ILLINOIS BIOLOGICAL MONOGRAPHS

PUBLISHED QUARTERLY
UNDER THE AUSPICES OF THE GRADUATE SCHOOL
BY THE UNIVERSITY OF ILLINOIS

VOLUME I

Urbana, Illinois
1914-15

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ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. I January, 1915 No. 3

PUBLISHED UNDER THE
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STUDIES ON THE CESTODE FAMILY ANOPLOCEPHALIDÆ

WITH SIX PLATES

BY

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Contributions from the
Zoological Laboratory of the University of Illinois under the direction of
Henry B. Ward, No. 38

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INTRODUCTION

The present paper gives the results of studies begun at the University of Illinois in December, 1910, and carried on, between numerous interruptions, to the present time.

My purpose has been to make a comparative anatomical study of the Anoplocephalidae, but since so few of the individual representatives of the family have received adequate study, it has been necessary for me to give most of the time to the individual study of undescribed or poorly described species. The work lacks much of being complete; many of the genera I have not had opportunity to study myself. Other work compelled me to lay the task aside, and it seems advisable to make public the results already obtained.

My thanks are due to Professor Henry B. Ward for assistance of many sorts; to Professors Robert T. Young, M. J. Elrod, and R. A. Lyman, Drs. B. H. Ransom, and John E. Gutberlet, for materials placed at my disposal for study; also to Miss Bertha E. Martin for criticisms and assistance in preparing manuscript.

ANATOMICAL DESCRIPTION OF SPECIES AND GENERA

Andrya primordialis sp. nov.

[Figures 1-4]

Two specimens of this cestode, one without scolex, were taken from a red squirrel (*Sciurus hudsonica*) at Bemidji, Minnesota, in September, 1911. Since about 20 squirrels in all were examined, there and at Brainerd, Minnesota, it seems that this species is rare, at least as far as this region and host are concerned. Other species of squirrels from these and other localities were likewise uninfected with this species. Its close relationship to the ancestral types of the Anoplocephalidae seems evident, even tho based upon a study of so few specimens.

The worms, neither of which are fully grown, have a length of 40 mm. and the single complete specimen has 155 proglottids. The strobila increases in width to the posterior end, there being 1 mm. in breadth. The first proglottids are 290μ wide and one-eighth as long. Mature proglottids are half as long as wide, and the proglottids farther back

are somewhat longer. The scolex is compact, 700μ long by 475μ broad, the greatest width being near the anterior end. Posteriorly the scolex tapers uniformly, until it merges into the neck, which is 290μ broad. The suckers open nearly directly forwards. A circular groove about the scolex at the level of the suckers makes it appear as if the tip of the scolex were contracted somewhat within the rest.

The genital pore is always on the right margin, about four-fifths the length of the proglottid from its anterior end. It is relatively large and deep as compared with the same organ in related cestodes. The cirrus pouch is much larger than in other known members of the genus, both in length and breadth, its median end lying well across the excretory ducts. Its inner end is rounded and its lateral end only slightly tapering. Across the middle its diameter is considerably less than at either end so that its outline is somewhat like that of the figure 8. The median end is occupied by the vesicula seminalis. The vas deferens is not enlarged nor greatly coiled. An elongated prostate gland lying in the anterior end of the proglottid empties into the vas deferens near the cirrus pouch. The testes are dorsal, occupying the entire median field to the left of and anterior to the vitelline gland and receptaculum seminis, and partly underlying the latter. In the distal half of the left side the testicular field extends laterad beyond the ventral excretory duct. The testes number 30 to 40 and are mostly 70 to 80μ long, the breadth being somewhat less. They break down early, but the membranes remain intact and the individual testes are easily distinguishable.

The vagina lies entirely posterior to the cirrus pouch, and in the same dorsoventral plane. Its coils are thickly beset with glandular cells. The receptaculum seminis is large and slightly longer anteroposteriorly than laterally. It lies directly in front of the vitelline gland, and does not reach laterad to the ventral excretory duct as is the case in other species of the genus. The ovary is a semicircular mass, reaching nearly across the median field. In immature stages 12 to 15 lobes can be distinguished which radiate in all horizontal directions; but before the ovary matures these lobes become indistinguishable. The ovary is not located nearer the pore side than the other, the mouth of the oviduct being as often to the left as to the right of the median line. The vitelline gland however is distinctly nearer the pore side. It is of the shape most usually found in this group, being composed of a large median and a smaller lateral portion connected by a transverse portion.

The uterus, just before sexual maturity, is a network of tubes in the anterior two-thirds of the proglottid. In the median field it extends distad to below the upper limit of the ovary, ventrad of the latter. The

lateral tips extend a little farther distad than the median portion and cross the excretory ducts ventrally on either side. The anterior and lateral margins together form a semicircle, so that at this stage the uterus as a whole is somewhat semilunar in outline. The early development of the uterus will be taken up later (page 51). Development from the stage just described is first by enlargement and coalescence of tubes, forming a saccular structure; then by regular outpocketing, anteriorly, distally, and laterally. The anterior and lateral pockets together number about 22; the distal, 15. Since neither specimen possessed completely ripe proglottids, a study of the embryo was unfortunately not possible.

The dorsal excretory duct lies laterad of the ventral and usually somewhat more dorsal. The diameter of the ventral is 30μ and that of the dorsal 7μ. The transverse commissure is of very small diameter and is not visible at all in sections at hand except in proglottids past sexual maturity.

The presence of the prostate gland and the reticulate uterus show at once that this species is allied to the genus Andrya. It disagrees however with the accepted diagnosis in that (1) the pores are strictly dextral, (2) the ovary is not nearer the pore side than the opposite side, (3) the testes extend laterad across the ventral excretory duct on the aporose side; and (4) the later development of the uterus is by regular anterior and posterior outpocketing.

The first point of disagreement is not an important one since unilaterality is approached in all of the species of the genus. The second point, while significant in other aspects cannot be regarded as of generic import since the other female glands are displaced in the regular manner. The third point will be shown to be true also of known and new species of Andrya, Anoplocephala, and Bertiella; so that the descriptions of these genera are in error, and this character, supposed to be confined to the genus Aporina, is found in all the single-pored genera of the subfamily except Schizotaenia. As to the fourth, the discrepancy seems to be due to errors in the descriptions of the species already known; for while Stiles (1896), describing the uterus of *Andrya rhopalocephala* says it is in its final stages a simple sac or with "at most extremely fragmentary and rudimentary divisions", his figures of gravid uteri of this species and *A. cuniculi* (see his Plate VIII, fig. 1 and Plate IX, fig. 1) show for both species what is apparently regular outpocketing, correctly drawn tho misinterpreted.

This cestode shows several characters which mark it as the most primitive species known in the genus; and if the contention later made

be accepted, that Andrya is the most primitive genus of the family, then this becomes the most primitive known species. Its primitive characters are (1) the very broad distribution of the testes which occupy nearly the entire median field and part of the lateral; (2) the fact that the ovary is not nearer the pore side than the opposite side; and (3) the limitation of the receptaculum seminis to the median field and its simple globular character. In these characters this species is approached in some respects by *A. communis*, next to be described, which must be regarded as its nearest known ally.

Andrya communis sp. nov.

[Figures 5-8]

Professor R. T. Young collected in 1908 at Long's Peak, Colorado, cestodes from *Evotomys gapperi galei, Microtus pennsylvanicus modestus* and *Peromyscus* sp. They were examined by Hall who concluded and reported (1912) that those from Evotomys and Microtus represented a species of Anoplocephala, while those from Peromyscus represented a second species of the same genus. Professor Ward has secured for me the loan of this material for study. The cestodes from Peromyscus belong really in the genus Hymenolepis, except for one slide, apparently mislabelled, which is of the same species as those from Microtus. Those from Evotomys and Microtus prove to be two distinct species, the first being an Andrya and the other probably an Andrya also, tho the fragments at hand are all too far past sexual maturity to allow of certain generic determination. The latter species must therefore of necessity be omitted from consideration, tho it comes within the scope of this paper.

The species under consideration from *Evotomys gapperi galei* is represented in the material at hand by about 200 fragments in alcohol and 17 slides, most of which were prepared by Professor Young. Only one scolex is in this lot, this being in the form of oblique cross sections. Recently I have found in the collection of Professor Ward four fragments, evidently representing one worm, which were of the same lot of material, and were presented to Professor Ward several years ago by Professor Young. This material includes a scolex with a considerable number of proglottids attached, thus furnishing an idea of the appearance of the complete worm.

The total length is estimated to be about 3 or 4 cm; the number of proglottids, about 225. The greatest width is about 1.5 to 2 mm. The proglottids vary in shape from 12 times as long as broad shortly before

sexual maturity to longer than broad in the case of ripe proglottids. The length of the scolex is roughly 560μ. The greatest width, 350μ, is reached 95μ from the anterior end. The anterior end is rounded; posteriorly the scolex narrows regularly.

The genital pores are all on the right margin near the middle of the proglottid. The circular muscles surrounding the inner end of the cirrus pouch are usually contracted, compressing this part and making the pouch inversely pear-shaped. In older proglottids however the inner end becomes distended and much larger than the outer. In some specimens the cirrus pouch is separated by a distance equal to its own length from the ventral excretory duct; in others its median end extends across both ducts (Figs. 5 and 8). The different conditions do not seem to depend so much on the stage of contraction of the proglottid as upon differences in the position of the excretory ducts. An internal vesicula seminalis is present. The cirrus is generally extruded, tho usually it does not extend outside the genital pore.

The vas deferens is not enlarged and is not coiled, tho it is probable that some coiling would be found in more expanded specimens. A distinct prostate gland is present; it is tubular with a globular enlargement at its end. Lateral to the pore of the prostate gland the vas deferens is surrounded by a loose cellular mesh. The testes are all dorsal. On the left they may extend across both excretory ducts, or they may be strictly limited to the median field. To the right they extend as far as the prostate gland in the anterior part of the field. They extend distad as far as the vitelline gland and receptaculum seminis, and on the left of these they extend to the distal end of the proglottid. The number varies in eight proglottids counted from 24 to 41. They are mostly tranversely elongated, 55 to 80μ long in transverse axis by 30 to 50μ in longitudinal axis.

The vagina lies entirely posterior to the cirrus pouch and vas deferens and in the same plane. Up to the beginning of the receptaculum seminis its walls are glandular. The receptaculum begins where the vagina crosses the dorsal excretory duct; it enlarges gradually and uniformly to near its inner end then becomes abruptly smaller. The ovary is an asymmetrical mass most of whose bulk lies on the pore side, but it approaches no nearer to the excretory ducts on one side than on the other and the oöcapt is as often to the left as to the right of the median line. It shows rather obscure and uncertain evidence of partial division into about seven radiating lobes. The lateral and median lobes of the vitelline gland are but little larger than the transverse portion of the gland which connects them. This gland lies considerably to the pore side of the median line.

The uterus is a typical reticulum in its early stages. It lies entirely anterior to and to the left of the ovary, being never ventrad of it. To the left of the ovary it reaches the transverse commissure posteriorly. On either side it crosses the ventral excretory ducts ventrally. Development from this stage is as in *A. primordialis*.

The excretory ducts are dorsal and ventral in position in the head region; but the dorsal duct very early moves to a position laterad of the ventral, which it retains. The ventral duct is four times the diameter of the dorsal; the transverse commissure is very small. The ventral duct diverges from the central axis as it passes distad until near the distal end of the proglottid where it turns almost directly mediad to regain its position. The dorsal duct has a somewhat similar course but not so pronounced.

This cestode it will be seen is rather closely related to *Andrya primordialis*. Many of the differences in the two accounts are due probably to differences in the state of contraction in the material.

Andrya macrocephala sp. nov.

[Figures 9-13]

Fifteen specimens of this species were taken from pocket gophers (*Geomys bursarius*) living in swampy river bottom land at Brainerd, Minnesota, and one from a gopher living in low, heavy, black soil at Thief River Falls, Minnesota. Apparently they are entirely absent from sandhill regions if not from all uplands. For distribution and frequency see the table on page 62.

By far the most conspicuous anatomical feature of this cestode is the enormous development of the ventral excretory ducts and commissures. In the scolex anterior to the distal end of the suckers, the four ducts have a winding course, the diameter of each varying generally between 18 and 32μ. Distad of the suckers the ducts have a straight course, are approximately 15μ in diameter, and are arranged as a dorsal and a ventral pair. Near the distal end of the scolex the dorsal duct begins to move laterad and soon comes to lie directly laterad of the ventral. The diameter of the dorsal duct throughout the strobila is about 18μ. The ventral ducts increase considerably in size as they pass distad. As the proglottids approach sexual maturity this increase becomes much more rapid and the transverse commissures appear and develop rapidly. In a sexually mature proglottid the ventral aporose duct near the middle of the proglottid is 80μ in transverse diameter; at either end it is 145μ in diameter. On the pore side the transverse diameter is 125μ in the center; at either end, 150μ or more. The

dorsoventral diameter in the center is 225μ. The transverse commissure measures at its largest point about 100μ; at either end it becomes smaller. As the proglottids age the ducts keep on increasing in size. The largest dimensions observed for the transverse commissure were 320μ; for longitudinal ducts, exclusive of interproglottidal enlargements, both transverse and dorsoventral diameters reached 320μ; for interproglottidal enlargements, 430μ. As the proglottids lengthen prior to detachment, the ducts become smaller as the result of the stretching, and the interproglottidal enlargements which are not thus affected become prominent as spindle-shaped objects.

Since the maximum breadth of this worm is 1.5 mm. it will be seen that this development is truly enormous, the two ventral ducts extending in some cases through not far from one half the transverse measurement of the proglottid and dorsoventrally through the cortical layer. This is not due to reagents since the living worms exhibit the enormous ducts clearly visible to the naked eye, before being given any treatment whatever. Great as this development is however it will be seen that it is exceeded in *Andrya translucida,* the next form to be considered, tho with the difference that in the present species the dimensions are constant in any given stage of development of the proglottid while in the other they will suddenly develop enormously and then as suddenly decline. These enormous ducts make these two species quite transparent in life.

The cestode is contractile when alive; it is from 10 to 20 cm. long and is composed of from 345 to 455 proglottids, the average of 14 specimens being 393. In well expanded specimens the neck is 1.5 mm. long, in one case even 3 mm. while in some contracted specimens it is only 0.3 mm. The diameter varies from 0.2 to 0.6 mm. The strobila increases in width gradually to reach the maximum width of 1.5 mm. about one-third of its length from the anterior end. From this point back the width remains about constant. Sexually mature proglottids, which begin about the 145th in the strobila, measure in a typical specimen 0.3 mm. long by 0.9 mm. broad.

The very large scolex is nearly globular in form, being 600 to 800μ wide and 700 to 950μ long; eleven specimens which were measured averaged 709μ wide by 811μ long. One finds but slight indications of grooves between the suckers; the very shallow depressions fade out before reaching the apex. The suckers are very large, thin-walled structures, usually collapsed and opening directly forwards. Their diameter is 300μ and their depth, 415μ. Their muscular wall is 50μ thick and the orifice is 50μ across.

The genital pore is on the right margin, two-thirds the length of the proglottid from the anterior end. The cirrus pouch is a stout, pearshaped structure, 155μ long, 75μ in diameter at its inner end, and 35μ in diameter at its outer. The tip of the pouch lies dorsad of the ventral excretory canal just within its lateral boundary. Part of the vesicula seminalis lies within the pouch; a much larger portion lies without, dorsad of the ventral excretory duct and extending mediad of it. There is no prostate gland. The testes are dorsal, extending nearly if not entirely across the median field, and into the lateral field on the side away from the genital pore. On the pore side of the field they are confined to the region anterior to the ovary; on the opposite side they are slightly more posterior than anterior. They number 43 to 57 in eight proglottids counted and average about 50μ long, being slightly smaller in other dimensions. They break down early but each remains distinct within its membrane.

The vagina lies entirely posterior to the cirrus pouch, and in the same dorsoventral plane. Its walls are beset with glands. Dorsad of the ventral excretory duct and extending beyond it on either side is the very large receptaculum seminis which is somewhat constricted in the middle, giving it a two-lobed appearance. The ovary consists of about 15 distinct lobes, which radiate in all directions from the point of origin of the oviduct. The posterior lobes, which are much shorter than the rest, extend distad on the ventral side of the transverse commissure to near its posterior limit. The oviduct begins just anterior to the transverse commissure, four-tenths of the diameter of the proglottid from the pore margin.

The uterus is reticular tho there is a tendency for the tubes not to develop. The uterus thus tends to become what might be termed diffuse. Certain main ducts develop regularly; the rest of the cavity is usally formed by the mere expansion of these. In front of the ovary, near the median line, the uterus is represented by a single tube; to the right and left it widens distally until near the excretory ducts; it then crosses beyond these ventrally. The later development of the uterus is by regular outpocketing. The embryo is about 20μ in diameter. It bears a large pyriform body whose length plus that of the embryo is 30μ. The outer embryonic membranes are mostly elongate; when spherical, the outer membrane has a diameter of 30 to 32μ. The middle membrane is loose fitting and irregular. The uterus of this species is almost identical with that of the genus Andrya and therefore different from that of other closely allied genera. Likewise the distribution of the testes is fundamentally the same. This species however disagrees with other known Andryae in that it has no prostate gland, and in that

it has a well developed external vesicula seminalis. The extraordinary development of the ventral excretory system, moreover, is a character of which one finds no suggestion in its nearest allies. These points argue strongly for generic distinctness for this and the next species. Whether to create for them a distinct genus or include them in the genus Andrya is a question. However the uterine structure and testicular distribution, combined with certain other undefinable resemblances seem evidences of sufficiently close generic kinship to the known species of Andrya to permit the inclusion of these forms in this genus. Yet the diagnosis of the genus Andrya must be altered so as to admit these species.

Andrya translucida sp. nov.

[Figures 14-16]

Three specimens of this cestode were taken from a pocket gopher (*Geomys bursarius*) from low, semi-swampy river bottom land at Brainerd, Minnesota. The same gopher yielded also five specimens of *A. macrocephala* to which it is evidently closely related. Since a great many gophers were examined in this and other localities (see table, page 62) it would seem that the species is a rare parasite of the gopher.

The total length of the specimens at hand is 9 to 12 cm. The number of proglottids is 278 to 289. The greatest diameter of the strobila, 0.75 mm., is reached 3 cm. from the anterior end. Back of this the proglottids become longer and narrower, the most posterior becoming attenuated and some of those at hand measuring 0.3 mm. wide by 1.3 mm. long. The worm is quite transparent in life, due to the enormous development of the excretory ducts.

The scolex is 730 to 830μ long by 590 to 640μ wide. The suckers stand out rather prominently and are separated from each other by distinct grooves. They open obliquely forward, through orifices about 110μ across. A definite neck is present, 500 to 730μ in length and 350 to 410μ in diameter.

The genital pore is usually on the right margin but frequently a number of adjacent proglottids have their pores on the opposite side. The pore is located seven-tenths of the length of the lateral margin from the anterior end of the proglottid. The cirrus pouch at the time the sperms begin to enter is usually short and thick, being 75μ long by 40μ broad, and lying wholly laterad of the ventral excretory duct. In succeeding proglottids it lengthens rapidly, becoming 160μ long by 40μ wide at its inner end which lies mediad of the ventral excretory duct. The vesicula seminalis occurs both within and without the pouch, being represented without by a coiled tube which is about five times the

diameter of the vas deferens and extends forward and mediad in front of the receptaculum. The testes are usually confined entirely to the side opposite the pore but two or three may lie on the pore side of the median line; however they do not reach as far as the median line of the vitelline gland. Likewise, the testes are nearly all in the distal half of the proglottid. In both these features is seen a superficial resemblance to Anoplocephala. The testes extend well across the ventral excretory duct laterally. When not disturbed by the ventral excretory duct they extend entirely thru the medullary portion.

The vagina lies ventral of the cirrus pouch. Laterad of the excretory ducts its walls are glandular. Very early, long before sexual maturity, it expands at its inner end forming a receptaculum seminis. This cavity grows and extends laterad until it reaches the outer edge of the dorsal excretory duct. It is largest at its inner end and its diameter decreases gradually laterad so that it merges imperceptibly into the unenlarged portion of the vagina. The ovary is formed of about 15 lobes which radiate anteriorly, distally, and laterally; the female glands are situated slightly to the pore side of the median line. The vitelline gland is of rather unusual shape, owing to the size of the median lobe and its encroachment on the space within the circle of the gland.

The uterus is a very simple reticulum with its different branches wide apart and clearly distinct from each other. It lies anterior to the ovary and extends laterad to beyond the excretory ducts on either side. In front of the ovary two or three transverse tubes are to be found; in the lateral regions, six or eight. The lateral development of the proglottids is very peculiar, and apparently abnormal, in that the ova do not pass into the uterus. In one specimen, having in all 278 proglottids, the uterus had already begun to develop in the earliest proglottid sectioned, number 148. In proglottid number 186 the receptaculum had reached its full development and was filled with sperms. In succeeding proglottids it was fully developed but nearly always empty. Proglottid number 187 showed all evidences of sexual maturity. The vesicula and receptaculum are developed, and the branches of the netlike uterus have become open tubes. In the following 91 proglottids however only 11 uteri contain eggs, these being between the 222d and 240th proglottids. The uterus is distinguishable in all except the most posterior, attenuated proglottids; it never develops beyond the reticular stage. In proglottid number 260 the degeneration of the ovary is nearly complete. The other two cestodes at hand of this species were cleared and examined in toto. They showed the same condition; in only an

occasional uterus are eggs present. These two individuals have each 289 proglottids; in all three cases some proglottids have been shed.

I can offer no certain explanation of this condition. The genital ducts appear normal and the ova certainly do not pass into any other organ than the uterus. There can hardly be any doubt therefore that these cestodes were incapable of perpetuating themselves. 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, incapable of perpetuating itself; in this case it could hardly be thought to have arisen from *Andrya macrocephala*, the nearest known relative; for while these and that species resemble each other in a general way, they differ in nearly every organ. 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. Sterility as a result of unnatural environment is a very common phenomenon in both animals and plants; and there is no reason why the condition might not be found in cestodes. Each of these explanations is favored by the fact that the three individuals were all found in the same host and were of the same size and appearance, making it appear probable that they arose from a single infection.

The excretory ducts show striking features also. As in *A. macrocephala* the ventral ducts are enormously developed. In this case the development is much greater however, especially that of the transverse commissure, so that often the proglottid is nearly separated by the excretory ducts into dorsal and ventral parts, the testes being dorsal and the ovary and uterus ventral. The transverse commissures are frequently three or four times as wide as the space between them; and when the ventral longitudinal ducts are likewise thus developed, the medullary space within these commissures becomes a mere patch in the anterior part, not much larger than is necessary to contain the vitelline glands and the female ducts. This enormous development is not constant however; such a development as described may be in a proglottid adjacent to one with ventral ducts 60μ in diameter. This is still an unusual size but is not greater than that found regularly in *A. macrocephala*. The dorsal duct has a rather sinuous course and is of ordinary size. It lies laterad of the ventral.

Altho differing in practically every organ from *A. macrocephala*, there is a fundamental resemblance between these two which argues for generic relationship. The similarity to Anoplocephala in the distribution of testes is interesting but is not to be taken as of more than specific

import, since such a condition is easily derived from Andrya by the suppression of the most anterior testes.

ANATOMICAL CHARACTERISTICS OF THE GENUS ANDRYA

The additions here made to the knowledge of the genus Andrya necessitate a radical revision of our conception of the group. These changes, briefly, are as follows:

1. The definition must be changed so as to admit forms in which the testes cross beyond the excretory ducts on the side away from the genital pore. Also, the fact that *A. translucida* has the testes only on the side away from the pore and mainly in the distal part of the proglottid, must be recognized. In the way of more exact definition it should be stated that the testes are always chiefly found on the side away from the pore and usually mainly anterior.
2. The strictly dextral arrangement of the genital pores which is found in some species, must be given recognition.
3. It must be recognized that the ovary may be directly median in position.
4. It must be recognized that the later development of the uterus is by outpocketing, in a manner not different from that occurring in Anoplocephala and Bertiella.
5. The definition must be changed so as to admit species without a prostate gland.
6. The position of the vagina and vaginal pore has been shown to be a constant character and should be given recognition.
7. The point of origin of the oviduct should be mentioned as a distinction from Schizotaenia.

The diagnosis of Andrya then becomes as follows:

Anoplocephalinae, with segments much broader than long, except in the most distal parts of the strobila. A single set of reproductive organs to each segment. Genital pores mostly, or entirely dextral. Genital canals pass dorsal of longitudinal excretory vessels and nerves. Testes chiefly on the side away from the genital pore, usually mainly anterior, and usually extending nearly across the median field anteriorly; on the side away from the pore they usually extend beyond the excretory ducts. Vagina and vaginal pore strictly posterior to the cirrus pouch. Female glands on the pore side of the median line, or with the ovary median. Oviduct connects with ovary beneath the median lobe of the vitelline gland. Uterus reticular, becoming saccular,

then developing by regular anterior and posterior outpocketing. Eggs with pyriform apparatus. Adults in mammals.

Type-species: *Andrya rhopalocephala* Riehm 1881.

Representing the genus Andrya, six species are known; besides those here studied, these are *rhopalocephala* and *cuniculi* (for both of which see Stiles, 1896). In addition, Parona (1900) has designated a cestode from *Dypus aegyptius* as *A. dipi,* with no word of description. As it is a pure nomen nudum, it can not be taken into consideration. The six known species fall into two well-defined groups, the rank of which it is difficult to decide. They are here treated as subgenera:

1. *Rhopalocephala*-group. Testes mainly anterior. With a pedunculated prostate gland opening into the vas deferens near the ventral excretory vessel. Vas deferens not enlarged outside the cirrus pouch to form a vesicula seminalis. Excretory ducts of normal dimensions. Scolex normal in size. Four species.

A. rhopalocephala Riehm — *A. primordialis* Douthitt
A. cuniculi R. Blanchard — *A. communis* Douthitt

2. *Macrocephala*-group. Testes about uniformly anterior and posterior, or mostly posterior. No prostate gland. Vas deferens enlarged to form a vesicula seminalis outside the cirrus pouch. Excretory ducts enormously developed. Scolex of more than ordinary size. Two species:

A. macrocephala Douthitt — *A. translucida* Douthitt

Anoplocephala wimerosa Moniez 1880

[Figure 17]

Of this species but two specimens are at hand. Admittedly, this is not sufficient material to form a basis for a satisfactory account of anatomy; but there is need to know the structure of the older members of this genus, for comparison with the better known new ones, which do not fit old conceptions. *A. wimerosa* has been known for 33 years; but it has received scanty attention, and several of the statements concerning it I find to be in error.

The specimens studied were taken from *Lepus variabilis* at Briançon, France, by R. Blanchard in 1891. He gave several specimens to Stiles, who, after he had studied them, divided the lot, presenting two to the Ward Collection. These were placed at my disposal for study. One is a toto mount and the other was sectioned. The account here given is original, except for the statements applying to external form which are taken from the account of Stiles (1896).

Anoplocephala wimerosa has a length of 10 mm. and a breadth of 1.5 to 2.25 mm., and contains 10 to 28 proglottids. The proglottids are much broader than long, except the distal segments, which rarely become as long as broad. The head is 0.7 to 0.88 mm. in diameter, is cuboid in form, and is quite distinct from the strobila. The suckers are 0.4 mm. in diameter, are prominent, and open diagonally forward.

As would be expected in so short a strobila, each proglottid shows a distinct advance in development over the one before. The genital organs are fairly well formed in the first proglottid. The receptaculum seminis begins to fill with spermatozoa in the fifth. By the fifteenth the testes have practically disappeared, and the receptaculum, vesicula, and cirrus pouch are enormously distended with spermatozoa. A few remnants of the testes persist until the eighteenth. The ovary develops to its full size in the eighth or ninth proglottid and begins to discharge eggs into the uterus. In the next proglottid this process is completed and the ovary disappears.

The testes, which are frequently as much as 90μ long, are irregular in shape. They occur on the side away from the pore and reach laterad to beyond the excretory ducts. The number, in six proglottids counted, ranged from 31 to 42. Not more than two testes can lie in a row in the axis of the strobila. The cirrus pouch is enormous. In a mature proglottid it is 520μ long and at its inner end extends thru the entire length of the proglottid. Its median end is occupied by a portion of the vesicula seminalis, 190μ long. The portion of the vesicula outside the pouch has a length in mature proglottids of 100μ and is two-thirds as wide. In older proglottids the entire vesicula becomes much larger. The cirrus pouch lies of necessity almost entirely mediad of the excretory ducts.

The genital pores are dextral. When undisturbed, the cloaca is 200μ deep. When the proglottid enters the period of sexual activity, it turns inside out. In the third or fourth segment succeeding, it is again drawn back. In this feature and in the enormous size of the cloaca and the cirrus pouch this cestode recalls Schizotaenia, especially *S. anoplocephaloides*, described in this paper. The unexpanded portion of the vagina is about 300μ long. Throughout its entire length it lies ventrad of the cirrus pouch, as does also the vaginal pore. No indication of glandular structure in its walls was observed. The receptaculum seminis is 300μ long in mature proglottids and at its median end extends from the anterior to the posterior border of the proglottid. Latterly it narrows regularly and evenly. In succeeding segments it becomes enormously distended.

The toto mount shows the whole of the female glands to be situated slightly to the pore side of the median line; the other specimen shows decidedly the opposite conditions in most proglottids. The shell gland is very indistinct in the material at hand. Nothing could be made out concerning its structure. The vitelline gland is 135μ long in transverse measurement. The posterior border is straight. Near the left end the gland measures 76μ across anteroposteriorly; it narrows somewhat towards the right until 40μ from the end; it then narrows abruptly. The ovary in immature proglottids consists of ten lobes which radiate anteriorly and laterally from a transverse portion. In its fully developed stage, however, no such divisions can be recognized. The ovary has a width of 420μ and extends practically through the proglottid anteroposteriorly. It reaches its full development in the eighth or ninth proglottid and disappears completely in the succeeding one.

The uterus begins as a simple transverse tube which seems to be confined wholly to the region between the excretory ducts. It develops mostly by expansion of the primary lumen, this occurring first at the end away from the genital pore. Short anterior and posterior outpocketings are present. In toto mount it appears as if these pockets are separated by a considerable space from each other; this is due to the fact that the eggs are shrunken, the outlines of the egg-masses being taken for the outlines of the pockets. As the uterus becomes filled with eggs it appears to force itself into the region ventrad of the excretory ducts. The embryos in the uterus have three shells. The outer is usually somewhat compressed; when spherical it measures 48μ to 55μ in diameter. The embryo itself measures 13μ to 15.5μ in diameter. The length of the embryo plus the pyriform body is 17.5μ to 21μ. The appearance of the horns of the pyriform body could not be made out. These measurements would probably not hold true for fresher material. It was not possible to make out much concerning the excretory ducts. The dorsal duct lies laterad of the ventral, and usually, at least, in the same plane. The two ducts appear to be approximately equal in size. Transverse commissures are present, but can be made out only with difficulty.

It will be seen that this species is without doubt an Anoplocephala. Yet it disagrees with the accepted conception of the genus in that the testes are not confined to the median field, and in that the female glands may not be placed to the pore side of the median line. Both of these conditions were found in Andrya, where they were supposed not to occur; and the first was found also in another species of Anoplocephala; they cannot therefore be regarded as generic differences. The diagnosis

of the genus Anoplocephala must of course be altered to conform; this matter is taken up later on.

Anoplocephala variabilis sp. nov.

[Figures 18-24]

This cestode has been found in *Geomys bursarius,* from Springfield, Illinois, to Emerson, Manitoba; as yet, no examinations have been made south of this region. It seems to be wholly absent from the sandhill regions; at Bemidji, Minnesota a few were found in hosts from very wet, coarse sand mixed with humus, only a foot or so from the edge of a swamp. In fertile soil, both uplands and bottoms, they vary in frequency, being in some localities extremely abundant, and in others rare or apparently absent. Not infrequently as many as fifty will be taken from a single host; in one case 136 specimens of this and a species of Hymenolepis were taken from one gopher. For distribution and frequency, see the table on page 62. From this table it would seem probable that the range of this species is the same as that of its host tho it is absent in many localities where its host occurs. The following description is based on well expanded specimens from central Illinois.

The total length varies from 45 to 75 mm; in life they can contract to 20 mm. or possibly less. The proglottids number from 175 to 225, the average of 19 specimens counted being 196. A neck is usually present which is four-fifths the diameter of the head, and one-half to one and one-half times as long, depending upon the stage of contraction. The strobila increases gradually in width to the posterior end, being there 2 to 3 mm. wide; occasionally the last few proglottids become narrower and longer. The first proglottids are very short. Distad they lengthen rapidly, most of the proglottids being two-thirds as long as broad. In several specimens especially in immature regions they are longer than broad. This is true only in case of extreme expansion, however. The scolex is irregularly oval in outline with sometimes a suggestion of quadrilaterality. Ordinarily it is about 275μ long by 300 to 400μ broad. It is distinctly set off from the neck by a deep circular groove which however is not always apparent. The suckers stand out rather prominently, due to the presence of longitudinal grooves between them, the dorsal and ventral grooves being deepest and extending farthest distad. Opposite the anterior end of the suckers the dorsal and ventral grooves arch over, the arches being as prominent as or more prominent than the suckers. These arches are the ends of a transverse bar which stands out prominently as the most anterior part of the

scolex. In frontal section this bar shows as a projecting tip in the median line. In some specimens however the bar and arches are not recognizable. The grooves never extend to the tip. The suckers open obliquely forward, at an angle of about 45 degrees from the axis of the strobila. The cuticula surrounding the orifice may be a simple fold or there may be as many as four folds of varying prominence.

The genital anlagen are represented by deeply staining cells even before strobilization is evident. The organs begin to take on recognizable form about the 45th proglottid, and eggs begin to pass into the uterus about the 75th. The genital pore is on the right margin, two-thirds of the length of the proglottid from the anterior end and considerably nearer the dorsal than the ventral surface. In some specimens it is everted during sexual activity. The cirrus pouch is 200μ long by 75μ wide, and pear-shaped. It extends well across the excretory ducts, dorsad of them. The cirrus is not spiny. Part of the vesicula seminalis occupies the median end; outside the pouch the vesicula bends upon itself twice, enlarging greatly at its inner end. From here the vas deferens takes a somewhat convoluted course across the proglottid. The testes shrink and apparently break down very early so that individual recognition is difficult. The number varies from 60 to 85; they are about 65μ long antero-posteriorly and usually somewhat smaller in other dimensions. They occur in the side away from the pore, extending from the median line to the nerve trunk and from ten to twenty lie outside the excretory ducts. They extend forward to slightly beyond the uterus and in the central part of their field entirely through the medullary portion. In expanded specimens it is clear beyond doubt that they are to be considered distal in occurrence, rather than proximal. The vaginal pore is on the ventral surface of the cloaca. The vagina lies ventral of the cirrus pouch, and at its median end usually somewhat posterior to it. Its walls are glandular. Just within the excretory canals is the receptaculum seminalis, which is at first clearly divisible into a small lateral and a larger median portion, both of which are about globular in form. Within the circle of the vitelline gland the receptaculum becomes a short, thickwalled tube, which joins the oviduct.

The ovary lies mostly to the pore side of the median line. It consists of a bar in front of the vitelline gland, turning distad beneath the median end of the latter, with lobes radiating in all directions in the longitudinal plane except directly backwards. The oviduct arises from beneath the median end of the vitelline gland mediad of the central axis of the ovary. It takes a fairly definite, sinuous course laterad, then proximad, to join the vagina. The common duct takes an irregular course to where it passes into the shell gland. The vitelline gland is a

large, horseshoe-shaped body, just to the pore side of the median line. Its duct arises from near the median line of the gland. It can be traced inside the gland as an open passage which divides and goes to the two lobes. When it has emerged from the shell gland the uterine duct passes forward and median with several windings which are fairly constant in different individuals, to join the uterus near the median line. The uterus is at first a narrow, sinuous transverse tube, just below the upper limit of the ovary and testes. At either end it crosses beyond the excretory ducts ventrally, and turns distad beyond them. Just before the eggs begin to enter the uterus expands considerably. The later development is by outpocketing, the walls of the adjacent pockets touching. The anterior pockets number 28 to 40 being usually about 35; the posterior pockets, 22 to 33, being usually about 30.

The embryo has three membranes. The outer is spherical, 30 to 35μ in diameter; the middle is loosefitting and irregular. The embryo itself is 12 to 13μ in diameter. It bears a well developed pyriform apparatus. The dorsal excretory duct lies dorsal of the ventral in young proglottids. As the proglottid ripens it passes laterad and usually ventrad also. At sexual maturity the dorsal duct is usually lateral but it may be both strictly dorsal and strictly lateral in different parts of the same proglottid. The transverse commissure is sinuous.

The foregoing description, as already stated, is based on well expanded material from central Illinois. In the material from the same localities, however, are a number of very much contracted specimens which are so different from the forms already described that they would no doubt have been classed as separate species if only the preserved specimens were known. The main differences from the type already described are as follows:

The length is 30 to 33 mm. The proglottids are all very short and broad. Mature proglottids are 0.325 mm. long by 4.5 mm. broad. The suckers open directly forward. The scolex is half-moon shaped, and is not broader than the first part of the strobila. The genital pore is situated midway on the right margin nearer the dorsal than the ventral surface. The ovary extends from the ventral excretory canal on the pore side to not far from the corresponding canal on the opposite side. The oviduct arises from the median line of the proglottid, half its length lying mediad of the vitelline gland. The transverse commissure of the excretory duct is not sinuous. The dorsal excretory duct is always lateral to the ventral, except in the head region and vicinity. In making comparisons of these two types, the reader should refer to figures 18, 19, 22, and 23.

Perhaps the most striking of these differences is seen in the position of the genital pore. This is explained however when one notes that in the elongate proglottid the portion of the body wall anterior to the genital pore lies much nearer the longitudinal muscles, and more nearly parallel to them, than does the portion posterior. As a consequence the anterior part would be shortened much more than the posterior in the process of contraction. That such is the case is shown by the fact that in contracted specimens the cuticula is much thicker anterior to the pore and is thrown into many fine wrinkles.

In order to make sure that these were really of the same species, experiments were performed with the object of trying to produce the two types at will. Complete success was attained with the simplest methods of treatment. Living specimens, just removed from the host, were cut each into two pieces; one was placed in a dish of water, the temperature of which was estimated to be about 30° C; the other in a dish of about 37°, care being taken that the portions from different worms were not confused. Those in the warmer dish soon expanded, and while in this condition they were fixed in corrosive sublimate. Those in the colder water contracted, however, and could not be induced to expand. When sectioned the portions from warm water were found to be without exception of the type first described, and those from the cold water of the second type. This simple experiment shows the necessity in comparing cestodes of taking into account the state of contraction of the proglottid.

These descriptions, as already stated, apply to specimens from central Illinois. As one passes northward, however, it is found that the individuals grow steadily smaller, both in bulk and number of proglottids. In anatomical features only one difference was discerned: the testes become very regularly fewer; apparently their size remains about the same, tho their irregular shape does not permit of exact determination on this point. The most conspicuous difference between the worms from different localities is in size, those from the north being only about half the length and breadth of those from the south. The other differences are illustrated in the following table. The numbers in parentheses indicate the numbers of individuals or proglottids examined.

Locality	Latitude	Number of Proglottids	Number of Proglottid in which Eggs first in uterus	Number of Testes
Lincoln, Springfield and Clinton, Illinois	40°	196 (19)	75-81 (6)	68.9 (10)
Minneapolis, Minnesota	45°	190.5 (2)	76 (1)	53.4 (5)
Brainerd, Minnesota	45° 21′	154.8 (19)	65, 68 (2)	45.5 (10)
Wahpeton, North Dakota	45° 21′	147 (2)	63 (1)	
Bemidji, Minnesota	47° 28′ 30″	144.7 (3)	54 (1)	
Thief River Falls, Minnesota.	48° 7′	129 (3)	56 (1)	43.3 (7)
Emerson, Manitoba	49°	134.5 (2)	57 (1)	40.2 (10)

In judging from these figures it must be borne in mind that while Emerson, Manitoba is considerably farther north than Bemidji and Brainerd, Minnesota, it is, nevertheless, in the transitional zone while they are in the boreal. It will be observed from this table that while there is a considerable difference between the extremes, the intergradations are sufficiently regular to destroy the validity of these differences as specific characteristics. They are therefore here classed as one species, with the specific name "variabilis". The northern forms are further recognized as a variety, with the name *Anoplocephala variabilis borealis*.

Anoplocephala infrequens sp. nov.

[Figures 25 to 27]

This cestode was found rather sparingly in *Geomys bursarius* in northern Minnesota and just across the Canada line, at Emerson, Manitoba. Recently also, through Professor Ward I have received from Professor Young a cestode taken from Evotomys sp. at Grand Forks, North Dakota, which is identical with these. In all, ten specimens were secured from the gophers. All were taken from the last inch of the small intestine or the adjacent part of the large intestine, were unattached, and showed no signs of life. Whether or not they belong this far back cannot be said positively; but the fact that three were immature and that all but one were in good condition when found would seem to indicate that they had not died and drifted back. The following description was based upon three sectioned and three adult alcoholic specimens. Later, the specimen from Evotomys was sectioned and compared; no significant points of disagreement with the account here presented were discovered.

The total length is 12.5 to 20 mm. The number of proglottids is 61 to 72. There is no neck. The first proglottid is about 40μ long, and generally about five-sixths the diameter of the head. The strobila may increase rapidly in width in the first few proglottids, or the fourth or fifth may be four-fifths the diameter of the first. Mature proglottids measure 1.5 mm. wide by 145μ long. The maximum width of 2.5 to 5 mm. is reached about 7 mm. from the posterior end. Beyond this the proglottids usually narrow rapidly and lengthen somewhat. The posterior free border of each proglottid overlaps about half of the succeeding proglottid.

The scolex is 625 to 750μ broad near its anterior end. It narrows distad, passing abruptly into the first proglottid. It is nearly square in cross section with only slight indication of grooves between the suckers. On the anterior end grooves occur between the suckers, fading out just before the apex is reached. There is no indication of the circular groove found in the last species. The very large suckers open directly forward. Right and left suckers touch in the median line of the scolex, and reach very nearly to the lateral cuticula (see Fig. 26). The mouth is 70 to 90μ across. The muscular wall is 55 to 75μ thick.

The genital anlagen appear in the first proglottid. The receptaculum seminis fills in the 17th or 18th, and eggs are found in the uterus in the 21st or 22nd. The genital pores are located midway on the right margin and distinctly nearer the dorsal than the ventral surface. The cirrus pouch extends first proximo-mediad and then bends directly mediad, not enlarging beyond the bend. Its inner end lies well within the excretory ducts. The passage of the cirrus is tortuous. In the median end of the pouch is a portion of the vesicula seminalis which later enlarges to fill the entire pouch. Outside the pouch is a second portion of the vesicula. The testes shrink and apparently break down very early. They are 50 to 60 in number and are 70μ long, being usually somewhat longer than broad. Nearly all lie between the left ventral excretory vessel and the vitelline gland, but not infrequently a testis will lie wholly or in part laterad of the excretory vessel and two or three may lie dorsad of the anterior part of the vitelline gland. They extend entirely thru the medullary portion dorsoventrally.

The vaginal pore is on the ventral surface of the cloaca. The vagina lies ventrad to the cirrus pouch and partly behind it. Its walls are highly glandular. The receptacular seminis is large and elongate, reaching laterad to the ventral excretory vessel. A small part at the lateral end is indistinctly constricted off from the median portion, making it somewhat bilobed The oviduct arises just anterior to the lower median corner of the vitelline gland and passes laterad and

proximad with several turns over the ventral surface of the latter. The vitelline duct extends as a large channel into each lobe of the gland. The uterine duct, after passing thru the voluminous shell gland, takes a crooked but regular course forward and mediad to the uterus. The very slender transverse uterus extends laterad at either end to beyond the nerve trunks. Development is by extension and outpocketing in the usual manner. The anterior pockets number 44 to 51; the posterior, 28 to 34. The ovary, in individuals from the gopher, is small, just reaching to the median line on the left, and not reaching the excretory duct on the right. In the specimen from Evotomys, the uterus is somewhat larger. The ovary does not cross the uterus anteriorly.

The embryo is typical. The outer membrane is usually elongate, or of other shape, due apparently to pressure. When spherical, it measures 39 to 43μ in diameter. The middle membrane is loosefitting and irregular. The embryo itself measures 12μ in diameter. It has a typical pyriform apparatus whose length, plus that of the embryo, is 19 to 22μ.

The dorsal excretory duct lies laterad of the ventral. The inner duct curves very strongly laterad in the middle of the proglottid; the curve of the outer is much less. The transverse duct is sinuous in dorsoventral plane.

THE GENUS ANOPLOCEPHALA

The genus Anoplocephala has served as a refuge for inadequately described species throughout its history. Most of the older species of the family Anoplocephalidae have been placed here at one time or another; as they have become better known, they have been removed one by one to other genera. Many of the names given have also been shown to be synonyms. Recently, von Janicki (1910), studying the cestodes from the hyrax, found that five of these supposed species did not belong even to the subfamily. Deiner (1912) has recently given an excellent and thoro description of "*Anoplocephala*" *magna* Murie; for reasons stated on page 40 I have transferred this species to the genus Schizotaenia. I have made the same disposal of *Anoplocephala* (*Taenia*) *gigantea,* whose anatomy MacCallum and MacCallum (1912) have recently investigated in a thoro manner.

Unfortunately, however, many of the species assigned to the genus still remain practically unknown; and more unfortunately, still other inadequately described species are being added. Thus, Mello (1912) thrusts upon the world *A. minima,* without giving any information

whatever except to external form; and Galli-Valerio (1905) burdens science with *A. dentata,* with but two lines of information as to internal anatomy and these lines devoted to non-essential details. There is no proof that either of these two species belongs even to the subfamily; and indeed, the only important fact made known concerning *A. minima,* that the genital pores are regularly alternate, indicates that it does *not* belong to the genus Anoplocephala.

If consideration be given to these half-starved species, no anatomical generalization concerning the genus Anoplocephala is possible. Thus, "*A.*" *spatula* has the testes extending across the median field; "*A.*" *omphalodes* has the genital pores irregularly alternate, the vaginal pore posterior, and the testes sometimes extending across the median field; and "*A.*" *minima* has the pores regularly alternate. For about half the species assigned to the genus, no statement whatever is made concerning the uterus. There seems no alternative, then, if one would attempt any generalizations, but to base them only on those species whose position in this genus is assured, and to ignore seeming contradictions coming from the inadequately described species which are placed provisionally in the genus.

The diagnosis of the genus should be changed so as to admit species in which the testes extend beyond the excretory ducts on the side away from the genital pore. Also, it should state that the vagina and vaginal pore are ventral to the cirrus pouch. It seems probable that in all the proximal end of the oviduct lies beneath the median lobe of the vitelline gland; but information is needed concerning more species on this point.

The diagnosis of the genus Anoplocephala thus becomes as follows.

Anoplocephalinae, with segments generally much broader than long, occasionally longer than broad. A single set of reproductive organs in each segment. Genital pores unilateral. Genital canals pass on the dorsal side of the longitudinal excretory vessels and nerve. External vesicula seminalis present. Testes on the side away from the genital pore, sometimes extending laterad of the nerve trunk. Vagina and vaginal pore ventral to the cirrus pouch. Female glands to the pore side of the median field. Uterus a transversely elongated sac, with pocket-like appendages, anteriorly and posteriorly. Eggs with well developed pyriform apparatus. Adults in mammals.

Type-species: *Anoplocephala perfoliata* Goeze 1782.

The following species may be assigned with certainty to the genus Anoplocephala.

A. perfoliata Goeze
A. magna Abildgaard (syn., *A. plicata* & *A. zebrae*)
A. globiceps Diesing
A. mamillana Mehlis
A. wimerosa Moniez
A. variabilis Douthitt
A. infrequens Douthitt

The following species are not well enough known to allow of generic determination, but should be left here for lack of better disposal.

A. inermis von Linstow (syn., *A. arvicolae*)
A. blanchardi Moniez
A. omphalodes Hermann
A. dentata Galli-Valerio
A. restricta Railliet
A. paronai Moniez
A. transversaria Krabbe
A. spatula von Linstow

Schizotaenia americana Stiles 1895

[Figures 28, 29]

Stiles in 1895 gave a short description of this cestode and placed it in the genus Andrya. The next year he transferred it to the genus Bertia, (now Bertiella). In 1906 von Janicki, having proposed the genus Schizotaenia, included this form and *Bertiella americana leporis* in that genus, basing his action mainly upon the distribution of testes, since the description of Stiles was noncommittal or erroneous on other points that might be of importance. The results of the present studies justify completely von Janicki's disposal.

In 1906 Cohn expressed it as his opinion that this cestode was the one described by Leidy (1855) as *Taenia laticephala,* and that the specific name "*americana* Stiles" should be dropped as a synonym. I cannot agree that the evidence justifies such a conclusion. With full consideration for the ability of cestodes to contract and expand, it is a severe strain on one's credulity to conceive how a cestode 1.3 inches long and 2.8 lines broad could at will become 9 inches long, and ¾ of a line broad; and how a proglottid 12 times as broad as long could become square. Moreover, Leidy states that the width of the neck in the forms at his disposal is ¼ of a line, or one-half the diameter of the head. These specimens have no neck and strobilzation is very conspicuous even in the first proglottids. Leidy states that the anterior proglottids are oblong-square. If this means that they were longer than broad, we have a condition that is unprecedented in the Anoplocephalidae; if it means that they were broader than long, then Leidy's speci-

mens must have been composed of at least 225 proglottids, more probably of 350 or 400 proglottids.

The fact that Leidy's and Stiles' material were from the same host, the only point that Cohn seems to have taken into consideration, means nothing. I have taken 16 species of cestodes from Geomys, and have not exhausted the field; Stiles (1896) has reported still another. These species represent seven genera, and three families. The balance of evidence seems to be in favor of Stiles' view that Leidy's species was a species of the genus Davainea.

Cohn criticise Stiles for the inadequateness of his description; but with sectioned material before him he failed to add anything of importance to our knowledge. Incidentally he mentions that the female glands are situated at a considerable distance from the median line, which proves that he did not have before him Stiles' species but had probably *Schizotaenia variabilis,* the next species discussed in this paper.

There were available for study specimens from Stiles' material loaned by the Bureau of Animal industry; others were placed at Professor Ward's disposal by Professor M. J. Elrod, the original collector of the material; also, from the Bureau of Animal Industry a specimen from a porcupine taken at Mayfield, Michigan. The first lot is from *Erethizon epixanthus,* from Snake River, Wyoming; the second is from *Erethizon dorsatus.* I have also specimens (No. 1502, B. A. I. Coll.) identified by Stiles as this species; examination has shown that they are distinct.

External form (Stiles (1896)—"Strobila attains 33 mm. in length by 6 mm. in breadth and contains about 90 segments, the oldest of which are 8 mm. long. Head unarmed, measures 0.6 mm. broad by 0.38 mm. long by 0.32 mm. thick, and is nearly rectangular in apex view. The neck is absent, and the head is frequently retracted in the body, as in *Drepanidotaenia lanceolata.* Suckers round, 0.176 mm. in diameter, open anteriorly".

The genital organs alternate, in the specimens at hand, with perfect regularity from right to left. The genital anlagen are visible in the first proglottid. The specimen from Mayfield, Mich., shows the 70th proglottid still immature; apparently, maturity is reached about the 80th. No other specimen at hand gave information as to this point. One must conclude from this condition, either that Elrod's material was all immature since it shows the total number of proglottids to be about 90, or that the species is larger when inhabiting *Erethizon dorsatus.* The latter conclusion seems more probable, since some of the detached proglottids of the Elrod material are ripe.

The genital cloaca could not be studied as carefully as desired, on account of its habit of turning inside out at the approach of sexual maturity. A full comparison of the organ with that of *Schizotaenia anoplocephaloides,* to be described later, is therefore not possible. They agree however in all points that could be made out. In both the cloaca everts at the approach of sexual maturity; and in both it is drawn back at the close of sexual activity, but in none of the sectioned material at hand does it come back completely. In both the cloaca is very large tho in the present species it is not so extraordinarily large as in the other. The proglottids sectioned do not show whether the cloaca is divided into two parts, as in *S. anoplocephaloides.* The pore is located about midway on the margin.

The cirrus pouch is quite large, tho small as compared with that of *S. anoplocephaloides.* When the cloaca is not everted, about a third of it lies mediad of the excretory ducts; when everted it reaches usually just to the nerve trunk. It is 500-625μ long by 185-210μ wide. It is somewhat pear-shaped in outline, the inner half being about uniform in diameter. Laterad of the middle it tapers sharply to end in a slender neck 40μ in diameter and 150μ long. The cirrus is spiny. Extruded cirri however are smooth, from which it would seem that the attachment of the hooks is very light. This probably explains the apparent absence of spines observed by Stiles for *S. americana leporis.* The inner end of the cirrus pouch is occupied by a portion of the vesicula seminalis. Outside the cirrus pouch the vesicula is about 80μ in diameter in mature proglottids and extends mediad and proximad for a distance of about 850μ, coming to lie here near the anterior end of the proglottid. It then curves usually to extend mediad and distad for a distance of about 225μ where it ends in the slender vas deferens. The vasa efferentia are in a large part plainly visible. The vesicula seminalis if closely examined is seen to be somewhat sinuous; but the effect is that of a straight tube taking the course mentioned. At its extreme inner end just at this juncture with the vas deferens it has glandular walls. The testes are spherical and 65μ to 80μ in diameter. They are all dorsal and extend from excretory duct to excretory duct in the distal end of the proglottid. The number was found to be about 70 which agrees with the account of Stiles.

The vagina and vaginal pore are anterior to the cirrus pouch. For about the first 185μ of its length the vagina is a very small, heavy-walled tube which is perfectly distinct when once recognized. Beyond this point it is very indistinct and usually can be traced only by the vacuolated appearance of its course. In a few cases, however, it can be seen very indistinctly anterior to the cirrus pouch, crossing the

vesicula seminalis just beyond the pouch and then proceeding mediad to the receptaculum seminalis. Just before entering the receptaculum it again becomes distinct. Thus in position only does it resemble the conspicuous, glandular vagina of *S. anoplocephaloides*. The rather small, nearly globular receptaculum seminis lies just anterior to and laterad of the vitelline gland partly overlapping it.

The female glands are but slightly displaced from the median line. In proglottids 4 to 5 mm. wide the median axis of the shell gland is 55μ to 175μ distant from the median line. The female organs of the right and left sides therefore overlap largely. The transverse diameter of the ovary is about 1.3 mm. It is composed of a transverse portion in front of the vitelline gland from which numerous small lobes radiate in all directions except towards the vitelline gland. To either side of the vitelline gland the lateral portions turn distad and extend to near the transverse commissure of the excretory duct. The ova measure 12μ to 15μ in diameter. The oviduct is short; its attachment to the ovary is located anterior to the central axis of the vitelline gland. This latter gland is of the regular Anoplocephaline form, being composed of a small lateral and a large median lobe. Here, however, is a clear approach to the peculiar mulberry-like form found in the next species and in *S. hagmanni*. The two lobes approach each other anteriorly, thus restricting the space between them and making the gland more compact and show an indication of the division of the gland into many small radiating lobes. The transverse diameter of the gland is 400μ. The shell gland is 90μ in diameter; it needs no further description.

The uterus in the earliest stages observed is a continuous sheet of tissue extending through nearly the whole of the median field, except for the portion occupied by the ovary and vitelline gland. The two lateral portions are connected by a narrow strip above the ovary. There is abundant indication of thickening of the uterine tissue into definite lines, thus simulating a network such as is found in Moniezia. These do not develop into open tubes, however, so it is not really a reticulum. For a discussion of this type of uterus see under *S. anoplocephaloides*. The condition of the material unfortunately does not permit the development of this organ to be worked out in full detail. In its fully developed stage it is divided up into a great many small compartments, each containing several eggs, similar to the condition described later for *Moniezia expansa*. It seems, therefore, that the uterus does not break down into egg-capsules after the manner of the Linstowinae, but that the condition is due to unequal development of the original cavity at different points. In its fully developed stage the uterus is practically confined to the median field but a small branch extends out to occupy

the vacuolated space surrounding the cirrus pouch. The fully developed uterine embryos are 14.5μ to 15.5μ in diameter. The inner embryonic membrane is 18μ to 20μ across; the length of the embryo plus the pyriform body is 26.5μ to 29μ. The outer mebrane is 55 to 61μ in diameter; the middle is loosefitting and irregular.

The ventral excretory duct has a diameter of 45 to 75μ, and the dorsal is about half this size. Both lie in approximately the same dorsoventral plane. Near the distal end of the proglottid the ventral duct turns and runs abruptly mediad for a distance of about 275μ where it gives off the transverse commissure. Beyond the commissure and therefore in the next proglottid the duct turns laterad not so abruptly as before to regain its lateral position. Stiles records that he has observed the dorsal duct in open communication with the transverse commissure; since this occurs also in *S. variabilis* and *S. anoplocephaloides,* it seems to be a common occurrence in the genus.

Stiles in 1896 referred to this species five cestodes from a rabbit (host species and locality not known), giving them the rank of a variety with the name *Bertia americana leporis.* His description is very unsatisfactory being based upon poorly preserved, unsectioned material. In reading over carefully the description of the worms there does not appear a single anatomical character upon which to justify giving them the rank of a distinct variety. The cirrus is supposed to be smooth; but this conclusion is based upon extruded cirri, and as shown, extruded cirri of the forms from the porcupines are usually if not always smooth. The testes are stated to be probably fewer; but Stiles is not certain as to the count and the difference moreover is not so great as that between the extremes of the next species. The description of the position of the genital pore is vague but implies a difference; yet his figures (Stiles 1896, Pl. X, Figs. 7, 14, and 15) are identical for both. Some slight differences were observed in the first appearance of the genital anlagen; but such appearances when based upon unsectioned specimens and poor material, do not have any importance. No other points of difference were brought out which could not be accounted for as mere individual variations. There appears therefore to be no evidence to justify giving these specimens the rank of variety.

On the other hand there is very little evidence that these cestodes rightly belong to this species, or even to the genus for that matter. As will be shown in the succeeding paragraphs the supposedly homogeneous materials from the porcupine prove to be two distinct species. Until something is known of them however they should not be given separate recognition.

Schizotaenia variabilis sp. nov.

[Figures 30 to 32]

Some years ago Dr. A. K. Fisher collected cestodes from a number of porcupines (*Erethizon dorsatus*) at Lake George, New York. These in the Bureau of Animal Industry at present bear serial number 1502. Stiles (1896) examined them and identified them as *Bertia americana* (now *Schizotaenia americana*). Professor Ward secured the loan of these specimens. Examination has shown that they do not represent *S. americana,* but are a distinct species. The following description is based upon a single complete specimen, not sectioned, and several sectioned portions from the region of sexual maturity. The specimens reported by Cohn (1906) from *Erethizon epixanthus* from Alaska seem referable to this species rather than *S. americana,* since he reports that the female glands are located far from the median line.

The complete specimen at hand, which appears to be fully grown and has shed proglottids, is 20 mm. long and is composed of 60 proglottids. The greatest width, 8.5 mm., is reached 18 cm. from the head; back of this the strobila narrows somewhat. All the proglottids are very short in comparison with the width, except the last which is 6 mm. wide and 1.5 mm. long. The fragments at hand agree with this specimen, except that some have longer and thicker proglottids the width being the same; this would seem to indicate that they came from a larger specimen. Three scolices are present; they measure 450μ long by 875μ wide. One is retracted within the end of the strobila as in *S. americana.*

The genital pores are regularly alternate. The genital cloaca and cirrus pouch agree with the description just given for *S. americana,* except that the cirrus pouch is somewhat smaller being ordinarily 485 to 500μ long tho it is sometimes longer. Its width is 140 to 185μ. The vesicula seminalis is of necessity much shorter than in *S. americana* on account of the nearness of the female glands to the lateral margin. It is variable in form, being sometimes straight and sometimes in the form of large, wide loops, as shown in Fig. 30. The gland-cells on the inner end of the vesicula are usually more numerous than in *S. americana,* as shown in the same figure. The vagina is identical but of course shorter.

The testes are decidedly unlike *S. americana* in form and distribution. Nearly all are elongated anteroposteriorly, the breadth being to the length as 5:7. In some specimens they are 60 to 80μ long while in others they are 95 to 130μ long. These measurements were all taken at sexual maturity. They occur only in the median field and are

mostly on the pore side of the median line of the proglottid. Beyond the median line they are reduced to a single row which reaches as far as the median axis of the female glands of the proglottids before and behind. On the pore side of the field they are in 2½ to 5 rows when viewed from above. They are usually limited to the dorsal part of the proglottid but in one specimen they sometimes extend entirely through the medullary portion. Generally they lie almost entirely posterior to the female glands, but in one specimen they were found sometimes at the same level as the female glands and dorsal to them, and in some proglottids even anterior to them, and therefore if judged by position in the proglottid in front! These different types of distribution were all found in five adjacent proglottids. The number of testes was found to vary from 60 to 70 in one specimen to 110 in another. The number seems to be fairly constant for any given individual.

As already stated the genital organs alternate regularly from the left to the right side of the strobila. The median line of the female glands in mature proglottids is 600μ from the median line of the proglottid; in *S. americana* the distance was 55 to 175μ. The ovary is much smaller than in *S. americana,* its diameter varying from 650 to 900μ; it never reaches to the median line of the proglottid. Otherwise the ovary is not different from that of *S. americana.* The ova measure 12 to 14μ in diameter. The vitelline gland shows the peculiar mulberry-like appearance figured by von Janicki for *S. hagmanni.* In cross sections of the gland, i. e., longitudinal sections of the proglottid, about 25 radiating lobes can be made out. There is no trace of the usual bilobed condition. The shell gland is small and lies directly dorsad of the vitelline gland, having about one-third the diameter of the latter. The uterus in mature proglottids is apparently not so extensive as in *S. americana,* but statements concerning it must be qualified on account of the poor condition of the material. It does not seem to reach either the anterior or the posterior border of the segment. Otherwise, the description given for *S. americana* will apply equally well for the early stages. Unfortunately the later development could not be followed.

The description given for the excretory system of *S. americana* will answer for what seems to be the normal condition here. One individual however offers such radical departures from this type that a detailed description is given here. In the specimen in question the longitudinal portions of both dorsal and ventral ducts are of approximately the same size. In one sectioned portion having five proglottids, the large ventral transverse commissure extends laterad to make open connection also with the dorsal duct. Judged by its appearance, the commissure would seem to belong to the dorsal rather than

the ventral system in these cases, and the connection with the ventral system appears secondary. This effect is heightened by another remarkable feature, the presence of a secondary transverse commissure anterior to the first. This duct is a direct continuation mediad of the longitudinal ventral duct at the point where the latter dips distad just before communicating with the main transverse commissure. This secondary duct is usually of small diameter dorsoventrally but anteroposteriorly it may extend through one-fourth the length of the proglottid. Its diameter however is very irregular, and its course is sinuous. These secondary commissures are apparently analogous to the condition found in *S. anoplocephaloides.* The connections between dorsal ducts and transverse commissures were observed also in *S. anoplocephaloides,* and by Stiles in *S. americana.* In two proglottids the main transverse commissures are not fully developed, but are represented by strings of disconnected spaces. This may be due however to the fact that the proglottids are not quite mature. All these conditions are illustrated in Fig. 31.

Schizotaenia anoplocephaloides sp. nov.

[Figures 33 to 40]

Four gophers (*Geomys breviceps* Baird) from creek bottom land at Norman, Oklahoma, yielded of this species plentifully. About half of the 75 specimens taken were lost and tho many others are not in the best condition, some are good. For distribution and frequency of this species see the table on page 62.

The total length of the specimens at hand is 30 to 33 mm. The number of proglottids varies from 55 to 80, the average being 68. There is no neck. The first proglottids are about seven-tenths the diameter of the scolex and from one-eighth to one-twelfth as long as broad. The maximum width of 1.7 to 2 mm. is reached about the middle of the strobila; back of this the width remains constant or decreases slightly. At the middle of the strobila the proglottids are from one-fifth to one-third as long as broad. They increase in length as they become older, becoming finally two-thirds as long as broad. In those proglottids in which the eggs are being fertilized the large everted genital pore protrudes prominently.

The scolex averages 390μ in diameter and 320μ long and is quite distinct from the strobila. It is clearly separated into anterior and posterior portions by a slight transverse constriction near its middle. The apex is blunt, the anterior outline being a regular curve. The scolex is rather deeply four-lobed owing to the presence of longitudinal

grooves between the suckers, the dorsal and ventral grooves being the deepest. All four fade out before reaching the apex. The very prominent suckers face anterolaterad at an angle of about 45 degrees from the axis of the worm. The mouths of the suckers are from 25 to 40μ in diameter and the cavities are 70 to 90μ deep. The muscular wall of the sucker is from 25 to 50μ thick.

There is one set of reproductive organs to the proglottid, these alternating with practically perfect regularity from right to left; in a dozen worms examined only three cases were found of two adjacent proglottids with pores on the same side. The anlagen of the female glands can be made out in the first proglottid. Testes are to be recognized in the 15th and eggs pass into the uterus in the 40th. The genital cloaca presents an unusual appearance. It is clearly divisible into two parts, a lateral and a median. The lateral is an unusually large structure varying in shape in different specimens probably on account of contraction from nearly globular to angular, being even acutely angular at its inner end. The pouch has a length of about 140μ and a breadth of about 85μ. The anlage of this structure can be made out in about the 20th proglottid as a group of cells that stain deeply. Soon afterwards a mass of substance not distinguishable from the cuticula can be made out in it near the lateral margin. A lumen appears which increases in length mediad and then expands. Just before sexual maturity the cuticula of the outer body wall is broken through, and the cavity of the pocket becomes continuous with the outer surface. The pouch immediately turns inside out, projecting abruptly in some cases for more than 200μ from the margin. Fifteen or twenty proglottids farther back it is again retraced to remain thus to the end. In its fully developed stage the cuticula and wall of the pocket are directly continuous with the cortical layer and not distinguishable from it. Mediad of this and communicating with it is a second small pocket. It is rather small and is expanded at its inner end to embrace the end of the cirrus pouch. The vagina opens into its anterior border. Generally, the median end of the cloaca lies mediad of the longitudinal excretory ducts.

An unexpected condition was found in the position of the vagina and cirrus pouch with respect to each other and to the nerve and excretory trunks. When the pouch and vagina are on the right margin of the strobila they cross the excretory ducts dorsally; but when on the left, in two individuals out of ten studied, they more often cross the excretory ducts ventrally. In these two individuals out of 19 proglottids which had the pores on the left margin ten had the genital ducts ventral. Thus some proglottids have an arrangement that is charac-

teristic of the Linstowinae and has been observed nowhere amongst the Anoplocephalinae, except possibly in the genus Triplotaenia. It should be stated however that the identification of right and left sides in these specimens may be in error.

Still another interesting feature was observed in regard to the genital ducts. The vagina crosses the cirrus pouch ventrally in most cases; but in the two individuals mentioned in the paragraph above, 12 of the proglottids that had the excretory ducts dorsal to the genital ducts, had the vagina dorsal and the cirrus pouch ventral. This recalls at once Moniezia in which the vagina is regularly ventral to the cirrus pouch on the right and dorsal on the left. These same two individuals were unusual in the form of the ovary, as explained below. The cirrus pouch is very large. Before the evagination of the cloaca it lies usually entirely mediad of the excretory ducts; but when the cloaca is everted it may lie entirely laterad. In mature proglottids it is 275 to 370μ long, and 120 to 240μ broad. Before the development of the vesicula seminalis it may be elongated and spindleshaped; afterwards it is always pearshaped. The cirrus is straight in the lateral half of its length and has usually two spiral turns at its upper end. It is lined with many hundreds of small hooks which are arranged in spiral rows. The median end of the cirrus pouch is occupied by a portion of the vesicula seminalis. Proximad and mediad of the pouch is a second portion, 140μ long, which is only slightly coiled. This portion is thickly beset with glandular cells. Beyond the seminal vesicle the passage narrows and soon divides, sending a branch to either testicular field.

The testes, 70 to 110 in number, are dorsal and posterior. They occur in both lateral halves but are mostly on the side away from the pore. At either side they are grouped two or three deep dorsoventrally. Above the yolk-gland there is never more than a single layer and as often as not there are none here, the testes being separated into two groups. The testes are typically spherical in shape, averaging 35μ in diameter.

The vagina communicates with the genital cloaca on the anterior surface of the latter. It extends forward and somewhat mediad in front of the cirrus pouch then turns directly toward the median line, usually crossing the cirrus pouch ventrally. Mediad of the cirrus pouch it curves somewhat distad, the entire vagina thus describing a semicircle. Its middle portion in the anterior part of the proglottid is several times the diameter of the two ends. The surface is glandular. At about the same level as the lateral end is located the receptaculum seminis which is a simple expansion of the vagina, measuring 180 by

130μ. The ovary is distinctly, but not considerably, to the pore side of the median line. It is fanshaped in outline, being formed of a large central mass from which about 30 lobes radiate extending in all directions in the horizontal plane except towards the part of the field occupied by the vitelline gland. It is distinctly ventral in position. In two specimens however most of the proglottids which have the genital pore on the left side have the ovary separated into distinct dorsal and ventral portions with a narrow connection between them. The dorsal portion in these cases is of about half the area of the ventral and thin. These are the individuals that show the peculiarities of the excretory ducts already mentioned. The oviduct in all cases connects with the ovary at a point directly in front of the vitelline gland and is short. The vitelline gland is of the ordinary bilobed type which is found nearly everywhere in the subfamily and shows no suggestion of the type found usually in the genus. It lies posteriorly to the ovary, sometimes extending dorsad to the cortical layer and dividing the testes into two fields. In cross section it is distinctly horseshoeshaped, with the open face dorsad. Viewed from above it is U-shaped but with the median arm much larger.

The uterus is first recognizable as a sheet of deeply staining cells ventrad of the testes and dorsad of the ovary. Just beneath the margin of each testicular field the sheet is thickened into a heavy circular band. On the pore side there extends forward from the anterior tip of the circular band a strip of the same nature, which crosses the vagina laterad of the receptaculum seminis then turns and extends diagonally distad just underneath the anterior margin of the receptaculum and anterior to the vitelline gland. It joins with the other circular band at the corner of this gland. It is into this cross duct that the uterine duct empties. Within these circles and anterior to the transverse portion and connecting with them at frequent points, is a network of strands formed by thickenings of the uterine tissue which recalls strongly the reticulate uterus found in Moniezia. The transverse portion is of course the first part of the uterus to receive eggs; but the eggs pass immediately into the circular bands which have developed into canals. The extreme lateral portions fill and then the whole canals. As the uterus fills with eggs these passages expand centrally and the transverse portion anteriorly, so that the cavity of the uterus becomes one continuous sac. The extension from this stage is by regular outpocketing no different from that found in Anoplocephala and Bertiella, except that the pockets are of necessity shorter since the uterus does not begin as a simple tube. The development of the uterus continues until nearly all the organs of the proglottid are reabsorbed. The cirrus pouch and

vesicula persist to the last either in situ or crowded to one side. The receptaculum persists as a mere vestige. The shell gland persists as a structureless mass connected with the receptaculum and with the posterior end of the proglottid by a narrow bridge, such as has been described for *Moniezia carrinoi* and some of its relatives. All the other organs are reabsorbed, the testes being the last to give way. The proglottid becomes little more than a thin-walled egg capsule, the cortical layer being reduced sometimes to a thickness of 20μ.

The uteri of the three species of Schizotaenia here described agree in all essential respects but differ decidedly from the account presented by von Janicki (1906) for *S. hagmanni* which is accepted as the type of the genus. He recognized nothing comparable to the degenerate reticulum or diffuse uterus described here; also the three species described here show nothing comparable to the "äusserst feinen Schlitze, der als mannigfach gewellte Fläche durch den grössten Teil der Markschicht * * * * * sich hinzieht". Von Janicki does not figure this structure except in transverse section, in which way it gives very little information. In view however of the fact that such a structure would not be greatly different in appearance from that of the degenerate reticulum described here, I am inclined to believe the difference is one of interpretation rather than structure. Likewise von Janicki's drawings of the "Spaltenwerk" (Figs. 85, 86) resemble closely the condition observed in frontal sections of the early saccular stage when the thin uterus is applied to the uneven surface of the ovary and only parts of the cavity appear in each section. There is no ground therefore for considering these uteri as differing fundamentally in this regard. The possession of uterine outpocketings by the present species is striking and is significant as to its relationships; but the fact offers no barrier to its inclusion in the genus Schizotaenia; it is what should be expected in the more primitive members of the genus.

The uterine embryos have three membranes. The outer is spherical and 30 to 40μ in diameter. The middle is loose-fitting and irregular. The diameter of the embryo is 10 to 17μ with no considerable range of variation in any one individual. There is a perfectly developed pyriform apparatus whose length plus that of the embryo is 16 to 26μ. The two stout tapering horns cross at the tip and extend backwards as long, slender processes.

The excretory ducts lies in about the same dorsoventral plane, the originally dorsal duct outside. This arrangement is present in both strobila and scolex. The path across the proglottid is a curve. The dorsal duct is usually between 10 and 12μ in diameter at the ends of the proglottids, narrowing in the middle to 6 or 7μ on the side away

from the pore, and on the pore side to 3μ. The ventral duct at the ends of the proglottids is 40 to 50μ in diameter; it narrows in the middle to 30 to 35μ on the side away from the pore, and on the pore side to 3 by 10μ. The transverse commissure of the ventral duct is a straight tube 25 to 40μ in diameter. In three individuals the dorsal longitudinal duct is connected with the transverse commissure in very many cases (Fig. 40). In the present species these connections are always on the same side of the strobila, judged to be the right side, tho since the specimens are in longitudinal sections this could not be determined finally.

In the anterior aporose portion of the proglottid the transverse commissure becomes divided and with the aid of the main duct surrounds an "island" of medullary parenchyma which varies from 60 to 200μ long and may have its long axis either longitudinal or transverse. From this region but varying considerably in point of origin a large branch duct extends distad and mediad into the proglottid. This duct persists after the uterus is fully formed, projecting free into its cavity and invested by its walls. Frequently a similar duct will extend forward from the transverse commissure in the lower pore corner of the proglottid.

There appears to be no doubt but that this cestode is most nearly allied to the genus Schizotaenia. Yet it shows very clearly that it is related to the genus Anoplocephala and appears to be transitional between the two. Aside from the close general resemblances between the two genera the following characters show its close relationship to the known representatives of the genus Anoplocephala.

1. The testes are mainly on the side away from the pore.

2. The vitelline gland is of the type found in Anoplocephala, and shows no suggestion of the type occurring in most other known Schizotaenia.

3. The uterus develops by regular anterior and posterior outpocketing.

4. The cirrus pouch is unusually large.

THE GENUS SCHIZOTAENIA

Deiner (1912) has published an account of the anatomy of *Taenia magna* Murie 1870, under the name *Anoplocephala latissima*, the specific name "*magna*" being dropped because preoccupied by *A. magna* Abildgaard 1789. The account is very thoro and bears all the marks of being strictly dependable. A consideration of the anatomical features leaves no doubt whatever in my mind but that this cestode is a true repre-

sentative of the genus Schizotaenia. Briefly summarized, the following points brought out by Deiner support this conclusion.

1. The testes are mainly on the pore side; this agrees with some Schizotaeniae and disagrees with all known Anoplocephalae.
2. The cirrus is spiny.
3. The vagina and vaginal pore are anterior to the cirrus pouch.
4. The structure of the vagina is identical with that of *S. anoplocephaloides.*
5. The oviduct connects with the ovary directly in front of the vitelline gland.
6. The uterus, while relatively simple, shows clearly a resemblance to Schizotaenia.

These features are all characteristic of the representatives of the genus Schizotaenia. Some of them are found nowhere else; none of them are found in any species known to belong to the genus Anoplocephala. In one character only does this cestode resemble Anoplocephala: the genital pores are all dextral. This character however can not be considered to outweigh the other anatomical resemblances and the cestode is therefore placed in the genus Schizotaenia.

MacCallum and MacCallum (1912) have published a careful account of the anatomy of *Taenia gigantea* Peters 1856, usually referred to the genus Anoplocephala. This cestode also shows marked affinities for Schizotaenia and while the case is not so strong as in the other, the evidence is sufficient to indicate the position of the cestode. The evidence that *Taenia gigantea* Peters is a Schizotaenia follows.

1. The testes are mostly on the pore side.
2. The cirrus is spiny.
3. The vagina was not observed. Since the investigators expected to find it posterior to the cirrus pouch, an inconspicuous and transitory vagina, such as is found in *S. americana* and *S. variabilis,* anterior to the pouch might easily have been overlooked.
4. The vitelline gland is lobulated.

Taenia gigantea Peters is therefore here transferred to the genus Schizotaenia. Its specific distinctness from *S. magna,* long disputed, seems assured.

With six of the species of Shizotaenia well known it is now possible to judge the value of the various anatomical features much more satisfactorily than could von Janicki, who had before him but one that was satisfactorily described. It becomes evident that several of the characteristics he proposed must be restated and several others show themselves to be of generic rank. In making such generalizations the poorly

known *S. 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. The conception of the genus must be changed in the following particulars:

1. The testes do not necessarily extend "von Längsgefäss zu Längsgefäss" in the distal part of the proglottid. They may be in two lateral groups, or all on the pore side, and they may be mostly anterior.
2. In the main the genital canals "ziehen dorsal an den beiden Excretionsgefässen und dem Nervenstrang vorbei"; yet recognition must be given to the fact that the opposite may be the case in some proglottids.
3. The position of the vagina and vaginal pore anterior to the cirrus pouch is an absolute distinction from all other known genera of the subfamily and indeed from nearly all known cestodes, and should have recognition as perhaps the most important generic character. The unsatisfactory description of *S. decrescens* is noncommittal but gives no information opposed to the conclusion that the vagina is anterior here also.
4. The union of the oviduct with the ovary in all sufficiently known species of the genus is located directly anterior to the middle of the vitelline gland. This fact should be stated in the diagnosis.
5. The diagnosis should state that cirrus is spiny.

Accordingly the genus Schizotaenia should be characterized as follows:

Anoplocephalinae, 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, tho 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 towards 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: *Schizotaenia decrescens* Diesing 1856.

The genus Schizotaenia embraces the following well described species.

Magna group: Genital pores dextral. Testes mostly anterior and mostly on the pore side. Size of known species enormous.

S. latissima Deiner
S. gigantea Peters

Hagmanni group: Genital pores alternate. Testes posterior. Known species small.

S. hagmanni von Janicki
S. americana Stiles
S. variabilis Douthitt
S. anoplocephaloides Douthitt

"*Schizotaenia*" *decrescens* (Diesing 1856) Lühe 1895, which von Janicki unfortunately designated as the type of the genus, seems to belong to this group and should be treated as such until better known. "*Anoplocephala*" *transversaria* shows some of the characteristics of this group but not enough information is accessible to justify a change of position.

THE UTERUS OF MONIEZIA EXPANSA

The cestodes of the genus Moniezia have received more attention than those of any other genus of the family. As a result of the studies of Stiles and Hassall, Tower, Fuhrmann, and a number of other workers, most of the points of anatomy have been determined carefully. Strangely enough, however, practically no attention has been given to the uterus except to observe that it begins usually as a reticulum; one is left to assume that the later development is not different from that of related forms. My own observations however have tended to show that the development of the uterus is in many ways unique and furnishes hints as to the relationship of the genus. I had for study several specimens of *Moniezia expansa,* taken from sheep at Lincoln, Nebraska, and belonging to the collection of Professor Henry B. Ward. No observations at variance with accepted anatomical accounts were made so structures other than the uterus have not been taken up, except that a drawing of a mature proglottid is included for comparison (Fig. 41).

The uterus in *Moniezia expansa* begins as a reticulum (Fig. 42), whose slender branches are quite distinct and lie at a considerable distance from each other. In extends nearly the whole length of the proglottid in the space that lies between the shell glands. Beyond these glands on either side two branches, occurring respectively in the anterior one-third and the posterior one-third of the proglottid, extend laterad to beyond the excretory ducts on the dorsal side of the latter. Upon the entrance of the eggs the cavities of the various branches of the uterus enlarge somewhat. The eggs come to lie in bunches which are distributed equally to different parts of the proglottid. As the

embryos develop the portions of the uterus containing these bunches expand. This expansion continues until the enlarged spaces fill almost the entire medullary portion, the tissue substance beween the different regions of enlargement being reduced greatly in thickness but remaining to the last to separate these chambers from each other (Fig. 43). In no stage does the uterus force its way between the excretory ducts and the ventral cortical layer. Thus here in the ripe uterus is a condition that is very unusual in the Anoplocephalinae, and which indeed has been observed in only one other species of the group, namely, *Schizotaenia americana.* One recalls at once the uterus of the Linstowinae, tho there is no indication that the uterus ever really breaks down in the present species. It appears therefore it would not be correct to speak of the compartments as egg-capsules in the sense that the term is used, even tho it is probably a step in that direction.

Drawings by Stiles and Hassall (1893) of gravid uteri of *Moniezia planissima* and *M. alba* indicate structures which, tho not so represented, may be identical with the walls of the compartments found in *M. expansa.* There is a slight indication of such structures also in their drawing of the gravid uterus of *M. neumanni.* Their drawing of *M. trigonophora* shows no such structures but since they give no indications of such structures in their drawing of *M. expansa,* the absence means nothing. Thus no evidence available is opposed to the conclusion that the Monieziae from mammals have the uterus similar in all essential respects to the condition here described for *Moniezia expansa.* The excellent account of Fuhrmann (1902) shows however that the uteri of the Monieziae from birds differ in almost every point from the type just described. The difference between these two groups, if the condition for *M. expansa* is likewise the condition for other mamalian Monieziae, may be summed up as follows:

Monieziae from mammals	*Monieziae from birds*
Mature uterus crossing excretory ducts	Mature uterus not crossing excretory ducts
Mature uterus a complicated reticulum	Mature uterus a simple transverse tube, or with a few simple branches
Gravid uterus in the form of many separated or nearly separted compartments	Gravid uterus saccular, or with simple anterior and posterior pockets
Embryos with pyriform apparatus, the horns of which end in disk	Embryos without pyriform apparatus
Dorsal excretory duct median to ventral	Dorsal excretory duct dorsal to ventral

Diamare (1900) who was first to give more than mention of the Monieziae from birds, created the genus Paronia for the species he was considering (*Moniezia carrinoi*). His conclusions, however, were not based upon a sufficient knowledge of the cestodes in question or the Anoplocephalidae in general, and Fuhrmann very properly included this cestode and other related ones which he described in the genus Moniezia. If, however, the additions here made to the knowledge of *Moniezia expansa* should hold true for the other Monieziae from mammals, there seems to be little question but that the genus Paronia should be revived for the forms from birds. It would be rash to conclude, however, that the other Monieziae from mammals agree with *M. expansa* in this regard. If one considers the different members of the genus Schizotaenia, one finds as great a diversity in uterine structure as is here exhibited. As to the other differences noted, they are not by themselves sufficient reasons for the separation of the genus Moniezia, since other Anoplocephalid genera show both conditions for each structure. Any division of the genus Moniezia would seem premature, therefore, without first examining several species. Consideration of this step is left to some worker who has access to such material.

For reasons stated on page 49 I have transferred Zschokke's "*Moniezia*" *diaphana* to the genus Cittotaenia. Von Janicki's description of *M. beauforti* is not accessible to me; but since it is an avian parasite, it is here considered as belonging in the *carrinoi*-group I can not find evidence to support Parona's action in placing *Taenia frontina* (Dujardin 1845) in this group. Until something more is known of this cestode it should by all means be left where it will do no harm. The genus Moniezia as here accepted includes therefore the following species:

1. *Carrinoi*-group
   - *M. carrinoi* Diamere
   - *M. ambigua* Fuhrmann
   - *M. columbae* Fuhrmann
   - *M. variabilis* Fuhrmann
   - *M. beauforti* von Janicki

2. *Expansa*-group
   - *M. expansa* Rudolphi
   - *M. trigonophora* Stiles and Hassall
   - *M. oblongiceps* Stiles and Hassall
   - *M. planissima* Stiles and Hassall
   - *M. benedeni* Moniez
   - *M. neumanni* Moniez
   - *M. alba* Perroncita
   - *M. amphibia* von Linstow
   - *M. rugosa* Diesing
   - *M. festiva* Rudolphi

Apparently in all Monieziae the oviduct connects with the ovary directly in front of the vitelline gland and the uterus crosses the excre-

tory ducts dorsally or not at all. These points should be stated in the diagnosis of the genus.

The diagnosis therefore becomes as follows:

Anoplocephalinae, with segments generally broader than long. Two complete sets of reproductive organs in each segment, or with but one continuous uterus. Uterus generally reticular, either confined to the median field or crossing the excretory ducts dorsally only. Oviduct joins with ovary directly in front of the middle of the vitelline gland. Genital canals cross on dorsal side of longitudinal excretory vessels and nerves. Interproglottidal glands often present. Vagina ventral and cirrus dorsal on right side of the proglottid; the reverse on the left side. Pyriform apparatus present or absent; when present, the horns end in a disk. Adults in mammals and birds.

Type-species: *Monieza expansa* Rudolphi 1810.

THE CITTOTAENIAE OF NORTH AMERICAN RABBITS

There have been described and named as parasites of North American rabbits four Cittotaeniae, namely, *C. perplexa, C. mosaica, C. pectinata,* and *C. variabilis.* Of *variabilis* I had at hand the material studied by Lyman (1902) and several specimens I collected at various points in Kansas and Oklahoma. The observations confirm Lyman's statements and need be discussed no farther. A drawing is given (Fig. 44) for purposes of comparison.

Of *C. pectinata* there is at hand Lyman's material from Kansas and Nebraska and also two individuals which I collected at Neosho Falls, Kansas. I have been unable to find any confirmation of Lyman's statement that the uterus in anlage extends beyond the excretory ducts. Stiles (1896) and Hall (1908) also conclude that it does not. In some instances I have observed that the fully developed uterus extends slightly beyond the excretory ducts dorsally; but usually it is confined to the median field at all stages. Lyman states that the greatest diameter of the lobes or pouches of the ovary is 16μ. My own measurements of Lyman's material and my own show a diameter of 40 to 60μ as the usual condition. Since the ova themselves are 15 to 18μ in diameter his figures seem most probably a typographical error.

The specimens taken at Neosho Falls, Kansas, are in some respects quite different from Lyman's. The testes are practically absent from the middle part of the proglottid and somewhat more numerous in the lateral parts than in Lyman's material. These two specimens which have shed some proglottids are 45 mm. long and consist each of 85 proglottids. Lyman's specimens were up to 71 mm. long and had when

complete 110 to 140 proglottids; Stiles' material measured up to 400μ long. Eggs begin to pass into the uterus in the 45th proglottid in one of my own specimens. My measurements of the heads of the two specimens show diameters at the base of 700 and 745μ respectively but confirm Lyman's measurements for the specimens he studied. There seems no reason to doubt Stiles' figures which give the diameter of the head as 250μ or less. These different figures show little reliance is to be placed upon these characters.

In certain features the American representatives of this species are different from the European and should be designated as a distinct variety to avoid confusion. The following is the characterization.

Cittotaenia pectinata: Strobila up to 400 mm. long. Sexual maturity about 30 mm. from the anterior end. Testes about 150, extending uniformly across the distal end of the proglottid, from excretory duct to excretory duct. Hosts *Lepus timidus* and *Lepus variabilis.* Known distribution, Germany and France.

Cittotaenia pectinata americana: Strobila 44 to 71 mm. long. Number of proglottids, 85 to 140. Sexual maturity reached in about the 45th proglottid, about 10 mm. from the anterior end. Testes 100 to 125, extending from excretory duct to excretory duct in the distal end of the proglottid, sometimes nearly absent from the median part of the field. Host, *Lepus californicus melanotus.* Known distribution, eastern Kansas and Nebraska, U. S. A.

Of *Cittotaenia perplexa,* I have studied U. S. National Museum cestode No. 1110, which is one of the specimens upon which Stiles (1896) based his original description and which was designated by him a cotype. Permission was given to dismount and section the specimen. Inasmuch as it had been mounted in balsam for 18 years, this was obviously a difficult task to accomplish; but by careful work two series of sections have been made, which, while by no means suited for careful study, are sufficient to show that all the differences supposed to exist between this cestode and *C. mosaica* (Hall, 1908) are due to errors or incorrect conclusions as to the former. These points will be taken up one at a time.

The cirrus pouch Stiles (1896) records as being 288 to 320μ long in *C. perplexa.* Eighteen pouches I measured, however, were all 530μ long. Hall found the pouch in *C. mosaica* to be 475 to 640μ long, with an average length of 550μ. There is therefore no difference in this regard. In position and form the cirrus pouch and vagina are identical with Hall's descriptions. The specimen at hand is not suited for histological study and comparison. According to Stiles' description the testes of *C. perplexa* are absent from the median part of the pro-

glottid. In the specimen at hand, however, they extend across the field continuously in a manner identical with the description by Hall for *C. mosaica*. There is of course no reason to doubt the correctness of Stiles' observation; but it seems evident that the condition he described is not diagnostic. As mentioned, I have found the testes in *C. pectinata* almost separated in two fields.

Hall recognizes in his specimens some differences from Stiles' account as to the time of first appearance of genital organs. He acknowledges that such differences may be due to differences in technique and mentions that Stiles' account was based upon unsectioned material. I have not attempted to section the anterior end of the specimen at hand since it is not in condition for close study. However there is no valid reason for considering the specimens different on this point. The mosaic markings mentioned by Hall can hardly be considered of importance; anyway, they are shown to a slight extent by the specimen at hand.

There are no other points of difference between the two accounts. I have compared Stiles' cotype in nearly every particular with Hall's account and find only two points of difference: (1) eggs appear first in the uterus in the 94th proglottid; and (2) the ovary is 850μ across, and of somewhat different appearance from the condition Hall describes. These points of difference are taken up in the paragraph after the next.

Specimens of this form from cottontails (*Sylvilagus floridanus*) at Blair, Oklahoma, show the ovary exactly as described by Hall and of the same dimensions, that is, about 600μ across. The cirrus pouch is somewhat smaller, and old pouches, when gorged with sperm, shorten up and become pearshaped. In two specimens sexual maturity is reached in the 90th proglottid. In other points they do not differ from Hall's description. Figures 46 to 49 are from this material. These Oklahoma specimens, it will be seen, resemble the Maryland specimen in that maturity is reached about the 90th proglottid. The gorging and shortening up of the cirrus pouch suggests an explanation of the basis of Stiles' measurements. The general appearance of the worms is identical with both the Maryland and the Colorado forms, and the form of the ovary is identical with that of those from Colorado. It seems very probable that the appearance of the ovary presented by the Maryland specimen is due to the flattening process to which it was subjected preparatory to mounting in toto. The lobes stretching out laterally at full length are in just the position they would assume with such treatment. As to the difference in the stage at which maturity is reached, the same explanation would apply here as for *Anoplocephala*

variabilis (page 22). Bowie, Maryland, and Blair, Oklahoma, are in the Upper Austral faunal zone, while Seven Lakes, Colorado, is in the Boreal.

The Colorado forms may deserve the rank of a separate variety, on account of the difference in stage of sexual maturity; but until the character has been determined for more than two or three individuals on each side, such a step would not be justified. Variations of far greater import have been recorded in this paper which were found in individuals of the same species and from the same host, and even in different proglottids of the same individual. The name, *Cittotaenia mosaica,* should therefore be dropped, and the excellent description by Hall (1908) applied to *C. perplexa,* the only change necessary being to recognize that sexual maturity may not occur until the 95th proglottid and that in addition to occurring in *Sylvilagus pinetis* of Colorado it also occurs in *Sylvilagus floridanus* of Maryland and Oklahoma. There seems no reason to doubt that the testes are sometimes separated into two groups, as described by Stiles.

C. pectinata and *C. perplexa* are strikingly similar in several unique characters, and it seems not improbable that their differences may be due to environmental conditions, since one is a parasite in the cottontail and the other in the jack rabbit; but my present opinion is that such a decision would be premature, without testing it by breeding experiments. *C. perplexa* differs from *C. pectinata* in the following points, all of which are quantitative:

1. The testes are fewer
2. The cirrus pouch is smaller
3. There is a more complicated network of excretory ducts in the lateral portions of the median field
4. The ovary is smaller

THE GENUS CITTOTAENIA

Zschokke in 1907 described a cestode from *Phascolomys wombat,* giving it the name *Moniezia diaphana.* His excellent description however seems to be that of a perfectly normal Cittotaenia, and disagrees with Moniezia on every point in which these two genera differ. The species is here transferred to the genus Cittotaenia for the following reasons:

1. The vagina is not ventral on the right and dorsal on the left, as in Moniezia.
2. There are no shields on the ends of the horns of the pyriform body.

3. The uterus is tubular—not reticular.

4. The dorsal excretory duct is dorsolatral to the ventral.

Two changes should be made in the diagnosis of the genus Cittotaenia. It should be stated that the oviduct joins the ovary directly in front of the median axis of the vitelline gland and that the uterus crosses the excretory ducts dorsally only, or not at all.

The diagnosis therefore becomes as follows:

Anoplocephalinae, with segments broader than long. Two sets of reproductive organs in each segment. Genital canals pass dorsal of longitudinal excretory vessels and nerves. Interproglottidal glands absent. Vagina ventral of cirrus pouch on both sides of the segment. Oviduct joins ovary directly in front of the median axis of the vitelline gland. Uterus either confined to the median field or crossing the excretory ducts dorsally only. Development usually by simple anterior and posterior outpocketing. Eggs with well developed pyriform apparatus of ordinary type, or without pyriform apparatus. Adults in mammals and birds.

Type-species: *Cittotaenia denticulata* Rudolphi 1804.

The genus Cittotaenia includes the following species, most of which are fairly well known:

1. *Marmotae*-group. Cirrus pouch pyriform, distinct. Dorsal duct lateral or dorsal of ventral (no statement concerning *C. bursaria.*

C. marmotae Braun	*C. praecocquis* Stiles
C. denticulata Rudolphi	*C. ctenoides* Railliet
(*C. latissima* Riehm	*C. diaphana* Zschokke
(*C. goezei*)	*C. zschokkei* von Janicki
C. bursaria von Linstow	*C. quadrata* von Linstow

2. *Pectinata*-group. Cirrus pouch much elongated, resembling nozzle of a hose, and indistinct; becoming pyriform occasionally in old proglottids. Dorsal excretory duct median to ventral.

C. pectinata Goeze (in part)	*C. rhea* Fuhrmann
C. variabilis Stiles	*C. psittacea* Fuhrmann
(*C. mosaica* Hall)	*C. avicolae* Fuhrmann
C. perplexa Stiles	*C. kuvaria* Shipley

COMPARATIVE STUDIES ON THE ANOPLOCEPHALIDAE

Fuhrmann's classification of the Cyclophyllidea (1907) which is accepted here recognizes in the subfamily Anoplocephalinae the genera Triplotaenia, Cittotaenia, Moniezia, Anoplocephala, Andrya, Bertiella, Schizotaenia and Aporna. Each of these genera is well defined and

distinct; and except for Triplotaenia and Aporina they form a compact and orderly group. But little attention has been given to the relationships of these genera to each other. In the following pages the various resemblances in the different organs are considered, with reference to the question of relationships between the various genera.

1. *The Structure of the Uterus.*—Two general types of uterus have been recognized in this group: the tubular, found in Bertiella, Anoplocephala, and most Cittotaeniae,and the reticular, found in Andrya, most Monieziae, and some Cittotaeniae. In addition the uteri of Schizotaenia, Triplotaenia, and Aporina have been recognized as each being a distinct type in itself, tho the uterus of Triplotaenia is not really different from the tubular. The uterus of Schizotaenia has been shown in this paper to be of the reticular type, the reticulum being apparently in the process of degeneration. There appears no reason to regard the uterus of Aporina as of any other than the tubular type. As to the relationships of the reticular and tubular types to each other, very little has been done in the way of investigation except to conjecture. Generally the reticular type has been supposed to be derived from the tubular by the outgrowth and anastomosis of proximal and distal branches. Following are offered the conclusions from studies of the reticulate uteri of different species of Andrya, made with the view of studying the relationships of these two types to each other.

In the earliest stages in which indications of the uterus were observed it occupies the entire region later occupied by the fully developed reticulum. This stage is long before any lumina appear. The uterine tissue is more or less diffuse, there being no indication of segregation along lines, except that it is more or less "stringy" in transverse axis. As the proglottid increases in size, the cells segregate more and more into definite lines which run in all directions and connect at frequent intervals, forming a network. These lines of segregation do not spread from any central locality but appear in situ and so far as could be observed, at about the same time in all parts of the proglottid. Later cavities appear in these tubes; these again do not spread out from any central source but appear in situ and without the stimulus of entering ova. When fully developed they form a continuous network of open tubes. As these tubes become filled with ova they expand and coalesce, forming a single saccular cavity. Development then proceeds by regular outpocketing, anteriorly and posteriorly. Thus in the early stages of development there is no indication that the reticulate uterus has been derived from a transverse tubular type by outgrowth and anastomosis of branches, as was suggested by Stiles (1896). It is true of course that the uterus spreads from some original source in the course

of development; but there is no evidence that there intervenes a transverse tubular stage which is comparable in any sense to the uterus of Anoplocephala.

On the other hand it seems much more probable that the reticulate uterus has been derived by lateral spreading from a median longitudinal uterus, such as we find in more primitive cestodes, and is the first step in the evolution of the transverse uterus rather than the last; that the tubular uterus of Anoplocephala has been the product of simplification. Schizotaenia seems to be in an intermediate condition; the uterus appears in a widely diffused condition but the cavity appears first as an anterior transverse tube. Some such view becomes necessary if Andrya is regarded as a primitive type, as other characters indicate. It is a matter of sincere regret to me that other matters prevent making a careful study of the uterus at this time.

Aporina, Andrya, and Anoplocephala agree in that the uterus, in nearly all species, extends laterad beyond the excretory ducts, crossing them ventrally. Never does it cross them dorsally in anlage and at all stages it lies mostly ventral. In Schizotaenia, and apparently always in Bertiella, it is confined to the median field in mature proglottids and in its fully developed stage crosses the ducts mostly on their dorsal side, if at all. In Cittotaenia and Moniezia the uterus in anlage usually crosses both excretory ducts dorsally but in some species is confined at all stages to the median field. Apparently it never penetrates between the excretory ducts and the ventral cortical layer. These points furnish very important indications of the relationships of the varied genera to each other. The development of the uterus by outpocketing must be recognized as a very general character of the subfamily, and in general, a primitive one. It has been shown to be the method of development in Andrya, where it was supposed not to occur, and in one species of Schizotaenia.

2. *The Distribution of Testes.*—The genus Aporina has been considered unique in that the testes extend laterad beyond the excretory ducts. In the present paper however are described four species of Andrya and two of Anoplocephala in which the testes do extend across the excretory ducts on the side away from the pore, and in the other species of Anoplocephala here taken up they do in many proglottids. Likewise, Zschokke's figures for Bertiella edulis (1899, Taf. XX, Fig. 2) shows that in this species the testes may extend nearly across the ducts. It seems probable that they occur in the lateral fields in all or nearly all species of Anoplocephala and Andrya, and in the median field in all species of Schizotaenia and most species at least of Bertiella. The double pored genera of course, cannot be compared in this regard.

The genus Aporina remains distinct in that the testes cross the excretory ducts on the side in which the pore would be, if one were present.

The testes of Bertiella and most species of Andrya are anterior; those of Andrya occupy almost the entire median field except for the space above the ovary. Those of most species of Schizotaenia and at least some species of Anoplocephala are mainly posterior; and for Cittotaenia and Moniezia they are posterior in all cases where one can judge. However, *Andrya translucida* has the testes posterior and two species of Schizotaenia have them mainly anterior. It is therefore impossible to form any final conclusions as to the paths of evolution in this regard. In looking however for the type that has the most generalized distribution of testes, attention is at once attracted by the conditions found in Andrya. Here, especially in *Andrya primordialis,* is found a near approach to a distribution that could give rise by suppression to any distribution found in the subfamily, with the exception of Aporina.

3. *The Vaginal Pore and Vagina.*—The position of the vagina and vaginal pore with reference to the cirrus pouch appears from these studies to be the most stable generic character. In Aporina and Andrya the vaginal pore and vagina are directly posterior to the cirrus pouch, which position is primitive among cestodes. In Bertiella the pore and vagina are either posterior or somewhat dorsal. In Anoplocephala the pore is ventral to the pouch, and the vagina is ventral, and for at least the lateral half of its length is not posterior. In Cittotaenia the pore and vagina are ventral but may be at the same time posterior also. In Moniezia they are ventral to the pouch on the right side and dorsal on the left and usually they are also somewhat posterior. In Schizotaenia both vagina and vaginal pore are directly in front of the cirrus pouch. The evidence provided here points to the conclusion that the three genera first mentioned are the most primitive.

4. *The Ovary.*—Two types of ovary can be distinguished. In one the lobes radiate in all directions in the horizontal plane from the point of attachment of the oviduct; in the other the lobes radiate from a transverse bar, which forms the basal part of the ovary. The second type is perhaps the only one found in Anoplocephala and Schizotaenia, and it is present with modifications in Moniezia and Cittotaenia. The first type is typically represented in Andrya. Unfortunately most of the drawings of species of Bertiella and Aporina are obscure on this point. At any rate the character is not of much systematic importance because the two conditions are not very distinct from each other and are obscured by modifications.

5. *The Excretory ducts.*—Nothing is known as to the excretory ducts of Triplotaenia. Bertiella and Moniezia have the dorsal ducts

either dorsal or dorsomedian, and Cittotaenia has them dorsal, lateral or dorsomedian. Usually the dorsal duct is lateral in Anoplocephala and Schizotaenia; but in certain stages of contraction it has been observed to be directly dorsal in both genera. In Andrya the dorsal duct is lateral in all cases observed. In the scolex of all species of Andrya and Anoplocephala which were observed however, the dorsal duct is dorsal while in *Schizotaenia anoplocephaloides* it is lateral in the scolex. It would appear therefore that little evidence as to relationship is provided by the excretory ducts.

THE EVOLUTION OF THE ANOPLOCEPHALIDAE

The following arguments favor the conclusion that Andrya approaches most closely of all the genera to the ancestral type of the Anoplocephalidae.

1. In Andrya the ovary is either median, or very close to the median line, and none of the female glands are far from the median line.
2. In Andrya the vagina and vaginal pore are directly posterior to the cirrus pouch.
3. In Andrya is found the most generalized distribution of testes, with the possible exception of Aporina.
4. In the generalized species of Andrya is found a primitive, unmodified vas deferens, which character is found in no other genus except Aporina.
5. In Andrya is found the most genuine and least modified reticulate uterus.
6. In Andrya, the uterus in anlage, crosses the excretory duct ventrally.

As characters of more doubtful value, the following may be noted.

1. The pyriform body is simple (no pyriform body in Aporina).
2. The vesicula seminalis is, in the most generalized species, a simple, globular expansion.
3. The genital pores are in some species irregularly alternate.

As specialized characters of Andrya I can see but one; the genital pores are either dextral or tend towards dextrality, whereas one would expect the ancestor of the Anoplocephalidae to have single, irregularly alternating genital pores. Such a point constitutes but a slight departure however in the light of the different arrangements that have arisen in the family; and in this regard evolution could easily reverse its action. The possession of a prostate gland would seem at first to be a specialized character; but this structure appears to be associated with

an unmodified vas deferens and to cease to have a purpose for existence when the vas deferens comes to function as a storehouse for spermatozoa, as is the case in all other genera except Aporina.

Within the genus Andrya there has been a wide range of evolution. *A. primordialis* is decidedly the most primitive in structure of ovary and uterus and testicular distribution; and only in the arrangement of genital pores is it unlike what should be expected in the ancestors of all the Anoplocephalidae. In *Andrya macrocephala* and *A. translucida* on the other hand is found a rather high degree of specialization. As regards position in the scale Aporina is a close contestant with Andrya for the most primitive position, each having distinct points in its favor. Aporina must be regarded however as an offshoot since certain characters which it possesses exclude it from the direct line.

From forms like the most primitive Andryae there sprang apparently a line destined to give rise to all the other Anoplocephalidae, except possibly Bertiella. The characteristics of this line, many of which were subsequently modified, were as follows:

1. The lobes of the ovary did not radiate from the point of attachment of the oviduct, but instead extended out from a transverse bar which formed the base of the ovary.

2. The vagina and vaginal pore had begun to move anteriorly and ventralwards.

3. The testes had come to lie mostly in the posterior part of the proglottid.

4. The cirrus pouch had begun a conspicuous development in size, foreshadowed in *Andrya primordialis*.

5. The female glands remained in the primitive position, near the median line.

6. The prostate gland was lost and the vesicula seminalis was acquired.

The genus Anoplocephala apparently separated from the rest early, and developed along somewhat different lines. It retains the following Andryan characters.

1. The uterus, in anlage, crosses the excretory ducts ventrally.

2. The testes extend into the lateral field on the side away from the pore.

3. The proximal end of the oviduct lies beneath the median lobe of the vitelline gland.

4. The tendency towards dextral arrangement of genital pores is retained and perfected.

After Anoplocephala had split off the common line became modified as follows:

1. The uterus ceased to cross the excretory ducts, in anlage.
2. The ovary moved forward and laterad so as to lie directly in front of the vitelline gland with the proximal end of the oviduct in front of the median line of this gland.
3. The testes become confined to the median field.

From this line developed Cittotaenia, Schizotaenia, and Moniezia. Cittotaenia resembles Anoplocephala in some respects but the following evidences of relationship to Moniezia outweigh them:

1. In both, the uterus crosses the excretory ducts dorsally only, never ventrally as in Anoplocephala, Andrya, and Aporina. In some cases in each of these two genera, the uterus is confined to the median field at all stages.
2. At least one Cittotaenia has a reticulate uterus.
3. Both have two sets of genital organs.
4. The dorsal excretory duct is dorsal or median to the ventral in most species of each.

The points arguing for close relationship between Moniezia and Schizotaenia are as follows:

1. Each retains at least remnants of the reticulate uterus.
2. Some individuals of Schizotaenia show asymmetry in regard to the relations of the genital glands.
3. Moniezia has, to a considerable extent, at least, the mulberry-like vitelline gland, such as is found in most species of Schizotaenia.
4. The ripe uterus is divided into compartments in some species of both genera.

Although retaining the reticulate uterus Moniezia and Schizotaenia are in many ways the most specialized representatives of their subfamily, except of course for Triplotaenia. They have specialized along different lines and the decision as to which is nearest the ancestral line depends upon the criteria adopted.

The position of Bertiella in this scheme is somewhat doubtful. I had no specimens at hand for study and so must depend upon the accounts of others. The following points argue for close relationship with the higher representatives of the genus Andrya rather than with other genera.

1. The vagina and vaginal pore are directly posterior, or posterior and dorsal to the cirrus pouch.
2. The cirrus pouch is either identical with the higher Andryae

in form and size, or much smaller (the pouch is larger in the other genera).

3. The testes are mainly anterior.

4. In species concerning which information is available, the oviduct and ovary are related to each other as in Andrya, and not as in Schizotaenia.

The following points argue for relationship rather to Schizotaenia-like forms, however.

1. The cirrus is sometimes spiny.

2. The genital pores are sometimes regularly alternate.

3. The uterus, at least in anlage, is confined to the median field.

4. The dorsal excretory ducts are often dorsomedian, as in relatives of Schizotaenia.

5. The testes seem to be confined to the median field, as in Schizotaenia; in some species of Schizotaenia, also, the testes are anterior.

I am inclined to consider the aguments for closest relationship to the genus Andrya as the most important, and to attribute the resemblances to Schizotaenia to parallel evolution.

The relationships of the genus Triplotaenia are problematical and will probably always remain uncertain. The possession of two sets of reproductive organs suggests relationship to Cittotaenia or Moniezia. The following points argue for relationship to Schizotaenia.

1. The uterus, in anlage, is confined to the median field.

2. The horns of the pyriform body are long and filamentous.

3. The vagina is inconspicuous and apparently ephemeral.

These points argue for little more than general relationship however and all of them might easily be accidental.

The following points argue that Thysanosoma is most nearly related to the higher representatives of the Anoplocephalinae and is descended from forms like Moniezia and Schizotaenia.

1. There are sometimes two sets of reproductive organs in Thysanomosa.

2. The genital ducts sometimes cross the excretory ducts ventrally in Schizotaenia.

3. The genital organs are placed far laterad, in Thysanosoma.

4. The vaginal pore may be dorsal, or anterior to the cirrus pouch, in Thysanosoma.

5. Accessory transverse commissures of the excretory ducts are present in species of both Schizotaenia and Thysanosoma.

These arguments however are at best inconclusive. The most that can be said is that Thysanosoma seems to be related to the higher Anoplocephalinae.

That Stilesia and Avitellina are quite closely related to Thysanosoma is too evident to need discussion. The exact position of these genera with respect to each other must be left unsettled, however, until the species of Thysanosoma have received more careful study. At present we can do no better than accept Gough's decision (1911) that Stilesia and Avitellina represent a subfamily distinct from Thysanosoma.

In the subfamily Linstowinae, conditions are unsettled and uncertain, owing to the recent efforts of Beddard (1911, and 1912), and others. It seems little short of absurd to decide from external characters (1911:652) as to which of about 20 genera a given cestode should be referred to, the possible list including such genera as Anoplocephala, Zschokkeella, Thysanosoma, Davainea, Hymenolepis, Oochoristica and Taenia. Within two years, Beddard has actually placed one cestode (whose latest name is *Zschokkeella gambianum*) in three genera, representing two subfamilies; and there is no assurance that the present disposal is final. Since Beddard has proved his worth as an investigator by his researches in other fields, one might expect better things in the future; but as yet, while he has dwelt at great length upon the significance of the size and appearance of sucker and scolex, the presence or absence of a neck, and other such features, he has failed to tell, in any instance, whether the genital ducts cross the excretory ducts dorsally or ventrally, or pass between them; at least, several hours were spent in search in his voluminous articles without finding any information on this point. Bischoff (1912) has likewise contributed considerably towards a state of general confusion in this group. He has added to the genus Inermicapsifer several species, without giving, apparently, any adequate study to each. The few facts that he gives are not sufficient in most cases to show that the species exist; and if they do exist, there is no evidence in many cases that they should be placed in the Inermicapsifer group rather than in some allied group.

In the present condition of affairs, there are no characters except trivial unimportant ones upon which to separate the so-called genera Zschokkeella, Inermicapsifer, Thysanotaenia and Hyracotaenia from each other. My own opinion is that they all belong in one genus, with the exceptions of *Zschokkeella remota* and *Thysanotaenia lemuris* which seem to belong elsewhere. In the present condition of our knowledge of most of the species of the group, however, any alterations would merely add to the confusion already existing. *"Taenia" anoplocephaloides* must be given a place amongst the Linstowinae, close to the genus Linstowia. Of the genera of the Linstowinae, Linstowia shows, by the

position and form of genital organs and excretory ducts, that it is the most generalized, unless "*Taenia*" *anoplocephaloides* be given a lower place. The following facts argue that Linstowia is descended from the higher Anoplocephalinae, from forms somewhat like Schizotaenia and its relative Moniezia.

1. The uterus, in some Schizotaenia and Monieziae, in its fully developed stage is divided up into compartments much like the embryocapsules of the Linstowinae.

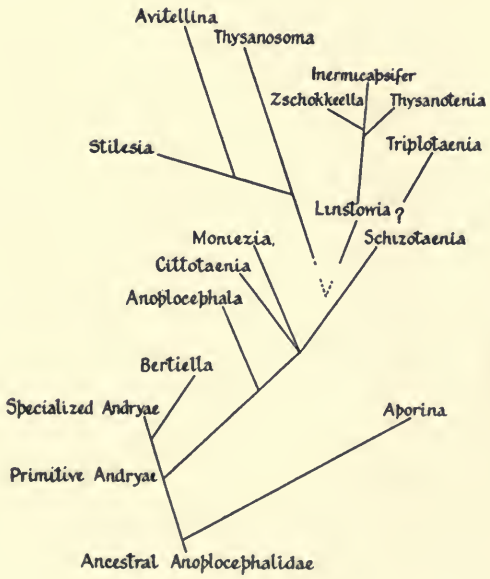
3. The uterus of the Linstowinae, in anlage, is not different in type from the diffuse uterus of the genus Schizotaenia.

3. The uterus apparently crosses the excretory ducts dorsally in the Linstowinae; information is vague or wanting as to most species, however.

4. The genital ducts have been observed to cross the excretory ducts ventrally in some individuals in Schizotaenia.

5. The cirrus pouch is unusually large in Schizotaenia and Linstowia.

The following diagram represents the scheme of evolution here proposed.



LIFE HISTORIES OF POCKET GOPHER ANOPLOCEPHALIDS

Throughout the present studies attention has been given to the problem of the life-histories of the cestodes of the pocket gopher. This problem has been attacked in three ways: by experimental feeding, by examination of suspected hosts for cysticercoids, and by observations on the habits of the gopher. Either the first or second method, or both, have been tried out on all the parasites and commensals of the gopher which I have been able to find, with only negative results as yet; it is my intention to keep steadily at this quest whenever opportunity offers. Observations on the habits of the gopher however have yielded information which may prove of decided value in the quest of the intermediate hosts of the Anoplocephalidae, and this information is given here in the hope that the facts may be of assistance to other workers who are giving attention to this subject. In order to make the matter clear a brief statement is necessary concerning the habits of the gopher.

I have found *Geomys personatus* always in infertile, sandy ground. *Geomys breviceps* I have caught at various points in Texas and Oklahoma; but nowhere except at Norman, Oklahoma, have I caught them in anything except upland regions in very sandy soil. At Norman, gophers were taken along a stream valley in soil that is of a sandy nature but fertile and moist. *Geomys bursarius* I have found to range over about every conceivable locality. They thrive on the borders of swamps, on hilltops, on open plains, in heavy pine forests, in windblown sand, and in heavy clay soil, whether uplands or lowlands.

Wherever he occurs, the gopher leads a life wholly apart from his fellows except at the mating season. His tunnel is seldom as much as 50 meters long. This tunnel is practically the gopher's world except during the mating season. In the evening he may come to the top of the ground for a few moments; but he does not wander more than a few feet from the mouth of the burrow. In regard to the occurrence of all the species of Anoplocephalidae found infesting the gopher, one rule has proved to be invariable: they occur only in gophers inhabiting rich soils, preferably clay soils, but occasionally in sand when it is mixed with humus and is of a swampy nature. To this rule I have found not a single exception. Apparently not all regions of fertile soil are infected, and lowlands in the main are most heavily infected. Swampy places have been found to yield the best of all.

A specific instance is illuminating. At Brainerd, Minnesota, fifteen gophers were caught in the sandhills; on examination one cestode was found which belonged in the genus Hymenolepis. The traps were then moved to Bean Flat, 200 meters away. Bean Flat is a low, almost

swampy region in which the gophers can live only along the margins of the low river terraces which cross the flat. With a single exception, every adult gopher examined was infected, this locality and another 200 meters away which was similar yielding five species of Anoplocephalid cestodes of three genera. Twenty-six specimens, representing three species, were taken from one host. When one considers that the gopher never wanders more than a few feet from the mouth of his burrow except during the mating season this fact becomes all the more significant. The conclusion is forced upon the student that there is some connection with the nature of the soil that determines the infection; it seems most probable that the intermediate hosts are plant-feeding insects that live only in fertile soil preferring wet lowlands.

Since this rule holds true for six species of four genera of the Anoplocephalidae it seems probable that it will hold true for the family generally; that there is something associated with fertile soils and swampy places that is necessary for the continued existence of these parasites; that if cattle and sheep could be confined to sandhill pastures (which assuredly would not be practical), they would not become infected with Thysanosoma and Moniezia. This rule is at least worth trying out by other workers who are giving attention to the life-histories of these cestodes. The camel cricket (Ceuthophilus) has been found to abound in the tunnels of the pocket gopher in localities where these cestodes occur and to be absent from localities where the cestodes do not occur. However all attempts to infect these animals have resulted in failures. It is my intention to continue these experiments both with these animals and others whenever opportunity offers.

The following table shows the infections found in adult gophers. All gophers that were less than 8 months old, even tho fully grown were without exception uninfected. The separation of the various species of Hymenolepis which were found was rather hastily done and only approximate correctness was aimed at. The species of Cittotaenia from Brainerd, Minnesota, was unfortunately immature and could not be worked out. It is not *C. praecocquis* described by Stiles (1896) from the same host-species. The examinations were all made by me, with the exception of those from Nebraska for which I have to thank Dr. John E. Gutberlet.

CESTODE INFECTION OF ADULT GOPHERS

Host	Locality	Habitat	Time of Collection	No. animals examined	No. infected	CESTODE PARASITES FOUND															
						Anoplocephala variabilis	Anoplocephala infrequens	Cittotaenia sp.	Schizotaenia anoplocephaloides	Andrya macrocephala	Andrya translucida	Oochoristica sp.	Davainea sp.	Hymenolepis sp.	Hymenolepis sp.	Hymenolepis sp.	Hymenolepis sp.	Hymenolepis sp.	Hymenolepis sp.	Hymenolepis sp.	Hymenolepis sp.
Geomys bursarius Shaw																					
	Hardy, Nebraska	Upland, clay soil	June-July	12	0																
	Springfield, Illinois	Upland, clay soil	July	9	9	104										38					
	Lincoln, Illinois	Heavy, black, upland clay soil	July	5	5	97										1					
	Clinton, Illinois	Heavy, black, upland clay soil	All months	26	14	140										2	108				
	Havana, Illinois	Sandhills	June, August	8	0																
	LaCrosse, Wisconsin	Infertile, upland, sandy soil	August	8	1													1			
	Sanborn, Minnesota	Infertile, upland, sandy soil	September	4	0																
	Minneapolis, Minnesota	Heavy, black, upland clay soil	August	8	1	2															
	St. Cloud, Minnesota	Fertile, upland clay soil	August	6	0																
	Brainerd, Minnesota	Bean Flat, swampy, black soil	August	9	8	44	4	1		3		2									
	Brainerd, Minnesota	Stroeh's Pasture, " " "	August	4	4		1			13	3										
	Brainerd, Minnesota	Sandhills	August	15	1													1			
	Bemidji, Minnesota	Mixed sand and humus, swampy	September	10	4	4	2														
	Thief River Falls, Minn.	Heavy, black, upland clay soil	September	6	2	3				1											
	Warren, Minnesota	Heavy, black, upland clay soil	September	4	0																
	Wahpeton, No. Dak.	Heavy, black, alluvial soil	September	6	2	2												1			
	Grand Forks, No. Dak.	Heavy, black, upland clay soil	September	12	3													3	36		
	Emerson, Manitoba	Heavy, black, upland clay soil	September	6	1	2	2														
Geomys breviceps Baird																					
	Norman, Oklahoma	Fertile, sandy soil, wet valleys	May, August	11	3				50												
	Norman, Oklahoma	Sandhills	September	5	1								2								
	Sulphur, Oklahoma	Fertile, sandy soil, upland	August	4	1															4	
	La Grange, Texas	Pure sand, river banks	August	3	3															6	3
Geomys personatus True																					
	Katherine, Texas	Pure sand, semi-arid	August	1	0																
Geomys personatus fallax																					
	Corpus Christi, Texas	Mixed sand and marl, [semi-arid	August	5	2									25	2						
Thomomys talpoides																					
	Emerson, Manitoba	Heavy, black, upland soil	September	6	0																

KEY TO KNOWN SPECIES OF ANOPLOCEPHALIDAE

Owing to the fact that the literature of this group is scattered, uncoordinated, and often inaccessible, the task of identifying material is often very difficult and time-consuming. The writer in taking up for the first time the several groups here studied, has had good cause to realize this. In the hope that it will spare to others this waste of labor in becoming acquainted with the field, the following key to all the known species of Anoplocephalidae is presented. A great many poorly described species are represented here, species as to whose affinities no one has any means of judging. In order to avoid confusion they are left in the genera to which they have been assigned, tho in many cases there is no proof that they belong even in the family. To prepare a key for such species has been found very difficult and in some cases the only thing that could be done was to list them with such descriptions as are possible.

In order not to hamper the serviceableness of the key only the more important synonyms are given and usually only the best reference is given for each species. For an exhaustive bibliographic account of the various species and genera, the reader is referred to Stiles & Hassall's excellent summary (1912). True phylogenetic characters have been used wherever possible; and wherever such exist, classifications previously proposed have been accepted. No attempt has been made to treat the Linstowinae critically; they are included here merely to make the key complete and critical study is left to someone better fitted to take up the work.

Family Anoplocephalidae: Scolex and suckers unarmed. Segments nearly always broader than long, generally many times broader than long. Genital pores marginal (absent in Aporina). Testes numerous, except in Triplotaenia. Uterus transverse. Embryos with thin, transparent shells, usually with a pyriform apparatus borne upon the innermost shell. Adults in mammals and birds, mostly in herbivorous mammals; larval stages unknown. Four subfamilies 1

1. Genital canals dorsal to longitudinal excretory vessels and nerves, except possibly in Triplotaenia, and in some proglottids in some Schizotaenia. Uterus at the stage of sexual maturity tubular, netlike, or diffuse, or, in Triplotaenia,

saclike. Development usually by outpocketing, the uterus rarely breaking up into separate compartments, never with paruterine organs. Vitelline and shell glands always present. ..... *Anoplocephalinae* 2

Uterus breaks down early into egg capsules. Genital canals pass ventral to excretory ducts or between them. Cortical parenchyma usually very thick. A single set of reproductive organs in each segment in all known species. Vitelline and shell glands always present ..... *Linstowinae* 51

Paruterine organs present. Genital canals pass between the excretory vessels and dorsal to the nerve. Embryos with two shells, usually with pyriform apparatus which is devoid of horns. Testes in two lateral groups which cross the excretory ducts on either side. Vitelline and shell glands present ..... *Thysanosominae* 70

Paruterine organs present. Genital canals pass dorsal to excretory ducts or between them. Eggs with two shells, no pyriform apparatus. No vitelline gland or shell gland. All known species inhabit ruminants. (See Gough, 1911.) *Avitellininae* 71

ANOPLOCEPHALINAE

2. Without genital pores. Testes crossing excretory ducts on both sides of the proglottid. No pyriform apparatus. One genus and species. (See Fuhrmann, 1902.) ..... *Aporina alba*

With genital pores. Testes not crossing excretory ducts on pore side 3

3. With not more than one cirrus pouch in each lateral half of the segment. With numerous testes. With external evidences of segmentation 4

With four or five cirrus pouches in each lateral half of the segment. With but one testis in each lateral half of the segment. Without external evidences of segmentation. One genus and species. (See von Janicki, 1906.) *Triplotaenia mirabilis*

4. With but one set of reproductive organs in each proglottid 5

With two sets of reproductive organs in each proglottid 6

5. Vaginal pore posterior to cirrus pouch. Uterus reticular. Either with a pedunculated prostate gland or with ventral excretory ducts enormously developed. Genital pores all, or nearly all dextral. (See present paper.) ..... *Andrya* 7

Vaginal pore posterior, or posterior and dorsal to cirrus pouch. Uterus tubular. No prostate gland. Ventral excretory ducts normal in size. Genital pores alternate, except in the doubtful *Bertiella pinguis* where they are unilateral. Testes anterior. (See Bourquin, 1905.) ..... *Bertiella* 12

Vaginal pore and vagina ventral to cirrus pouch. Uterus tubular. No prostate gland. Genital pores dextral except in the doubtful *Anoplocephala omphalodes* and *A. minima.* testes only on the side away from the genital pore, except in *A. spatula* and occasionally in *A. omphalodes.* (See present paper.) ..... *Anoplocephala* 21

Vagina and vaginal pore anterior to the cirrus pouch. Uterus diffuse, degenerate reticular. No prostate gland. Testes either posterior or anterior, and usually mostly on the pore side. (See present paper.) ..... *Schizotaenia* 30

6. Vagina crosses cirrus pouch ventrally on both sides of the segment. (See Stiles, 1896, and present paper.) ..... *Cittotaenia* 34

Vagina crosses cirrus pouch dorsally on the left, and ventrally on the right side. (See Stiles & Hassall, 1893.) ..... *Moniezia* 44

Genus Andrya

7. Scolex large. Excretory ducts enormous. No prostate gland. With external vesicula seminalis 8

Scolex and excretory ducts of ordinary dimensions. With prostate gland. Vesicula seminalis confined to cirrus pouch 9

8. Length 10 to 20 cm. Number of proglottids, 350 to 450. Width of strobila, 1.5 mm. Vesicula seminalis very large. Host, *Geomys bursarius,* Minnesota. (See present paper.) *A. macrocephala*

Length 9 to 12 cm. Number of proglottids, 290. Width of strobila, ¾ mm. Vesicula seminalis only two or three times the diameter of the vas deferens. Host, *Geomys bursarius,* Minnesota. (See present paper.) ..... *A. translucida*

9. European; over 60 cm. long, and 5 to 10 mm. broad 10

North American; 3 to 5 cm. long, not over 2 mm. wide 11

10. Prostate gland elongate. Testes comparatively few, mostly on the side away from the pore. Host, *Lepus timidus,* Saxony. (See Stiles, 1896.) ..... *A. rhopalocephala*

Prostate gland round. Testes scattered thru entire median field. Hosts, *Lepus cuniculus* and *L. timidus,* Europe. (See Stiles, 1896.) ..... *A. cuniculi*

11. Testes transversely elongated. Genital pore near middle of lateral margin. Uterus not extending ventral to ovary. Host, *Evotomys gapperi galei,* of Colorado. (See present paper.) ..... *A. communis*

Testes not transversely elongated. Genital pores near distal end of lateral margin. Uterus extends ventral to ovary. Host, *Sciurus hudsonica,* Minnesota. (See present paper.) *A. primordialis*

GENUS BERTIELLA (Synonym: Bertia)

12. Genital pores alternate 13

Genital pores unilateral. Host, *Bucorax abyssinicus.* Not properly described, position not assured. (See Fuhrmann, 1904.) ..... *B. pinguis*

13. Dorsal excretory duct actually dorsal. Three longitudinal nerve trunks on either side. Cirrus pouch very small (except in *B. polyorchis*). Female glands in a dorsoventral row 14

Dorsal excretory duct dorsomesial to ventral. Cirrus pouch of ordinary size, and well developed (except in *B. rigida*). One longitudinal nerve trunk on either side (no statement for *B. rigida*). Female glands arranged in a transverse row. (always?) 16

Dorsal excretory duct not known, apparently absent. One nerve trunk. Cirrus pouch of ordinary size, egg-shaped. Female glands in a dorsoventral row. A long, convoluted vas deferens. Host, *Lagidium peruanum.* Not properly described. Assigned by von Linstow (1904) to the genus Bertia, but it is by no means certain that it belongs amongst the Anoplocephalidae ..... *B. forcipata*

The following poorly known species is placed in the genus Bertiella, perhaps correctly so. Strobila 245 mm. or more long by 10 mm. broad. Number of segments about 350. Genital pores very small, irregularly alternate. Dorsal canal lateral to ventral. Cirrus pouch large and elongate. Host, *Simia satyrus.* (See Stiles, 1896; or R. Blanchard, 1891.) *B. satyri*

14. Genital pores regularly alternate. Receptaculum seminis poorly developed. Ovary extends through one-sixth of the field between the excretory ducts and is not bilobed. Host, *Troglodytes niger,* Africa. (See Bourquin, 1905.) ..... *B. studeri*

Genital pores alternate, frequently with regularity. Ovary extending through about one-fourth the width of the proglot-

tid, divided into two nearly separated lobes, which are connected by a slender neck. Host, *Cercopithecus callitrichus.* (See Beddard, 1911.) ..... *B. cercopitheci*

Genital pores irregularly alternate. Ovary not bilobed 15

15. Strobila 14 cm. or more long. Receptaculum seminis globular. Eggs enter uterus in 350th segment. Host, *Mycetes niger,* Paraguay. (See Meyner, 1895, or Stiles, 1896.) *B. mucronata*

Strobila 84 mm. long. Receptaculum seminis oval. Eggs enter uterus in 130th segment. Host, *Macacus radiatus.* (See Meyner, 1895, and Stiles, 1896.) ..... *B. conferta*

Strobila 51 cm. long. Cirrus pouch of ordinary appearance. Host, *Macacus cynomolgus,* India. (See von Linstow, 1905.) ..... *B. polyorchis*

16. More than 21 cm. long. Sexually mature proglottids 26 times as broad as long, ripe proglottids 30 times as broad as long. Cortical layer exceptionally thick, in young proglottids forming five-sixth of total thickness, in older proglottids about three-fourths of thickness. Female glands far from median line. Testes numbering about 110. Host, *Phalangista* sp., New Guinea. Not adequately described. (See von Janicki, 1905.) ..... *B. rigida*

Proglottids not so short. Cortical layer of ordinary thickness 17

17. Cirrus spiny 18

Cirrus not spiny 19

18. Length, 30 to 60 cm. Number of proglottids, 600 to 850. Eggs pass into uterus in 300th proglottid. Testes 70 to 90. Ovary extending past the median line of the proglottid. Host, *Galeopithecus volans,* Sumatra. (See Bourquin, 1905.) *B. elongata*

Length, 2 to 6 cm. Number of proglottids, 80 to 200. Genital pores approach regular alternation. Testes 50 to 70. Ovary distant by more than twice its width from the median line. Host, *Galeopithicus volans,* East Indies, Sumatra, Java. (See Bourqin, 1905.) ..... *B. plastica*

19. Vitelline gland posterior to the ovary. Length, 14 cm. Number of testes 90, extending to the distal end of the proglottid. Diameter of ovary, 0.95 mm., not greatly displaced from the median line, its mesial edge extending across the median line. Hosts, doves and pigeons. (See Fuhrmann, 1902.) ..... *B. delafondi*

Vitelline gland not posterior to the ovary 20

20. Length, 50 to 60 cm. Several thousand proglottids. Testes about 200, reaching the distal limit of the proglottid. Ovary lying one-third beyond the median line of the proglottid. Host, *Phascolarctus cinerus,* Australia. (See Zschokke, 1898.) ..... *B. obesa*

Length, 66 cm. Number of proglottids, up to 1500. Testes fewer than in *B. sarsinorum,* extending nearly to the posterior limit of the proglottid. Ovary reaching just to the median line of the proglottid. Host, *Phalanger ursinus,* Australia and vicinity. (See Zschokke, 1899.) ..... *B. edulis*

Length, 7 cm. Number of proglottids, 220. Testes 30 to 40, mostly in a single row at the anterior end of the proglottid. Ovary distant by nearly half its width from the median line of the proglottid. Host,*Phalanger ursinus,* Australia and vicinity. (See Zschokke, 1899.) ..... *B. sarsinorum*

Genus Anoplocephala (Syn.: Plagiotaenia)

More than half the species placed in this genus are poorly known, and the statements made are often not dependable; some of the species probably do not exist, and others probably belong even in other families. For this reason, a logical key is out of the question, and no attempt has been made to make one; the following arbitrary division is made.

21. At least fairly well known species, generic position assured 22

Improperly described, position not assured 27

22. Cirrus pouch enormous, 0.8 mm. or more long, lying mostly within the excretory ducts 23

Cirrus pouch ordinarily not over 0.3 mm. long, more than half of it lying outside the excretory ducts 24

23. Length, 25 to 40 mm. Number of proglottids, 30 to 40. Sexual maturity reached in 10th or 12th proglottid. Receptaculum seminis globular, small. Host, *Tapirus americanus,* Brazil. Not fully known anatomically; all points known are essentially in agreement with the next species. (See Lühe, 1895.) ..... *A. globiceps*

Length, 10 mm. Number of proglottids, 10 to 28. Sexual maturity reached in eighth or ninth proglottid. Receptaculum seminis large and oblong, mostly ventral to cirrus pouch. Cirrus not spiny. Ovary not bilobed. Hosts, *Lepus cuniculus* and *Lepus variabilis,* France. (See present paper.) *A. wimerosa*

Length, 6 to 30 mm. 35 to 55 proglottids. Cirrus spiny. Sexual maturity reached about the 15th proglottid. Host, *Equus caballus,* Europe. (See Stiles, 1896; and R. Blanchard, 1891.) ..... *A. mamillana*

24. Ovary consists of two practically separate lobes. Receptaculum seminis greatly elongated. Host, *Equus caballus,* Old World. (See Kahane, 1880.) ..... *A. perfoliata*

Ovary not bilobed 25

25. (The better descriptions are not accessible to me; information compiled from several sources). 9 to 80 cm. long. Scolex 4 to 6 mm. in diameter. Maximum width, 5 to 20 mm. Synonys: *A. plicata, A. zebrae,* etc. (See Scheibel, 1895.) *A. magna*

Scolex considerably less than 1 mm. broad. Maximum breadth not over 5 mm. 26

26. Over 3 cm. long. Over 125 proglottids. Host, *Geomys bursarius,* North America. (See present paper.) ..... *A. variabilis*

Length, 12.5 to 20 mm. Number of proglottids, 60 to 75. Hosts, *Geomys bursarius* and *Microtus* sp., North America. (See present paper.) ..... *A. infrequens*

27. Genital pores irregularly alternate. Length, 12 to 21 cm. Number of proglottids, 250 to 300. Cirrus spiny. Hosts, *Mus arvalis* and *Mus amphibius.* (See von Janicki, 1906; and Stieda, 1862.) ..... *A. omphalodes*

Genital pores regularly alternate. Length, about 2 mm.; breadth, about 0.34 mm. Number of proglottids, 50 to 70. Host, pheasant, Italy. Description worthless; nothing to indicate that it belongs even in the family, if it exists. (See Mello, 1912.) ..... *A. minima*

Genital pores unilateral 28

28. Testes extending across median field. Length, 25 to 45 mm. Number of proglottids, 100. In *Heterohyrax mossambica.* Most likely does not belong in this genus. (See Bischoff, 1912; and von Janicki, 1910.) ..... *A. spatula*

Testes confined to the side away from the genital pore 29

29. Length, 16 cm. Cirrus spiny. In *Arvicola campestris.* (See von Linstow, 1878; and von Janicki, 1906.) ..... *A. inermis*

Length, 3 to 4 cm. In *Agricola campestris.* (See Moniez, 1891; and von Janicki, 1906.) ..... *A. blanchardi*

Length, about 8 mm. Breadth, 5 mm. Number of proglottids, 40 to 50. In *Arvicola nivialis,* Italy. Description worthless. Species may not belong to family, if it exists. (See Galli-Valerio, 1905.) ..... *A. dentata*

Length, 10 to 16 cm. Breadth, 6 to 8 mm. 200 to 300 segments. 60 to 80 testes. In *Arctomys* sp., Turkestan. (See Zschokke, 1888; and Stiles, 1896.) ..... *A. transversaria*

No information available. · (See Railliet, 1893.) ..... *A. restricta*

Genus Schizotaenia

30. Genital pores regularly alternate. Testes posterior, except in occasional proglottids in one species. Less than 20 cm. long 31

Genital pores irregularly alternate. Testes posterior, extending uniformly across the median field. About 3 cm. long. Hosts, *Dicotyles albirostris* and *D. torquatus,* Brazil. Not well known, position not assured. (See Lühe, 1895.) ..... *S. decrescens*

Genital pores unilateral. Size enormous, up to 120 cm. long, and 7.5 cm. broad. Testes mostly on pore side 33

31. Testes extending nearly uniformly across the median field in only two or three rows anteroposteriorly. Female glands near the median line so that the ovaries of the two sides overlap for most of their width 32

Testes nearly all in the half that contains the genital pore. Female glands far from the median line, the ovary not reaching the median line of the proglottid. Hosts, *Erethizon dorsatus* and *E. epixanthus,* North America. (See present paper.) ..... *S. variabilis*

Testes either extending across the median field, or in two groups separated from each other by the vitelline gland; in either case mostly on the side away from the genital pore, where they are in six or seven rows in the anteroposterior axis. Female glands quite large very near the median line. Host, *Geomys breviceps,* Oklahoma. (See present paper.) ..... *S. anoplocephaloides*

32. Length, 14 cm. Number of proglottids, about 280. Vitelline gland compact, formed of many small radiating lobes. Walls of vesicula seminalis glandular throughout. Vaginal walls glandular. Host, *Hydrochaerus capybara,* Brazil. (See von Janicki, 1906.) ..... *S. hagmanni*

Length, 3 to 4 cm. Number of proglottids, about 100. Vitelline gland formed of a large median and a smaller lateral lobe. Walls of vesicula seminalis not glandular, except at inner end. Vagina ephemeral, walls not glandular. Hosts,

Erethizon dorsatus and *E. epixanthus*, N. America. (See present paper.) ..... *S. americana*

33. Testes relatively few, confined to the anterior portion of the proglottid, mostly on the pore side. Ovary small, pear-shaped. Host, *Rhinoceros sondiacus* (and other rhinoceroses?) (See MacCallum & MacCallum, 1912; *Taenia gigantea.*) ..... *S. gigantea*

Testes very numerous, filling almost the entire field dorsally. Ovary consists of a transverse portion which extends nearly across the median field, and of numerous clubshaped lobes leading from it. Host, *Rhinoceros indicus* (and other rhinoceroses?) (See Deiner, 1912.) For reasons for transferring to Schizotaenia, see present paper..... *S. latissima*

GENUS CITTOTAENIA (Syn.: Ctenotaenia)

34. Cirrus pouch pyriform, distinct. Dorsal excretory duct lateral or dorsal of ventral (no statement for *C. bursaria*)..... 35

Cirrus pouch much elongated and slender, resembling the nozzle of a hose, and less distinct; in old proglottids, sometimes becoming pyriform on account of being gorged with sperm. Dorsal excretory duct generally median..... 39

35. Uterus not a simple transverse tube, but a rather simple reticulum. Length, 40 to 80 cm. Breadth, 15 mm. Number of proglottids, 200 or more. Genital pores in posterior corner of segment. Testes very numerous, scattered thru the dorsal portion of the median field. Host, *Lepus cuniculus*, Europe. (See Stiles, 1896, and others.)..... *C. denticulata*

Uterus a simple transverse tube..... 36

36. Testes 100 to 150, confined to the region between the two ovaries, not separated into two lateral groups. Host, *Arctomys* sp., France. (See Blanchard, 1891; and Stiles, 1896.) *C. marmotae*

Testes extending nearly or quite to the excretory ducts on either side anterior to the ovaries, and not separated into two lateral groups..... 37

Testes arranged in a group about each ovary, absent from the median part of the field..... 38

37. Length, 55 mm. Each set of genital organs occupies one-fifth the cross diameter of the proglottid. Cirrus pouch short and clubshaped. Testes numerous, spherical, 44μ in diameter, reaching the posterior end of the proglottid in the

median part of the field. Host, *Lepus nigricollis*. Locality, Nedunkeni. Inadequately described. (See von Linstow, 1906.) ..... *C. bursaria*

Length, 180 mm. Testes very numerous, mostly dorsal, 88μ long by 53μ broad. Cirrus spiny. Each ovary occupies one-seventh of the cross diameter of the proglottid. Host, *Lagidium peruanum cuvieri*. Locality, Peru. Not well known. (See von Linstow, 1904.) ..... *C. quadrata*

Length, 40 mm. Number of proglottids, about 150. Dorsal canal lateral. Host, *Geomys bursarius*, Iowa. More thorough description needed. (See Stiles, 1896.) ..... *C. praecocquis*

38. Length, 80 cm. 500 to 750 proglottids. 60 to 80 testes in each group. With pyriform body. Hosts, *Lepus cuniculus* and *Lepus cuniculus domesticus*. Distribution, Europe. Not well known. (See Stiles, 1896.) ..... *C. ctenoides*

Length, 8 to 9 cm. Number of proglottids, 250 to 350. Testes about 15 or 20 on each side, all dorsal. With pyriform body. (See Zchokke, 1907, under name *Moniezia diaphana;* and present paper.) ..... *C. diaphana*

Length, 13 to 16 cm. Three longitudinal excretory ducts, true dorsal duct outside. Testes 30 on each side, extending thru medullary portion. No pyriform body. (See von Janicki, 1905.) ..... *C. zschokkei*

39. Diameter of scolex, 1.5 mm. Cirrus pouch 600μ lond and 20μ in diameter. Testes about 110. Host, *Rhea americana*, of South America. Description very incomplete. (See Fuhrmann, 1904.) ..... *C. rhea*

With prostate cells on vas deferens 40

Without prostate cells on vas deferens 41

40. Length, 10 cm. Diameter of scolex, 230μ. Testes about 200, dorsal. Cirrus pouch 520μ long and 20μ wide. Host, *Stringops habroptilus*. Description very incomplete. (See Fuhrmann, 1904.) ..... *C. psittacea*

Length, 15 to 22 cm. Diameter of scolex, 800μ. Testes 120 to 140, confined to the region between the ovaries. Cirrus pouch 1 mm. long, 120μ in diameter. Host, *Anas* sp. (See Fuhrmann, 1897.) ..... *C. avicolae*

41. Dorsal excretory vessel lateral to ventral. Length, 5 cm. Cirrus pouch 300μ long and 40μ broad. Hosts, *Carpophaga vanwycki* and *Ptilopus jambu*. Localities, Karavia (New Britain) and Sumatra. (See Fuhrmann, 1902; and Shipley, 1900.) ..... *C. kuvaria*

Dorsal excretory duct median to ventral 42

42. Testes confined to the region between the ovaries. Uterus in anlage crosses excretory ducts dorsally. Excretory system simple. Cirrus pouch 400μ long. Hosts, *Sylvilagus floridanus* and *S. palustris,* North America. (See Stiles, 1896; Lyman, 1902; and present paper.) ..... *C. variabilis*

Testes extending laterad beyond the ovaries. Uterus in anlage confined to the median field. Fifteen or more large, prominent ducts crossing the proglottid lengthwise and connecting the transverse commissures of the excretory ducts with each other 43

43. Cirrus pouch about 1 mm. long, extending some distance mediad of the longitudinal excretory canals. Testes 100 to 125. Hosts, *Lepus timidus, L. variabilis,* and *L. californicus,* Europe and North America. (See Stiles, 1896; Lyman, 1902; present paper, and others.) ..... *C. pectinata*

Cirrus pouch not over 640μ long, often much shorter. Testes 60 to 80. Hosts, *Sylvilagus floridanus* and *S. pinetis.* (See Hall, 1908, under name *C. mosaica;* and present paper.) *C. perplexa*

GENUS MONIEZIA (Syn. partim: Paronia)

44. Description not accessible.—*Moniezia beauforti* von Janicki 1906b. Host, *Cyclopsittacus dioptahlmus,* in Sekanto. *M. beauforti*

Length, 20-27 cm. Host, *Macropus giganteus,* Australia. Poorly known, position uncertain. (See R. Blanchard, 1891; or Dujardin, 1845:593.) ..... *M. festiva*

Uterus tubular or slightly branched, not reticular, confined to median field in anlage. In its final stages saccular, or with anterior and posterior outpocketings. Embryos without pyriform apparatus. Dorsal excretory duct dorsal to ventral (not known in *M. variabilis*) 45

Uterus a very complicated, finely meshed reticulum, usually,if not always, crossing the excretory ducts dorsally in anlage. Embryos usually with pyriform apparatus, the horns of which generally end in a disk. Dorsal excretory duct median to ventral 47

45. Uterus in anlage inverted U-shaped, embracing ovary 46

Uterus in anlage a transverse bar, with a few simple branches at its median end. Communication of ripe uteri of two

sides of proglottid slight. Number of testes about 200. With prostate cells on vas deferens. Cirrus pouch 90μ long. Host, *Ptilopus* sp., Sumatra. (See Fuhrmann, 1902.) *M. columbae*

46. Uteri of two sides never united. Testes about 140. No prostate cells on vas deferens. Cirrus pouch 300 to 450μ long. Hosts, *Ptilonopus* sp., *Lorius erythrothorax, Trichoglossus novaehollandiae, Cyclopsittacus suavissimus,* and other parrots, New Guinea and Sumatra. (See Fuhrmann, 1902; also, Diamare, 1900 and 1901.) *M. carrinoi*

Uteri of two sides becoming connected very early, anteriorly. Number of testes, about 100. Host, *Chrysotis amazonica,* South America. (See Fuhrmann, 1902.) *M. ambigua*

Uteri of two sides becoming connected distally. Hosts, 4 species of Rhamphastos. Description poor. (See Fuhrmann, 1904.) *M. variabilis*

47. With interproglottidal glands, which are linear, and are not grouped around blind sacs (very indistinct in *M. benedeni.*) *Planissima*-group 48

With interproglottidal glands, which are grouped around blind sacs. *Expansa*-group 49

No interproglottidal glands. *Alba*-group 50

48. Length, 1 to 2 m. Ripe segments 12 to 26 mm. broad, and 1 to 1.75 mm. long. Interproglottidal glands large, distinct. Hosts, *Bos taurus* and *Ovis aries.* (See Stiles & Hassall, and others.) *M. planissima*

Length, 4 m. Ripe segments 12 mm. broad by 3 mm. long. Interproglottidal glands indistinct (absent?). Hosts, *Bos taurus* and *Ovis aries.* Better study needed. (See Stiles & Hassall, 1893.) *M. benedeni*

About 0.66 m. long. Largest segments 8 mm. broad by 1.5 mm. long. Testes in a quadrangle. Interproglottidal glands small. Host, *Ovis aries.* Better study needed. (See Stiles & Hassall, 1893.) *M. neumanni*

49. Length, 4 to 5 m. Testes in mature proglottids usually in a quadrangle, rarely in two triangles. Hosts, *Bos taurus* and *Ovis aries.* See Stiles and Hassall, 1893; Tower, 1900; present paper, and others.) *M. expansa*

Length, about 1 m. Testes less numerous and smaller than in *M. expansa.* Host, *Coassus* sp., Trinidad, South America. Poorly known. (See Stiles and Hassall, 1893.) *M. oblongiceps*

Length, 1.6 to 2 m. Testes usually in two triangles, absent from median part of the field. Orifices of suckers slitlike. Host, *Ovis aries*. (See Stiles and Hassall, 1893.)
M. trigonophora

50. Length, 0.6 to 2.5 m. Testes in a quadrangle. Genital pores in anterior half of the segment. Hosts, *Bos taurus* and *Ovis aries*. Description very incomplete. (See Stiles & Hassall, 1893.) ..... *M. alba*

Length, 41 cm. Testes in entire median field, except part occupied by female glands. No disk figured on pyriform body. Host, *Hippopotamus amphibius*. Description poor, generic position not established. (See von Linstow, 1901.)
M. amphibia

Length probably not over 10 cm. Poorly described. Host, *Ateles hypoxanthus*, Brazil. See Lühe, 1895) ..... *M. rugosa*

LINSTOWINAE

51. Genital pores alternate. Cirrus pouch well developed. Female glands near the median line 52
Genital pores unilateral. Cirrus pouch weakly developed. Female glands far from the median line, except *Thysanotaenia lemuris* and *Zschokkeella remota* 53

52. Genital canals ventral to excretory canals and nerve. Cortical layers of great thickness ..... Linstowia, 54
Genital canals between excretory canals. Cortical layer of ordinary thickness (See Fuhrmann, 1902.) .....
"Taenia" anoplocephaloides

53. For the following so-called genera, no differences of generic import are known, with the possible exceptions of *Thysanotaenia lemuris* and *Zschokkeella remota*. It seems most probable that they all belong in the genus Zschokkeella, with the two exceptions mentioned. Most of the species are poorly described, so no attempts at rearrangement have been made. They are listed here merely to make the key complete.

Genus Zschokkeella 57
Genus Inermicapisfer 58
Genus Thysanotaenia 68
Genus Hyracotaenia 69

GENUS LINSTOWIA

54. Cirrus pouch very large, reaching to the median line of the proglottid or nearly so 55
Cirrus pouch relatively small, not reaching to the lateral excretory trunks. Embryos, in ripe proglottids, mostly in lateral portions of the segment 56

55. Testes about 40, mostly posterior. Host, *Perameles obesula,* Australia. (See Zschokke, 1898.) ..... *L. semoni*
Testes about 100, mostly anterior. Host, *Echidna hystrix,* Australia. (See Zschokke, 1898.) Tidswell, 1910, has declared *Taenia echidnae* Thompson 1893 and *Taenia phoptica* Cobbold 1879, to be synonyms. (I have been unable to find this article, or even to learn its title) ..... *L echidnae*

56. Number of proglottids, 160 to 200. Genital pore but slightly in front of the middle of the proglottid. Ovary of about 8 slender lobes, four of which extend towards each lateral margin. Host, *Peramys americana,* South Americana. (See Zschokke, 1904.) ..... *L. jheringi*
Number of proglottids, 90. Genital pore very near the anterior end of the margin. Ovary consists of two comparatively compact lobes each with very short, slender, radiating processes. Host, *Didelphys tristriata,* Brazil. (See von Janicki, 1906.) ..... *L. brasilensis*

GENUS ZSCHOKKEELLA (Syn. Zschokkea Fuhrman 1902)

57. Excretory vessels far medial. Testes about 140, largely outside the median field. Host, *Numida ptilorhyncha*.... (See Fuhrmann, 1902.) ..... *Z. linstowi*
Testes in median field. Cirrus pouch round, small, one-eighteenth the diameter of the proglottid. Very poorly described. Most of the facts known point to the conclusion that this cestode does not belong in the genus Zschokkeella; but not enough is known to justify placing it elsewhere. Host, *Oprecopithecus pyrrhonotus,* West Africa. (See von Linstow, 1905.) ..... *Z. remota*
Excretory ducts lateral in position. Testes in two groups, mostly on the side away from the pore. Host, *Cricetomus gambianum.* (See Beddard, 1911, 1912.) ..... *Z. gambianum*

GENUS INERMICAPSIFER

58. No information of importance. (See von Janicki, 1910.) ..... *I. gondokorensis*
Testes filling most of median field 59
Testes posterior, extending across field 60
Testes in two lateral groups 64
59. 70 to 80 embryo-capsules, with 8 to 10 embryos in each. Number of proglottids, 70 to 80. Length of cirrus pouch, 400μ. Host, *Hyrax* sp. (See von Janicki, 1910.) ..... *I. pagensteckeri*
30 to 50 embryo capsules, up to 6 embryos in each. Number of proglottids, 40. Length of cirrus pouch, 270μ. Host, *Hyrax* sp. Locality, Schoa. (See Bischoff, 1912.) ..... *I. paronae*
60. Number of embryo capsules, 100 or more. Number of proglottids, 300 or more 61
Number of embryo capsules, 75 or less. Number of proglottids 130 or less 62
61. (No valid point of distinction from next. Length, 111 mm. Number of proglottids, 300. Host, *Hyrax capensis*. (See von Janicki, 1910.) ..... *I. critica*
Length, up to 350 mm. Number of proglottids, 400 to 500. Host, *Procavia* sp., South Africa. (See von Janicki, 1910.) *I. hyracis*
62. Number of embryo capsules, 75; 5 to 7 embryos in each. Number of proglottids, 130. Number of testes, 80. Host, *Procavia* sp., South Africa. (See von Janicki, 1910.) ..... *I. interpositus*
Number of embryo capsules, 24 to 28. Less than 60 testes 63
63. Length, 40 mm. 8 to 10 embryos in each capsule. 50 to 60 testes. Host, *Hyrax*, sp., Erethrea. (See Bischoff, 1912.) ..... *I. abyssinicus*
Length, 15 to 20 mm. 5 embryos in each capsules. 40 testes. Host, *Hyrax* sp., East Africa. (See Bischoff, 1912.) ..... *I. prionodes*
64. Number of proglottids, 200. Host, *Procavia capensis*. (See Beddard, 1912.) ..... *I. capensis*
Number of proglottids, not over 70 65
65. 5 to 7 embryos in each capsule 66
10 to 15 embryos in each capsule 67
66. Cirrus pouch 130 μ long. Host, *Hyrax* sp., East Africa. (See Bischoff, 1912.) ..... *I. parvulus*

Cirrus pouch 270 μ long. Host, *Hyrax* sp., East Africa. (See Bischoff, 1912.) ..... *I. apospasmation*

67. 20 to 70 proglottids. Host, *Procavia* sp., South Africa. (See von Janicki, 1910.) ..... *I. settii*

12 to 15 proglottids. Host, *Hyrax* sp., Rikwasee. (See Bischoff, 1912.) ..... *I. lopas*

Genus Thysanotaenia

68. Female glands near the median line of the proglottid. No dorsal excretory duct. Host, *Lemur macaco.* (See Beddard, 1911b, 1912.) ..... *T. lemuris*

Genus Hyracotaenia

69. Ovary entirely, or partly laterad of ventral excretory duct. Vitelline gland dorsal. Host, *Procavia* capensis. (See Beddard, 1912.) ..... *H. procaviae*

Ovary entirely mediad of excretory ducts. Vitelline gland ventral. Host, *Procavia capensis.* (See Beddard, 1912.) ..... *H. hyracis*

Thysanosominae

Genus Thysanosoma

70. Length, 15 to 30 cm. Two sets of reproductive organs. Testes in median field. Posterior flap of segments fimbriate. With pyriform body, which has no horns. Reported from several species of Cervus, Cariacus, Bos & Ovis. (See Stiles & Hassall, 1893.) ..... *T. actinioides*

Length, 1 to 2 m. Seldom more than one set of reproductive organs to the proglottid, pores alternating irregularly. Testes in lateral fields. Posterior flap of segments fimbriate. With pyriform apparatus which has no horns. Hosts, Ovis, Bos, and Sus. (See Stiles & Hassall, 1893.) ..... *T. giardi*

Length, 1.5 m. Strobilization not distinct. Genital pores alternating rather regularly. No pyriform apparatus. Host, *Capreolus pygardus,* Siberia. Description unsatisfactory. (See Kholodskovi, 1902.) ..... *T. pygardi*

Avitellininae

71. Uterus single; a single paruterine organ. Testes in four groups. Genital canals pass dorsally of both excretory ducts ..... *Avitellina* 72

Uterus double; two paruterine organs. Testes in two groups. Genital canals pass between excretory canals ..... *Stilesia* 73

Genus Avitellina

72. Length, 2 or 3 meters. Host, *Ovis aries,* Africa, Italy. (See Gough, 1911.) ..... *A. centripunctata*

Genus Stilesia

73. Testes mostly median or dorsal to the ventral canal. Hosts, ruminants, Africa. (See Gough, 1911.) ..... *S. hepatica*
Testes all lateral to the ventral canal 74
74. Vas deferens forms a dense packet of convolutions (functionally a vesicula seminalis) between nerve and ventral canal before reaching cirrus pouch. Host, *Camelus dromedarius,* India and Algiers. (See Gough, 1911.) ..... *S. vittata*
Vas deferens forms at most 3 or 4 loose convolutions between the nerve and ventral canal, before reaching the cirrus pouch. Hosts, Ovis & Capra, Europe and India. (See Gough, 1911.) ..... *S. globipuncta*

SUMMARY AND CONCLUSIONS

1. The cestodes of the subfamily Anoplocephalinae are in some way dependant upon rich soils for their existence and they thrive best in wet lowlands. The evidence points to the conclusion that the intermediate hosts are some group of insects which is confined to such regions; and since the hosts of the Anoplocephalidae are almost exclusively herbivorous, it would seem as if this host were a small, plant-feeding insect.

2. The primitive Anoplocephaline uterus was of the reticulate type, which in turn was derived from a median longitudinal tubular uterus by lateral outgrowths. The transverse tubular and diffuse uteri of this group have been derived from the reticular by simplification.

3. In the early primitive Anoplocephalidae the uterus crossed the excretory ducts ventrally; subsequently it became restricted to the median field and later came to cross the excretory ducts dorsally.

4. The position of the vaginal pore and vagina is one of the most stable anatomical characters of the Anoplocephalinae and should be given recognition as one of the most important criteria of relationship. The primitive position of the vagina was posterior to the cirrus pouch.

5. The more generalized representatives of the genus Andrya approach the nearest of all known Anoplocephalidae to the ancestral types of the family. Leaving out of consideration the aberrant Triplotaenia,

the genera Moniezia and Schizotaenia constitute the highest types of the Anoplocephalinae; the other subfamilies of the family seem to have sprung from forms like these two genera.

6. Cestodes exhibit a high range of variability which should be taken strictly into account in morphological, phylogenetic, and systematic studies. Generalizations not founded upon plenty of material and careful study and reflection do more harm than good. The following reference list of variations and anomalies reported in this paper shows the need of extreme caution in coming to conclusions regarding structure and consequent relationships.

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EXPLANATION OF PLATES

Unless otherwise stated all drawings were drawn to scale, measurements being made with an ocular micrometer, and are dorsal side uppermost, with the anterior end towards the top of the plate.

ABBREVIATIONS USED

C	genital cloaca	*RS*	receptaculum seminis
CP	cirrus pouch	*SG*	shell gland
ExD	dorsal excretory vessel	*T*	testis
ExV	ventral excretory vessel	*UD*	uterine duct
ExT	excretory tubes connecting transverse commissures.	*Ut*	uterus
		Va	vagina
N	longitudinal nerve trunk	*VC*	ventral transverse commissure
O	ovary	*VD*	vas deferents (Plates V and VI)
Ovd	oviduct	*VD*	vitelline duct (Plates I and III)
Par	parenchyma-filled spaces between the compartments of the uterus	*VDef*	vas deferens (Plate I)
		VE	vasa efferentia
		VG	vitalline gland
PG	prostate gland	*VS*	vesicula seminalis

EXPLANATION OF PLATE

Figures 1 to 4. *Andrya primordialis.*

Fig. 1. Proglottid at sexual maturity, dorsal view; ovary and uterus omitted.
Fig. 2. Proglottid at sexual maturity, ventral view, to show ovary and uterus.
Fig. 3. Uterus of nearly ripe proglottid.
Fig. 4. Scolex, drawn from temporary mount.

Figures 5 to 8. *Andrya communis.*

Fig. 5. Proglottid at sexual maturity, dorsal view; ovary and uterus omitted.
Fig. 6. Proglottid at sexual maturity, ventral view, to show ovary and uterus.
Fig. 7. Ventral view of vitelline and shell glands and female genital ducts.
Fig. 8. Diagram of excretory ducts and cirrus pouch, showing a different arrangement from that shown in Figure 5.

Figures 9 to 11. *Andrya macrocephala* (see also next plate).

Fig. 9. Mature proglottid, dorsal view, uterus omitted.
Fig. 10. Mature proglottid, ventral view, to show uterus.
Fig. 11. Fully developed uterine embryo, middle membrane omitted.

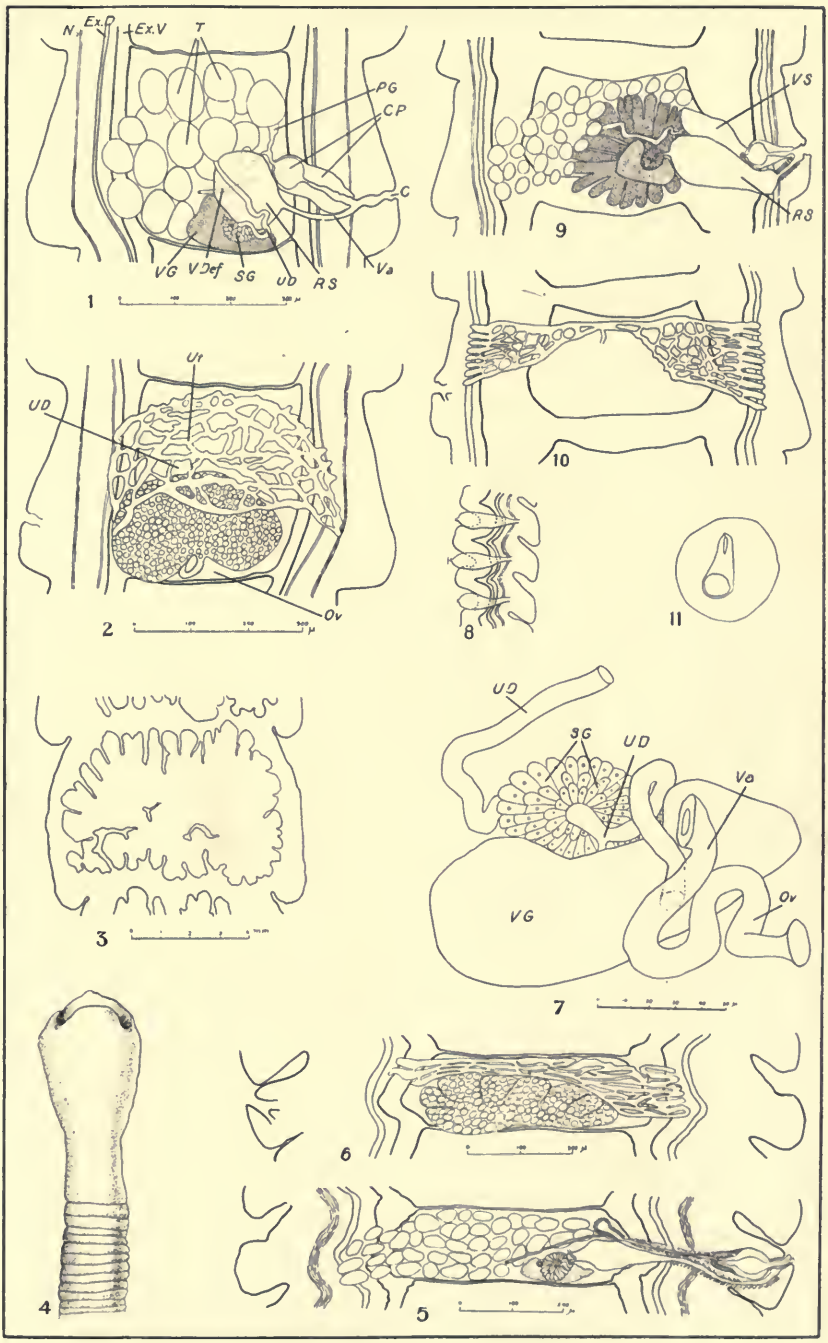
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PLATE I

PLATE II

EXPLANATION OF PLATE

Figures 12 and 13. *Andrya macrocephala* (see also Plate I).
Fig. 12. Uterus of ripe proglottid.
Fig. 13. Section of scolex.
Figures 14 to 16. *Andrya translucida.*
Fig. 14. Mature proglottid, dorsal view.
Fig. 15. Mature proglottid, dorsal view; ovary and shell gland omitted.
Fig. 16. Mature proglottid, ventral view, showing ovary and uterus.
Fig. 17. *Anoplocephala wimerosa.* Mature proglottid, dorsal view.
Figures 18 to 21. *Anoplocephala variabilis* (see also Plate III).
Fig. 18. Section of scolex in expanded condition.
Fig. 19. Section of scolex in contracted condition.
Fig. 20. Uterus of ripe proglottid.
Fig. 21. Uterine embryo, middle membrane not represented.

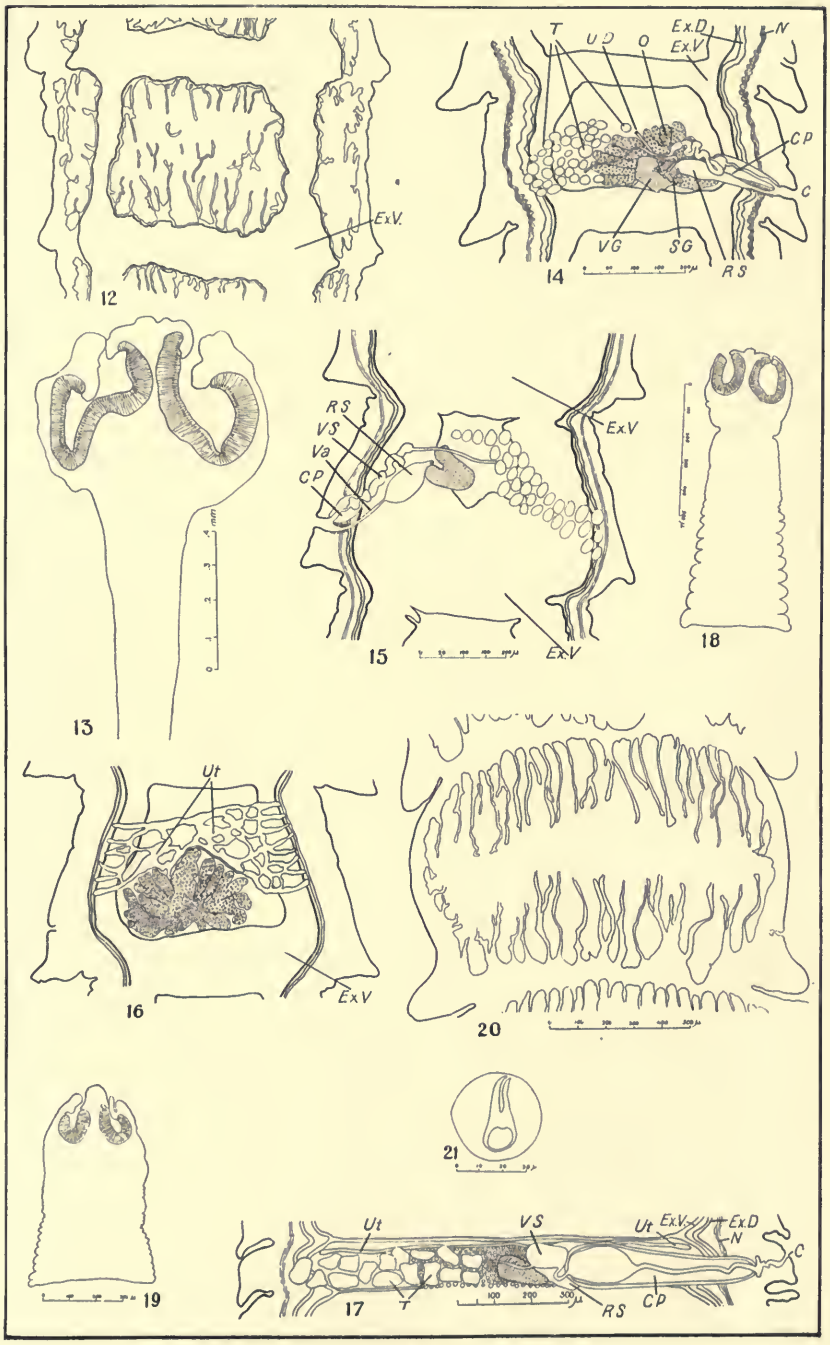
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PLATE II

PLATE III

EXPLANATION OF PLATE

Figures 22 to 24. *Anoplocephala variabilis* (see also Plate II).

Fig. 22. Mature proglottids in contracted condition; some structures omitted.

Fig. 23. Mature proglottid in expanded condition.

Fig. 24. Vitelline gland, shell gland, and female ducts; expanded condition, ventral view.

Figures 25 to 27. *Anoplocephala infrequens.*

Fig. 25. Mature proglottids in ventral view, some structures omitted. The transverse comissures of the ventral ducts which appear straight here are sinuous in dorsoventral plane.

Fig. 26. Section through the scolex.

Fig. 27. Vitelline gland, shell gland, and female ducts; ventral view.

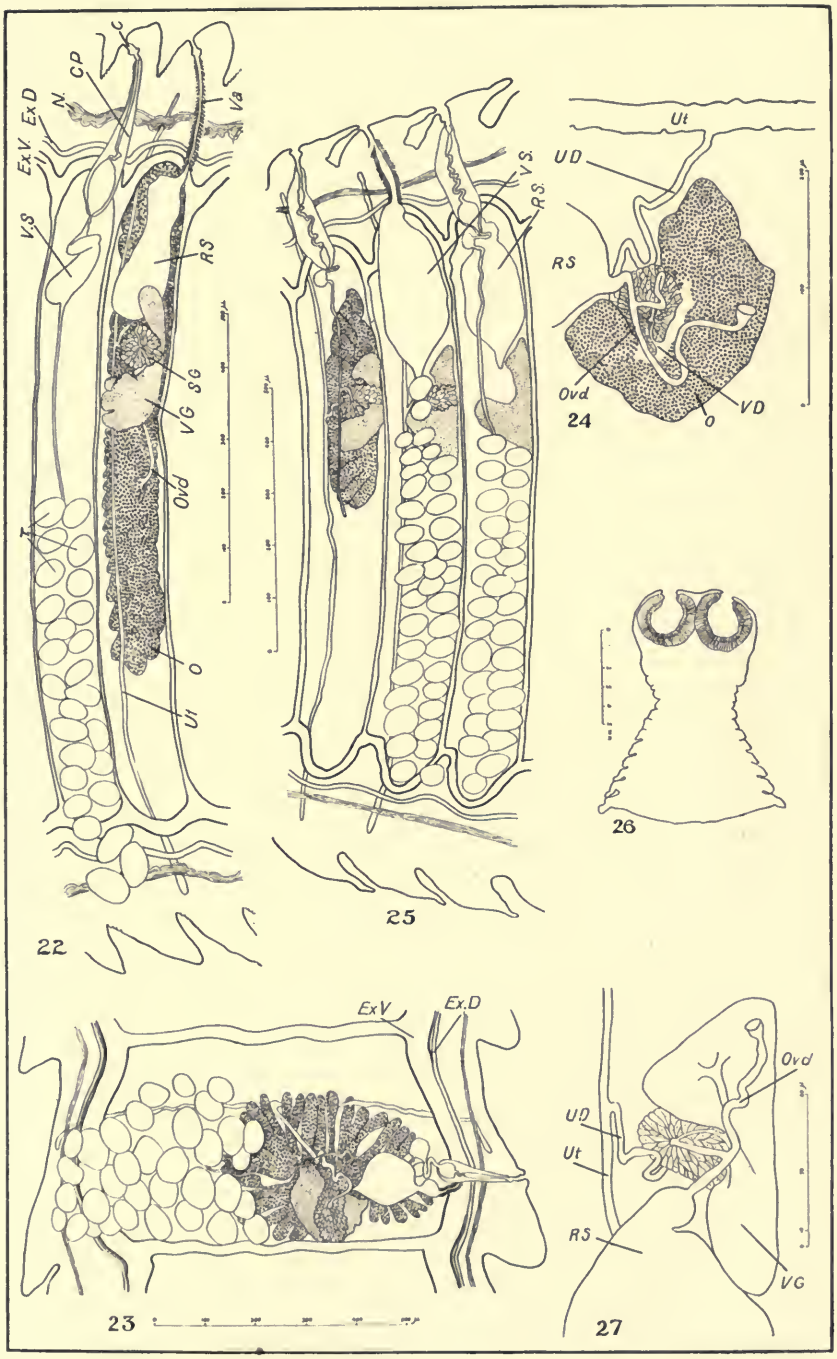
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PLATE III

PLATE IV

EXPLANATION OF PLATE

Figures 28 and 29. *Schizotaenia americana.*

Fig. 28. Mature proglottid, dorsal view; uterus not included.

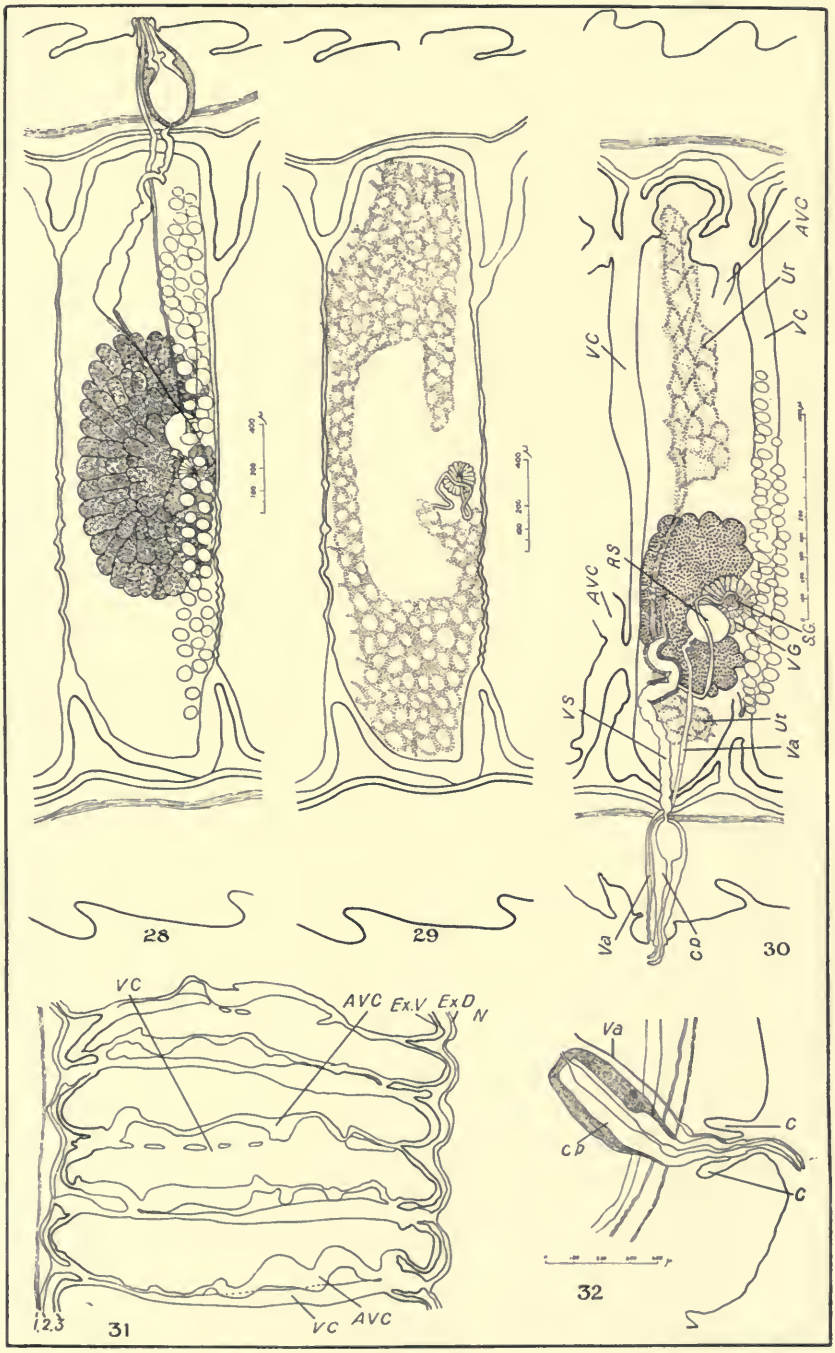
Fig. 29. Mature proglottid, showing uterus (dotted), oviduct, and shell gland.

Figures 30 to 32. *Schizotaenia variabilis.*

Fig. 30. Mature proglottid, dorsal view. After this drawing was completed the study of additional material showed that it is not normal in some respects, namely: (1) the testes are usually further forward, anterior to the transverse commissure; (2) the accessory ventral commissures were found in only one specimen; (3) the vesicula seminalis is usually not thrown into wide curves as here shown. The uterus may be somewhat more extensive than here shown; the poor condition of the material does not permit exact judgment as to the limits of this structure.

Fig. 31. Diagram of excretory system of five adjacent proglottids, showing accessory transverse commissures (*AVC*) and other features. The absence of the main transverse commissure in some cases may be due to the fact that the proglottids are not fully mature.

Fig. 32. Drawing showing the cloaca only partly everted and the cirrus pouch lying consequently mostly mediad of the excretory ducts.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VC
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32

PLATE IV

PLATE V

EXPLANATION OF PLATE

Figures 33 to 40. *Schizotaenia anoplocephaloides.*

Fig. 33. Proglottid just before sexual maturity, dorsal view; uterus and vas deferens omitted.

Fig. 34. Proglottid at sexual maturity. Ovary and testes omitted. Uterus dotted.

Fig. 35. Drawing to show the testes extending across the median field, the usual condition in the species.

Fig. 36. Ripe proglottid, showing fully developed uterus with short anterior and posterior outpocketings.

Fig. 37. Section of scolex thru suckers.

Fig. 38. Scolex and anterior regions from toto mount.

Fig. 39. Fully developed uterine embryo, middle embryonic membrane omitted.

Fig. 40. Diagram to show excretory system in a series of proglottids. Drawn ventral side uppermost.

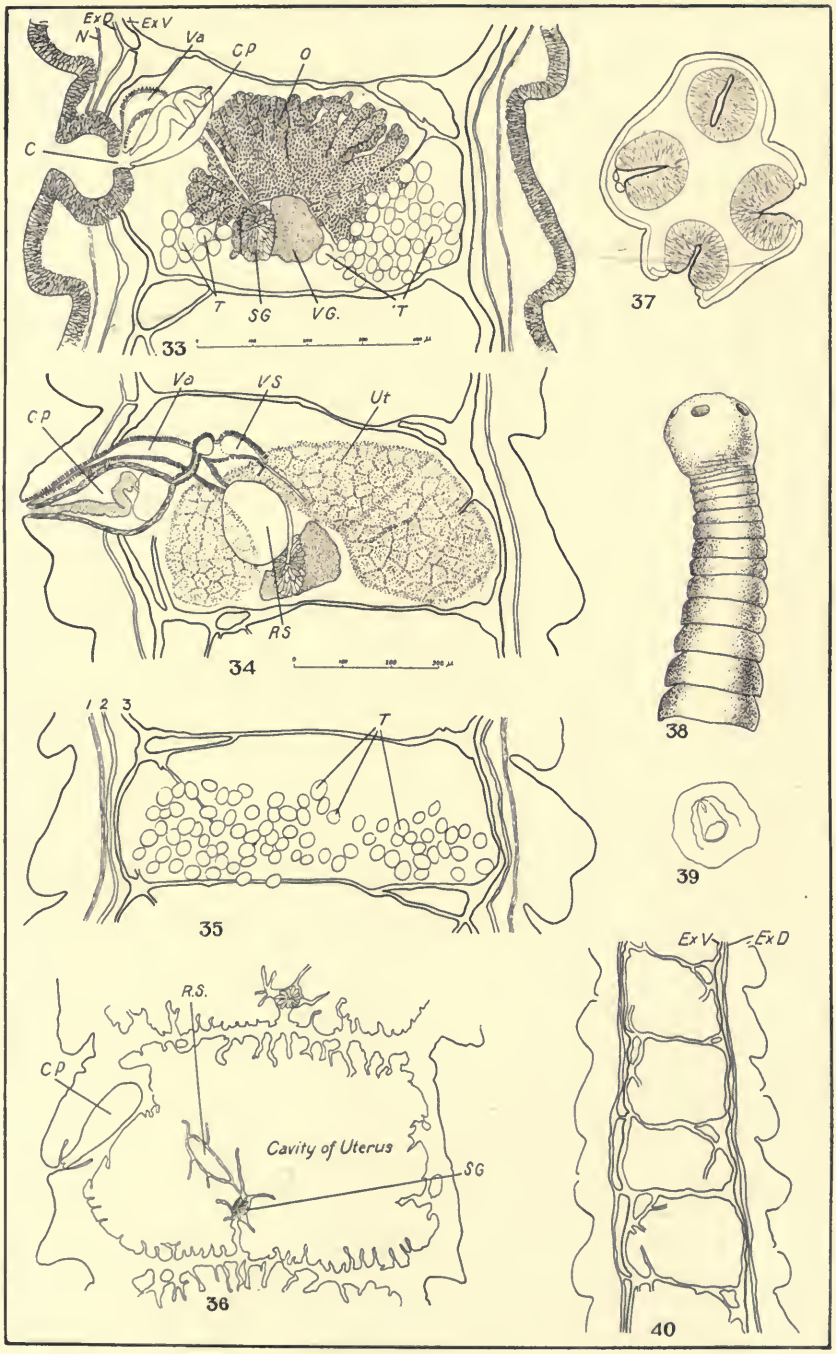
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PLATE V

PLATE VI

EXPLANATION OF PLATE

Figures 41 to 43. *Moniezia expansa.*

Fig. 41. Mature proglottid, dorsal view; shell gland and part of testes and genital ducts omitted from right side of proglottid.

Fig. 42. Uterus as it appears just prior to the entrance of the eggs, a complicated network of interconnecting small tubes.

Fig. 43. Uterus in its final stages, a system of separated or nearly separated compartments.

Figure 44. *Cittotaenia variabilis.* Proglottid at sexual maturity, dorsal view; parts of genital ducts and female glands omitted from left side.

Figure 45. *Cittotaenia pectinata americana.* Proglottid at sexual maturity, dorsal view.

Figures 46 to 49. *Cittotaenia perplexa* from *Sylvilagus floridanus alacer,* Oklahoma.

Fig. 46. One-half of proglottid at sexual maturity. The cirrus pouch is here shown to reach across both excretory ducts: usually it reaches just to the lateral nerve trunk. In other specimens at hand the testes are somewhat more numerous in the median part of the field, and less numerous in the lateral parts. In Stiles' figures they are wholly absent from the median part of the field.

Figures 47 to 49. Cirrus pouches, showing variations in size and form. All drawn to the same scale.

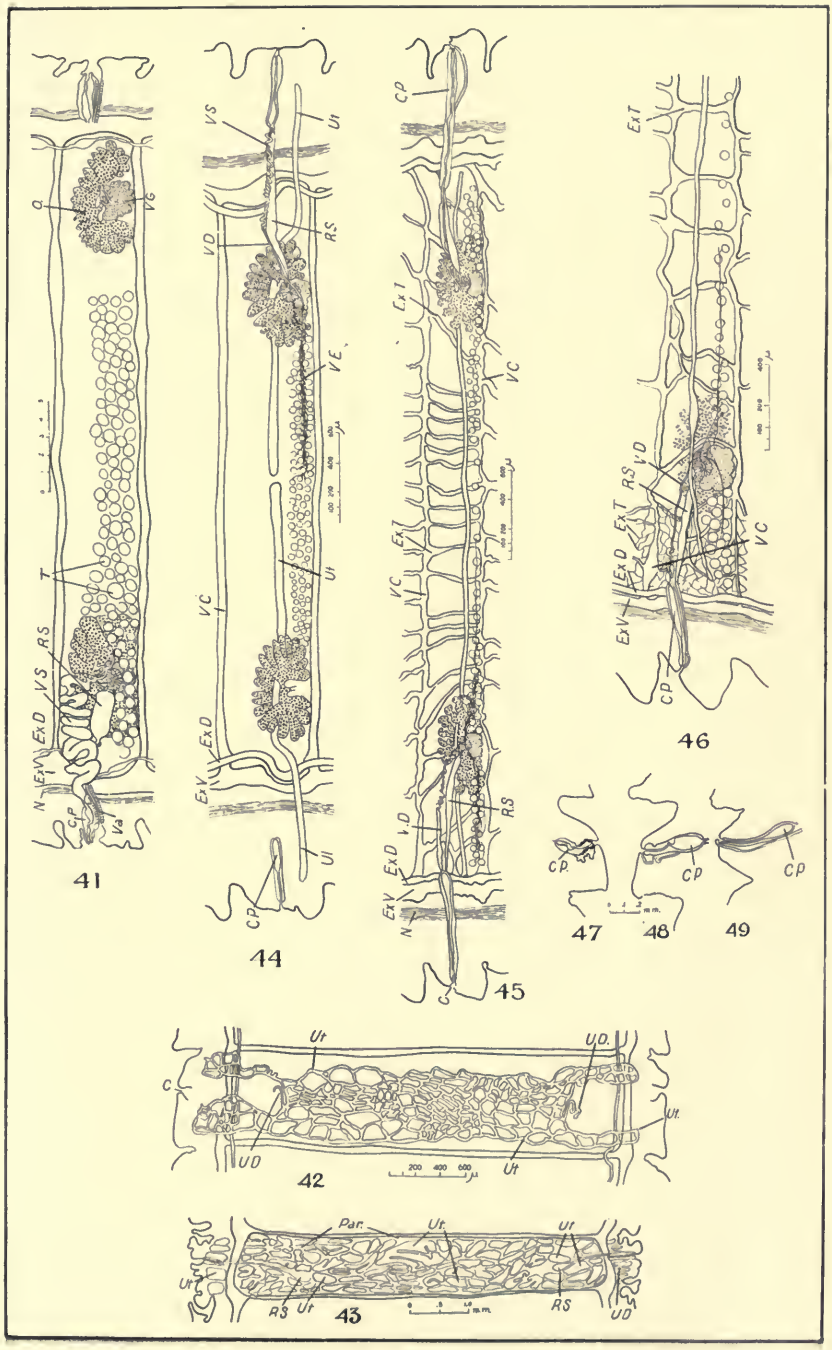

PLATE VI