Proc. Helminthol. Soc. Wash.
47(2), 1980, p. 157–164

Redescription of *Diandrya composita* Darrah, 1930 (Cestoda: Anoplocephalidae) from Nearctic Marmots (Rodentia: Sciuridae) and the Relationships of the Genus *Diandrya* emend.

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ABSTRACT: According to the original description of *Diandrya composita* Darrah, 1930 (the type and only species of the Nearctic genus *Diandrya* Darrah, 1930), this cestode would possess a combination of organs, the "interproglottidal glands" and "pedunculated prostate glands," otherwise unknown in any member of the Anoplocephalidae. Neither of these organs is present in *D. composita*. This species is redescribed and the generic diagnosis is emended accordingly. *Diandrya composita* has its closest affinities with cestodes of the genus *Andrya* Railliet, 1893, from which it differs significantly only in reduplication of the reproductive organs.

The monotypic genus *Diandrya* Darrah, 1930 was established for a cestode from the yellow-bellied marmot, *Marmota flaviventris* (Audubon and Bachman), in Wyoming. This cestode, *D. composita* Darrah, 1930, has been found to occur widely in western North America in five of the six Nearctic species of the genus *Marmota* (vide Rausch and Rausch, 1971).

On the basis of the original generic diagnosis, Spasskii (1951, p. 420) considered *Diandrya* to have some morphologic characteristics in common with the genera *Moniezia* Blanchard, 1891 and *Andrya* Railliet, 1893. However, the study of specimens of *D. composita* has shown that the affinities of the genus have been obscured by errors in the original interpretation of certain anatomic details. The present paper provides a redescription of this cestode and emends accordingly the diagnosis of the genus *Diandrya*.

Materials and Methods

The cestodes were routinely fixed in a hot solution of 10% formalin, stained in acetic carmine or acid hematoxylin, processed by standard methods, and mounted permanently. Superficial tissues were removed from selected strobilae before mounting to facilitate study of organs. Thick transverse sections as well as transverse and frontal sections prepared by the paraffin-embedding method also were studied. Of some hundreds of *D. composita* collected during the period 1949–1974, 110 specimens were used in the present study. These cestodes are listed below by host and general locality, with numbers of specimens indicated in parentheses. The holotype of *D. composita* (USNM Helm. Coll. No. 30263) also was examined.

Marmota caligata (Eschscholtz): (Alaska) Talkeetna Mountains (37); Chugach Mountains (15); Alaska Range (6); Kenai Peninsula (16); Hinchenbrook Island (1); (Alberta, Canada) Gorge Creek (2); (Washington) Mt. Rainier (2). *Marmota broweri* Hall and Gilmore: (Alaska) central and eastern Brooks Range (22). *Marmota olympus* (Merriam): (Washington) Olympic Peninsula (7). *Marmota vancouverensis* Swarth: (British Columbia) Vancouver Island (2).

Diandrya composita was compared with *Andrya rhopalocephala* (Riehm,

1881), the type species of the genus *Andrya*. The material studied included cotypes of *A. rhopalocephala* (USNM Helm. Coll. Nos. 1379, 1484, and 1485 (cf. Stiles, 1896, p. 158)) as well as specimens collected recently from rabbits, *Oryctolagus cuniculus* (L.), in Spain and from hares, *Lepus europaeus* Pallas, in Switzerland and Hungary. Also compared were cestodes of the genus *Moniezia*, representing the subgenera *Moniezia* Skriabin and Shul'ts, 1937 and *Blanchardiezia* Skriabin and Shul'ts, 1937, from wild ungulates of various species examined in northwestern North America.

Results

Numbers of *D. composita* found in individual marmots ranged up to 587. The wide variation observed in size of strobila and in state of development of the cestodes in some marmots indicated that acquisition of infective cysticercoids was more or less continuous after the rodents emerged from hibernation free of intestinal helminths. Because of age-related differences in size of fully developed (i.e., with gravid segments) strobilae, mean dimensions of organs have little significance and are not included in the following redescription. Measurements are in micrometers unless otherwise stated.

Diandrya composita Darrah, 1930 (Figs. 1, 2)

REDESCRIPTION: Strobila 46 to 625 mm long, with 108 to 817 segments. Maximum width 4 to 11 mm, attained in early gravid segments. Strobila attenuated anteriorly; margins otherwise essentially parallel and slightly serrate. All segments wider than long, with relative length increasing posteriad. Length/width ratio of mature segments (at level of first filling of seminal receptacle) 1:11 to 1:6; of gravid segments, 1:4 to 1:2. Scolex globular, distinctly set off from neck, 740 to 1.3 mm wide by 520 to 1 mm long. Suckers 360 to 600 in greater diameter. Neck 450 to 1 mm long and 550 to 800 wide. *Anlagen* of male genital ducts visible in first segments. Genital pores bilateral, situated posterior to middle of segmental margin in mature segments; farther posterior in gravid segments. Genital ducts passing dorsally across longitudinal excretory canals. Ventral canals 100 to 170 in diameter, connected across posterior margin of segment by transverse duct 50 to 140 in diameter; dorsal canals 12 to 40 in diameter, usually poral to ventral canals. Cirrus sac thick-walled, claviform, and somewhat curved; directed mediad, overlapping or sometimes extending mediad beyond, ventral excretory canals bilaterally. Size of cirrus sac increasing posteriad from area of mature segments with enlargement of internal seminal vesicle; maximum dimensions 370 to 700 long by 160 to 220 in diameter, attained in early gravid segments. Cirrus spinose, about 250 long when fully extended, with diameters of about 40 and 20 at proximal and distal ends, respectively. Internal seminal vesicle at first tubular, enlarging proximally in early mature segments with first appearance of spermatozoa; elongate-ellipsoidal in early gravid segments, attaining maximum dimensions of 190 to 450 long by 130 to 170 in diameter. Well developed retractor muscle, 8 to 40 in diameter and consisting of about 10 fibers, arising from proximal end of cirrus sac, extending anteromediad and fusing with fibers of internal (circular) layer of muscle anterolateral to ovary. External seminal vesicle first visible as aggregation of cells situated dorsally at proximal end of primordial cirrus sac;

cavity and ducts becoming visible with further development in immature segments. In mature and early post-mature segments, external seminal vesicle elongate, with long axis directed anteromediad; walls of vesicle provided with abundant glandular ("prostate") cells. External seminal vesicle enlarging posteriad, attaining maximum dimensions of 370 to 530 long by 130 to 410 in diameter in early gravid segments. Short afferent duct extending from distal end of external seminal vesicle, forming loop ventral to proximal end of cirrus sac and entering latter at apex. Vas deferens originating near anterior margin of ovary, formed by junction of 2 to 7 major ducts resulting from confluence of numerous vasa efferentia. Vas deferens extending directly laterad, forming reflex bend dorsal to external seminal vesicle and entering latter at anterior surface of proximal end. Testes subspherical, 287 to 327 per segment (av. 10 segments: 308), arranged 2–3 deep in dorsal layer extending across segment anterior to and between female genital organs; in some strobilae confined between ventral longitudinal excretory canals, sometimes overlapping canals, or with 1 to 8 testes disposed poral to canals bilaterally. Testes appearing before female genital organs in early immature segments and persisting in pregravid segments after disappearance of ovaries and vitelline glands. Testes 24 to 65 in diameter in mature segments, increasing to 97 to 129 in early gravid segments and thereafter disappearing. Vagina thick-walled with numerous glandular cells, about 50 in diameter in mature segments, extending mediad from genital atrium posterior to cirrus sac; enlarging just medial to ventral excretory canal, forming elongate seminal receptacle, latter extending mediad near posterior margin of segment and passing dorsally across poral side of ovary. Seminal receptacle attaining maximum dimensions of 630 to 800 long by 190 to 370 in post-mature segments. Short seminal duct arising from proximal end of seminal receptacle, joining oviduct just poral of Mehlis' gland. Ovary wider than long, situated bilaterally near posterior margin of segment; maximum dimensions of 360 to 650 wide by 250 to 400 long attained in post-mature segments. Fully developed ova, about 20 in diameter, abundant in ovary immediately before filling of uterus; ovaries disappearing in post-mature segments following expulsion of ova. Oviduct relatively long, extending porad to near proximal end of seminal receptacle, joining seminal duct, and then turning mediad to Mehlis' gland. Rudimentary ovaries or supernumerary masses of ovarian tissue frequently present near posterior margin of segment, between fully developed organs; sometimes associated with masses of vitelline cells or rudimentary vitelline glands and small, vesicular structures apparently representing rudimentary seminal receptacula. Vitelline gland entire to coarsely lobed, rounded to reniform, situated bilaterally dorsal to ovaries at posterior margin of segment, attaining maximum dimensions of 130 to 390 wide by 110 to 180 long in post-mature segments; persisting somewhat longer than ovaries. Vitelline duct extending anterolaterad to Mehlis' gland. As many as 7 rudimentary vitelline glands or masses of vitelline cells present in most segments of some strobilae, 30 to 170 in greater diameter, situated near posterior margin of segment between normally developed female genital organs. Such rudimentary organs persisting longer than functional female organs. Uterus first visible anterolateral to ovary, arising bilaterally as extensions from uterine duct, thereafter spreading ventrally as thin, cellular layer; early-stage uteri becoming confluent near midline of segment and extending laterad beyond ventral excretory canals. Uterus becoming reticulate posteriad, receiving

ova in early post-mature segments. Terminal gravid segments filled by uterus, in which reticular structure not evident but trabeculae visible when eggs lacking. Eggs subspherical to spherical, 71 to 90 by 68 to 83 (av. 81 by 75). Embryo 19 to 21 in greater diameter; embryonic hooks about 10 long. Cirrus sac and seminal receptacle persisting at posterior margin of gravid segments.

TYPE HOST: *Marmota flaviventris* (Audubon and Bachman); occurring in other Nearctic species of *Marmota* excepting *M. monax* (L.).

TYPE LOCALITY: Marquette Basin, Carter Mountain, south of Cody, Wyoming.

MATERIAL DEPOSITED: An entire mounted specimen of *D. composita* demonstrating the morphologic characteristics described above has been deposited in the USNM Helm. Coll. No. 75730.

The diagnosis of the genus *Diandrya* is here emended to accommodate the morphologic characteristics of the type species as redescribed.

Diandrya Darrah, 1930, emended

DIAGNOSIS: Monieziinae Spasskii, 1951. Strobila large, ribbonlike, with numerous segments. All segments wider than long. Scolex unarmed. Excretory system simple, with dorsal and ventral canals bilaterally. Genital pores bilateral. Two sets of genital organs in each segment. Genital ducts passing dorsal to longitudinal excretory canals. Vagina opening in genital atrium posterior to orifice of male duct. External seminal vesicle present. Testes numerous, distributed across segment anterior to and between female genital organs; may be poral to ventral excretory canals. Female genital organs situated posteriorly in lateral thirds of segmental width. Uterus reticulate, of bilateral origin, and filling gravid segments. Eggs with pyriform apparatus. Parasites of *Marmota* spp. (Rodentia: Sciuridae).

TYPE AND ONLY SPECIES: *Diandrya composita* Darrah, 1930.

Discussion

Diandrya composita was described from a small series of specimens, of which none was intact. The present redescription more adequately defines the range of nonsignificant morphologic variation of the species and corrects some errors in the original interpretation of anatomic details.

As originally described, *D. composita* would possess a combination of organs, the "interproglottidal glands," and the "pedunculated prostate glands," that otherwise is unknown in any cestodes of the family Anoplocephalidae. Interproglottidal glands occur in members of two of the three subgenera of *Moniezia,* and a pedunculated prostate gland has been considered characteristic of the genus *Andrya* s. str. (Spasskii, 1951). In reality, neither organ is present in *D. composita.*

The rudiments of supernumerary female genital organs so often present in *D. composita* were taken to be interproglottidal glands by Darrah (1930), who remarked (p. 254) that they ". . . are very inconstant in both size and number. They appear as globular, or small compact masses of spherical follicles along the posterior margin of the proglottids between the ovaries." These rudimentary organs are identifiable as genital tissue from both their form and microscopic structure, and when present they occur always in a row in the parenchyma of the

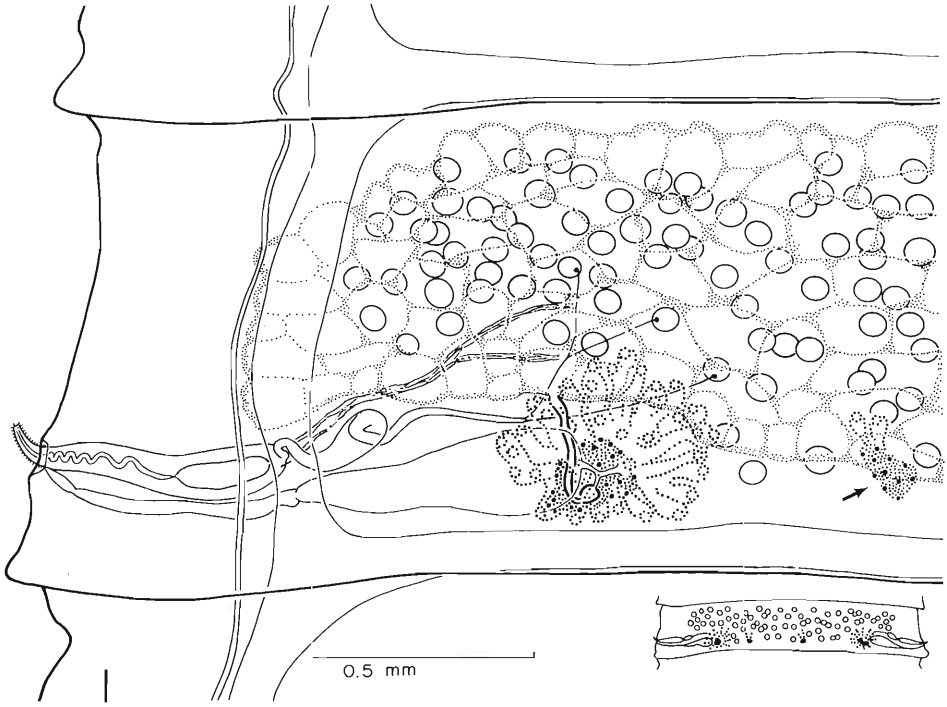
segment at the level of the functional female organs, rather than superficially at the anterior margin of the segment in parallel, dorsal and ventral rows, as do the interproglottidal glands in cestodes of the subgenus *Moniezia* (e.g., *M.* (*M.*) *expansa* (Rud., 1810)). In *D. composita,* the rudimentary organs persisted after the functional ovaries and vitelline glands had degenerated and disappeared, perhaps indicating that the former are not subject to the same degree of hormonal influence. In the absence of the "interproglottidal glands," the morphologic similarity of *Diandrya* to *Moniezia* is much diminished. However, that the uterus of *Diandrya* is reticulate permits retention of the genus in the subfamily Moniezinae.

The concept of a pedunculated prostate gland in certain cestodes now included in the family Anoplocephalidae had its origin with Riehm (1881), who believed such an organ to exist in *Taenia rhopalocephala* Riehm, 1881 (=*Andrya rhopalocephala* (Riehm, 1881), type species of the genus *Andrya* Railliet, 1893) and *T. rhopaliocephala* Riehm, 1881 (=*A. cuniculi* (Blanchard, 1891)), both described from leporids in Germany. With reference to his interpretation of the structure of the male genital duct in *T. rhopalocephala,* Riehm (1881, p. 9) stated that "Das Vas deferens . . . ist unschwer zu erkennen. Bevor dieses in den Cirrhusbeutel eintritt, nimmt es noch einen Gang auf, welcher an dem Excretionskanal entlang zieht und mit einer kleinen, ovalen bis spindelförmigen Blase blind endigt." Riehm considered the content of this vesicle to be the product of the glandular cells covering its surface. Compared with that of *T. rhopalocephala,* the prostate gland in the second species (*rhopaliocephala*) was stated (p. 20) to have a shorter peduncle. The pedunculated prostate gland as conceived by Riehm was portrayed in his figures (1881, Taf. VI, figs. 1 and 3).

With publication of Riehm's dissertation, the grounds were established for perpetuation of the concept of a pedunculated, blindly ending prostatic vesicle in cestodes in the family Anoplocephalidae. The uniqueness of such a structure in the Cestoda was noted already in 1897 by Braun (p. 1408), who remarked "Sind auch diese Angaben gewiss nicht erschöpfende, so dürften sie doch so viel beweisen, dass in der That bei wenigen Taenien am männlichen Leitungsapparat Drüsen vorkommen, die man mit Recht Prostatadrüsen nennen kann; freilich weichen dieselben von den Prostatadrüsen anderer Plathelminthen ab." Such a gland was subsequently reported to occur in additional species of *Andrya,* as well as in *Diandrya.*

In describing *Diandrya composita,* Darrah (1930) considered the published work of Stiles (1896), Douthitt (1915), and Baer (1927) concerning the morphologic characteristics of *Andrya* spp. Stiles (1896) had examined some of Riehm's original material, but its condition was so poor (p. 155) that he was ". . . unable to enter into a detailed study of the organs." Baer's (1927, p. 31) descriptions of the two species from leporids were evidently based on the data published by Riehm (1881). Douthitt (1915) described two additional species, *A. primordialis* Douthitt, 1915 and *A. communis* Douthitt, 1915 (=*A. primordialis*), which he placed in a "*rhopalocephala*-group" characterized in part (p. 367) by the presence of a ". . . pedunculated prostate gland opening into the vas deferens near the ventral excretory vessel." The existence of the latter organ has been generally accepted until only recently (cf. Spasskii, 1951; Yamaguti, 1959; etc.).

From the study of cestodes identified as *A. rhopalocephala* and *A. cuniculi*



Figures 1, 2. ***Diandrya composita.*** **1. Relationships of organs, ventral view. Arrow indicates rudiments of supernumerary ovary and vitelline gland. 2. Details of genital ducts, dorsal view. Abbreviations: cs = cirrus sac; esv = external seminal vesicle; rm = retractor muscle; sr = seminal receptacle; ut = early-stage uterus; v = vagina; vd = vas deferens; ve = vas efferens.**

(now considered to be a synonym of the former (cf. Sugár et al., 1978)), I determined (Rausch, 1976) that neither possessed a pedunculated prostate gland such as was described by Riehm and concluded that the typical structure of the male genital duct in these cestodes had been misinterpreted. At the same time (p. 523) it was noted that the structure of the male genital duct in *Diandrya composita* had been similarly misinterpreted. A figure of the "prostate gland" of *D. composita* published by Joyeux and Baer (1961, p. 394) showed a duct entering at the proximal end. However, the origin of the figure was not given, and the organ was described in the text (p. 395) as consisting of a blindly ending vesicle from which

an efferent duct entered the vas deferens: "Chez *Diandrya* ainsi que chez certaines espèces du genre *Andrya*, les cellules prostatiques déversent leur contenu dans la portion dilatée en cul-de-sac d'un canalicule qui vient se jeter dans le canal déférent à l'endroit où celui-ci pénètre dans la poche du cirre. Une 'prostate' sous la forme décrite ne s'observe que rarement chez les Cestodes. On peut même se demander quel en est le rôle, puisque dans un même genre (*Andrya*) quelques-unes des espèces seulement en sont pourvues." In any case, it is evident that the structure of the male genital duct is fundamentally identical in cestodes of the genera *Andrya* (sensu Rausch, 1976) and *Diandrya*.

The relationships of the female genital ducts in *D. composita* also were misinterpreted by Darrah (1930), who stated (p. 254) that "There is no oviduct, the eggs passing directly into the uterus when the ovary breaks down." In this species, the uterine duct (=oviduct of Darrah) arises bilaterally and extends somewhat anterolaterad to the margin of the ovary, where the early-stage uterus is first visible (Fig. 2). When in early post-mature segments the uterus has become a well-defined reticulum, it rather abruptly fills with ova, after which the ovaries degenerate and soon disappear. The process is like that in *Andrya* spp. and other anoplocephalids, such as *Anoplocephaloides* spp. (Rausch, 1976).

The genus *Diandrya* appears to be a derivative of *Andrya*, from which it differs only in the doubling of the reproductive organs. The rudiments of supernumerary genital organs frequently present in this cestode probably had their origin with the process that led to reduplication of the functional organs. The diploid number of chromosomes in *D. composita* is 10 (V. R. Rausch, unpublished). Although the chromosomes of cestodes of the genus *Andrya* have not been studied, the low number in *D. composita* indicates that it is not autopolyploid. *Diandrya* evidently arose in Nearctic marmots during the early Pleistocene, after the trans-Beringian dispersal of *Marmota* to the Palaearctic.

Acknowledgments

Marmots or cestodes from marmots were provided by Dr. M. L. Johnson, University of Puget Sound Museum of Natural History, Tacoma; Dr. I. McT. Cowan and Mr. D. G. King, University of British Columbia, Vancouver; Dr. John C. Holmes, University of Alberta, Edmonton; and Dr. Allen McIntosh, Animal Parasitology Institute, Beltsville. Specimens of *Andrya rhopalocephala* were provided by Dr. F. Simón Vicente, Centro de Edafologia y Biologia Aplicada, Salamanca; Dr. J. M. Tarazona, Departamento Higiene y Sanidad Animal, Madrid; Dr. M. Graber, École Nationale Vétérinaire, Lyon; Dr. B. Hörning, Universität Bern; Dr. T. Kubelej, Âllatorvostudományi Egyetem, Budapest; and Dr. J. R. Lichtenfels, Animal Parasitology Institute, Beltsville. The figures were prepared by Ms. V. R. Rausch, who also determined the diploid number of chromosomes in *D. composita*. These contributions are gratefully acknowledged.

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