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POSTONCOSPHERAL DEVELOPMENT AND CYCLE OF *TAENIA POLYACANTHA* LEUCKART, 1856 (CESTODA: TAENIIDAE)

First part

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SUMMARY. The postoncospheral development and cycle of *Taenia polyacantha* Leuckart, 1856, an holarctic species of cestode, were investigated in the laboratory as well as in the tundra of northern Alaska. Foxes, *Alopex lapogus* (L.) and *Vulpes vulpes* (L.), serve as final host of *T. polyacantha*; the northern vole, *Microtus œconomus* (Pallas), and the brown lemming, *Lemmus sibiricus* (Kerr), are important as the intermediate host. As determined in experimentally infected voles and lemmings, the oncosphere of *T. polyacantha* transformed to a primary vesicle in the liver. On the 6th day postexposure, coinciding with its migration to the peritoneal cavity, the larval cestode consisted of a minute aggregation of secondary vesicles. By 9-10 days postexposure, the secondary vesicles dissociated, thereafter developing independently to infective cysticerci by 30-40 days postexposure. At an age of about 60 days, the infective larvae began to undergo further growth and morphological modification, which led to acquisition of some strobilar characteristics by the forebody. Such late transformation of a cysticercus to a more advanced form of larva is known otherwise only in *Taenia martis* (Zeder, 1803). Differences in numbers and sizes of rostellar hooks provided the basis for recognition of two taxa at the infraspecific level: *Taenia p. polyacantha* Leuckart, 1856, distributed in Eurasia to the south of the zone of tundra, and *T. p. arctica* ssp. nov., present throughout the holarctic tundra. Observations concerning interactions of *T. polyacantha* and its hosts are discussed.

Key-words: Cestoda. *Taeniidae*. Development. Morphology. Cycle.

Développement postoncosphéral et cycle de *Taenia polyacantha* Leuckart, 1856 (Cestoda: Taeniidae).

RÉSUMÉ. Le développement postoncosphéral et le cycle biologique de *Taenia polyacantha* d'Alaska sont décrits. Ce cestode holarctique est répandu en Eurasie en diverses zones biotiques et en Amérique du Nord dans les régions de la toundra. Les Renards *Alopex lagopus* et *Vulpes vulpes* servent d'hôtes définitifs. Le campagnol *Microtus œconomus* et le lemming *Lemmus sibiricus* sont d'importants hôtes intermédiaires. La transformation des oncosphères de *T. polyacantha*

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commence dans le foie de l'hôte intermédiaire. Six jours après l'infection initiale, un aggrégat de vésicules secondaires, qui constitue un caractère distinctif du cestode, apparaît dans la cavité abdominale de l'hôte. Les vésicules secondaires se séparent 3-4 jours plus tard et continuent à croître indépendamment. Environ 30-40 jours après l'infection initiale des Rongeurs, des cysticerques infectants apparaissent. Au 60e jour, les larves infectantes subissent une croissance et une modification morphologique qui conduisent à l'acquisition dans la partie antérieure du corps de structures proches de celles de l'adulte (un phénomène comparable n'est connu que chez *Taenia martis* (Zeder, 1803). Le nombre et les dimensions des crochets indiquent l'existence de deux sous-espèces de *T. polyacantha* : *T. p. polyacantha* Leuckart, 1856, distribuée en Eurasie jusqu'au Sud de la toundra, et *T. p. arctica* s. sp. nov., présente dans la toundra holarctique. Quelques relations hôte-parasite dans le cycle naturel sont discutées.

Mots-clés : Cestoda. *Taeniidae.* Développement. Morphologie. Cycle.

The cestode *Taenia polyacantha* Leuckart, 1856 and its hosts make up a faunal assemblage that occurs widely in the Holarctic, present in Eurasia in diverse biotic zones and in North America in the zone of tundra. Our report primarily concerns that cestode in the Nearctic, where its cycle involves the arctic fox, *Alopex lagopus* (L.), and the red fox, *Vulpes vulpes* (L.), as final host and rodents of the family Arvicolidae as intermediate host. The first record of *T. polyacantha* in North America was that of Schiller (1953), who found the larval (metacestode) stage in the peritoneal cavity of a northern vole, *Microtus œconomus* (Pallas), on the delta of the Yukon River. The strobilar stage was later identified and redescribed on the basis of specimens from arctic foxes collected near Point Barrow (Rausch, 1959).

The larval stage of *T. polyacantha*, first described by Baer (1932), undergoes an apparently age-related modification in form, and when fully developed closely resembles that of *Taenia martis martis* (Zeder, 1803). Baer considered it to resemble a tetrathyridium, and in accordance, the designation « armatetrathyridium » was proposed for it by Abuladze (1964, p. 70). At the same time, the genus *Tetratirotaenia* Abuladze, 1964 was established for this cestode, but it is now usually placed in the genus *Taenia* Linnaeus, 1758 (see Verster, 1969; Rausch, 1985).

In 1964, we initiated a study of the morphogenesis of the larval stage of *Taenia polyacantha* in experimentally infected rodents, supplemented by observations on natural interactions with the hosts in Alaska and elsewhere. The pattern of development was found to involve a process of asexual multiplication previously unknown in cestodes of the genus *Taenia*. Our findings are reported in the present paper.

Materials and methods

Eggs from gravid segments of cestodes removed *post mortem* from the intestine of the final host or from segments expelled with the feces of foxes maintained in the laboratory were used to infect laboratory-reared rodents. The rodents were mainly of species known to serve as the natural intermediate host of *T. polyacantha*:

brown lemming, *Lemmus sibiricus* (Kerr) (stock from Point Barrow); and northern vole, *Microtus œconomus* (Pallas) (stock from the Kenai Peninsula). We also exposed to infection a series of narrow-skulled voles, *Microtus miurus* Osgood (stock from Umiat, northern Alaska), eight intergrades between *M. miurus* and the St. Matthew Island vole, *Microtus abbreviatus* Miller (stock from St. Matthew Island) [the latter two taxa were considered to be strongly differentiated subspecies of a single species, for which the name *M. abbreviatus* is applicable on grounds of priority (see Rausch and Rausch, 1968)], six northern red-backed voles, *Clethrionomys rutilus* (Pallas) (stock from the Anchorage area), and a few muskrats, *Ondatra zibethicus* (L.). Individual animals while under ether anesthesia usually received 5 to 20 eggs introduced by means of a glass pipette into the stomach; a few animals received as many as 200 eggs. The rodents were examined at appropriate intervals from one to 108 days postexposure, or in the case of severe infections, when death occurred.

Naturally infected arctic foxes were captured at the following localities in Alaska and maintained in the laboratory: Point Barrow, 1; Beechey Point, 1; and St. Lawrence Island, 3. Six arctic foxes, produced at the Alaska State Fur Farm at Petersburg, were infected experimentally, as was one laboratory-reared dog (beagle). All canids were kept in individual cages, under conditions that prevented any access to wild rodents. Larvae from naturally and experimentally infected rodents were administered to canids. Data on the prevalence of *T. polyacantha* were derived from helminthological surveys conducted by us in Alaska.

The description of the postoncospheral development of *T. polyacantha* is based on findings in 41 northern voles, 5 narrow-skulled voles, and 1 brown lemming, all exposed to experimental infection. Also included are descriptions of larvae from infections of long but unknown duration in naturally infected rodents. Mammalian tissues were fixed in a 10 % solution of formalin, processed by the paraffin-embedding method, and sectioned at 5 or 7 micrometers. Larval cestodes at different phases of development were processed similarly and usually were sectioned serially at 10 or 15 micrometers. Sections of tissues were stained in hematoxylin-eosin; those of larvae were stained in hematoxylin-eosin, phosphotungstic acid-hematoxylin, Gomori's trichrome, Masson's trichrome, Alcian blue, van Gieson picric acid-acid fuchsin, Gomori's reticulum stain, Growcott's methamine silver, and by the periodic acid-Schiff method. Whole-mounts of larvae at different phases of development, as well as cestodes in the strobilar stage, were prepared after staining in acetic carmine or Ehrlich's acid hematoxylin. For study of rostellar hooks, the rostellum was removed and mounted separately with sufficient pressure on the cover-glass to cause the hooks to lie flat. Films of blood and peritoneal fluid were air-dried, fixed in absolute methanol, and stained by the Wright-Giemsa method. Blood-serum and ascitic fluid were compared by means of polyacrylamide gel electrophoresis, using gels with 5 % or 7 % acrylamide. Controls consisted of serum from non-infected voles and from man.

The terminology used for the various microscopic structures in the larval cestodes corresponds mainly to that of Morseth (1966) and Bilqees and Freeman (1969).

Results

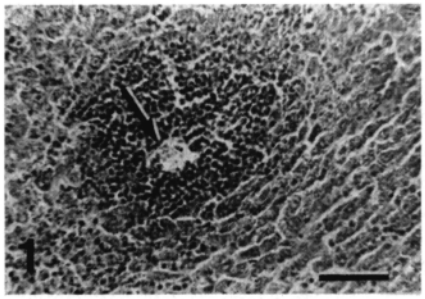
Of the rodents exposed to experimental infection, only the northern voles, brown lemmings, narrow-skulled voles, and muskrats became infected with *T. polyacantha*. None of the 8 *M. miurus* × *M. abbreviatus* intergrades became infected, nor did the series of northern red-backed voles. Neither *M. miurus*, *M. abbreviatus*, nor *C. rutilus* has been found infected naturally. The following description of larval development is based on findings in the experimentally infected northern voles. Findings in rodents of the other species are mentioned where appropriate.

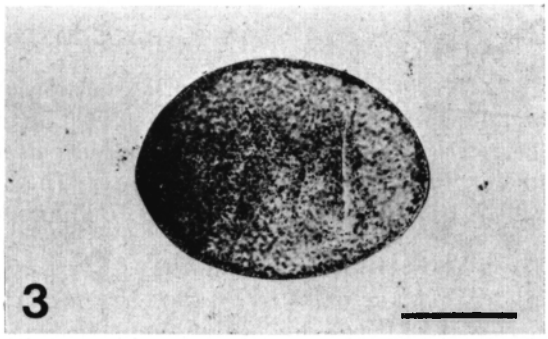
Chronology of Postoncospheral Development

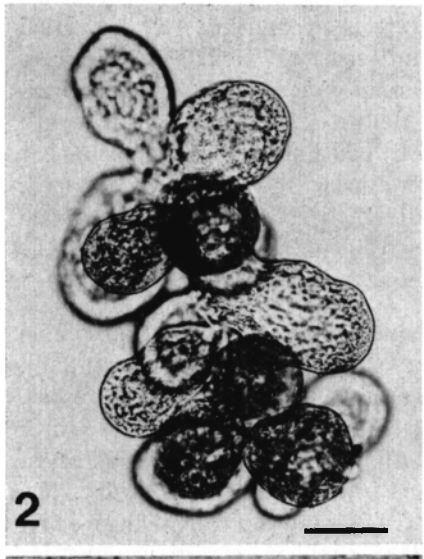
As is typical of cestodes of the genus *Taenia*, the oncospheres of *T. polyacantha* evidently passed by way of the portal vein to the liver of the intermediate host. They localized in that organ, where early development took place. Lesions produced by the youngest larvae were observed in sections of liver from several animals during the first 5 days postexposure; indications of their presence were not found in sections of any other organs. Following the administration of eggs, the first macroscopic indications of infection were noted on the 4th day postexposure, when a slightly turbid fluid began to accumulate in the peritoneal cavity. The quantity of fluid increased thereafter, and on the 6th day postexposure it contained minute larvae that had passed from the liver to the peritoneal cavity. At that time, sections of liver exhibited evidence of acute focal hepatitis. The quantity and cellular content of the ascitic fluid appeared to vary with the intensity of infection, but a comparatively large volume of fluid sometimes was associated with only small numbers of larvae. Ascites persisted in some rodents at least to the 16th day postexposure but was not evident thereafter. Residual effects of the inflammatory response were discernible indefinitely in animals that survived severe infections.

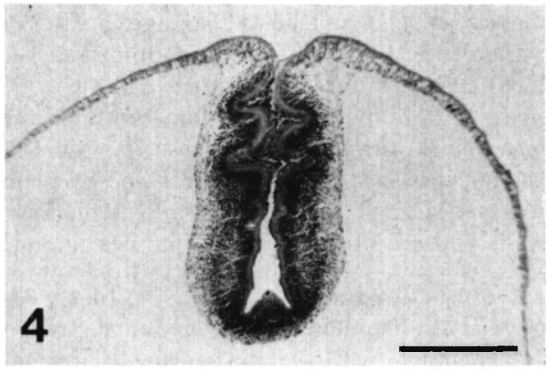
Figs. 1-9. — *Taenia polyacantha:* Developmental characteristics and structure.

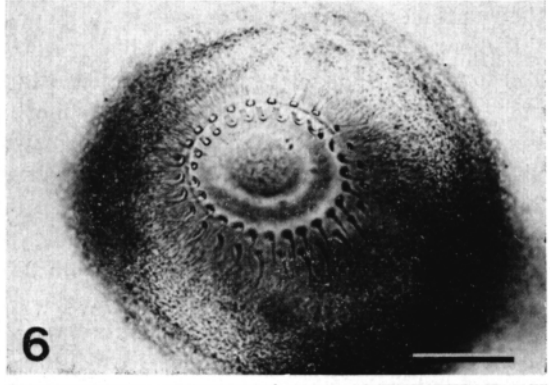
Fig. 1. Primary vesicle (arrow) surrounded by eosinophils in the liver of a northern vole, 120 h postexposure. Hematoxylin-eosin. Scale 50 μm. *Fig. 2.* Aggregation of secondary vesicles from the peritoneal cavity of a northern vole, 6 days postexposure. Formalin preserved. Scale 50 μm. *Fig. 3.* Detached secondary vesicle with the primordium of the scolex at the distal end, 9 days postexposure. Acetic carmine. Scale 200 μm. *Fig. 4.* Sagittal section of forebody, showing the early rostellar cone at the apex of the invaginal canal, 13 days postexposure. Hematoxylin-eosin. Scale 200 μm. *Fig. 5.* Lateral view of structures at the apex of the invaginal canal, 16 days postexposure. Ehrlich's acid hematoxylin. Scale 100 μm. *Fig. 6. En face* view of apex of invaginal canal, with two rows of developing rostellar hooks, 16 days postexposure. Ehrlich's acid hematoxylin. Scale 100 μm. *Fig. 7.* Microtriches on distal cytoplasm near apex of the invaginal canal, 18 days postexposure. Gomori's trichrome. Scale 25 μm. *Fig. 8.* Partial *en face* view of developing rostellum and suckers, 18 days postexposure. Acetic carmine. Scale 300 μm. *Fig. 9.* Projections or folds from the walls of the invaginal canal, 30 days postexposure. Masson's trichrome. Scale 250 μm.

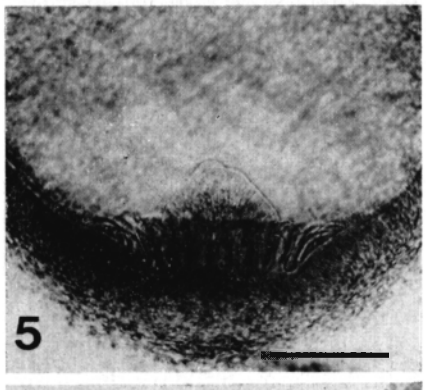


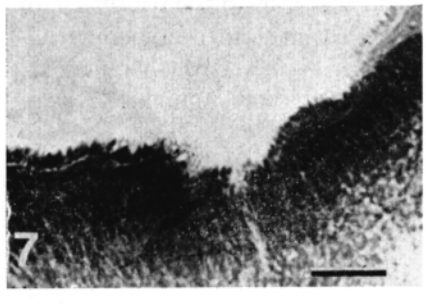


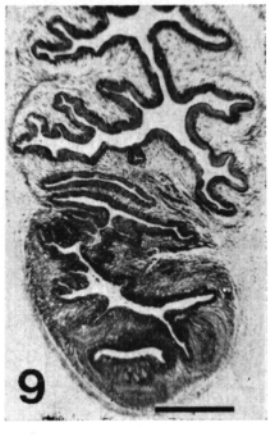












5 DAYS POSTEXPOSURE. The earliest postoncospheral phase observed in the liver, at 120 hours postexposure, consisted of primary vesicles, 19 and 22 μm in greater diameter, occurring within aggregations of eosinophils *(fig. 1)*. The individual lesions were about 200 μm in diameter. The vesicles were subspherical and thin-walled, with well developed lumina. Budding was not evident.

6 DAYS POSTEXPOSURE (7 ANIMALS). The larvae, each a minute aggregation of exogenous structures derived from the primary vesicle, appeared in the peritoneal cavity of the voles 144 to 146 hours postexposure. At that time, the individual masses ranged from 176 to 298 μm in greater diameter by 173 to 270 μm, and were composed of 3 to 16 buds in the process of becoming vesicular *(fig. 2)*. Such incipient bladders were subspherical to somewhat elongate, 70 to 110 μm in length by 62 to 110 μm in greatest diameter. Each was attached at the pole opposite that at which the primordium of the scolex would later appear. In those least advanced, the lumen was still partially occluded by filaments of tissue; in others, the lumen was well defined, and the walls of the bladder were 15 to 27 μm in thickness. The walls appeared to be a syncytium containing numerous nuclei.

9 DAYS POSTEXPOSURE (4 ANIMALS). In 4 voles given 10-15 eggs each, the volume of peritoneal fluid on the 9th day ranged from only a slight amount to at least 2 ml. In the animal with the most severe ascites, more than 100 bladders were present, their surfaces completely covered by a layer of leukocytes as much as 24 μm in thickness. In all voles, most of the bladders had separated from the original mass, and occurred singly, but some remained attached in groups of two to eight. The unattached bladders were somewhat pleomorphic, but were typically elongate and somewhat attenuated at the posterior end, where a slight projection usually was visible. Formalin-preserved specimens, measured without pressure, ranged from 262 μm to 1.3 mm in length by 140 to 467 μm in greatest diameter; average length was near 400 μm. The walls of the bladders ranged from about 20 to 30 μm in thickness. In the largest, the early primordium of the scolex, appearing at the anterior pole as an accumulation of nuclei 64 to 80 μm in thickness, was most clearly visible when stained in acetic carmine *(fig. 3)*. The distal cytoplasm of the tegument of the bladders was 1 to 2 μm in thickness.

Four larvae found in a narrow-skulled vole on the 9th day postexposure appeared to be retarded, since they consisted of typical aggregations of buds in which the lumina were little developed, comparable to larvae in northern voles on the 7th day postexposure. Also present were two large bladders, both 150 μm in length and still attached. A second vole, which died after 9.5 days, had two single bladders, 400 and 470 μm long, of which the walls contained numerous calcareous corpuscles. A third bladder, 440 μm in greater diameter, was anomalous, and consisted of four lobes of similar size with interconnected lumina. All were covered by a layer of leukocytes.

11 DAYS POSTEXPOSURE (3 ANIMALS). All bladders had become detached but showed some lack of uniformity in state of development. Seventeen specimens

from one animal were the most advanced, ranging from 1 to 1.9 mm in length by 497 to 936 μm in greatest diameter ($\bar{x}$ = 1.4 mm by 768 μm). Formation of the invaginal canal had begun, the invagination extending 140 to 337 μm posteriad into the lumen. The depth of the canal ranged from 100 to 270 μm. The bladders were somewhat elongate, with the posterior end still attenuated. Their walls ranged from 17 to 30 μm in thickness for the most part, increasing to as much as 66 μm at the posterior pole. The distal cytoplasm of the tegument was about 2 μm in thickness anteriorly, but less elsewhere. Calcareous corpuscles were numerous in the bladder-walls of living specimens, but were not discernible in those preserved. At 11 days, accumulations of leukocytes were limited to the lumen of the invaginal canal and the surface of the bladder immediately surrounding its orifice.

The 34 larvae from the second vole were smaller and more pleomorphic, ranging from subspherical to somewhat elongate, and 300 to 750 μm in length by 262 to 525 μm in maximum diameter ($\bar{x}$ = 557 by 386 μm). In all but the smallest was a shallow concavity at the anterior pole, beneath which nuclei formed a layer 54 to 112 μm in thickness. The surfaces of the bladders were covered by leukocytes. A single bladder in the third animal measured 861 by 750 μm, and resembled those from the first vole in state of development.

12 DAYS POSTEXPOSURE (2 ANIMALS). Twelve bladders with ca. 3 ml of ascitic fluid were present in the peritoneal cavity of a vole that had received 10-15 eggs. All were cysticercus-like, their anterior poles somewhat flattened and their posterior ends attenuated or with a small projection. Ten larvae ranged from 1.5 to 2.7 mm in length. In nine, a well defined invaginal canal was present; one anomalous specimen had developed a pole at each end. The tissues surrounding the canal formed a cylinder as much as 320 μm in diameter and 140 to 760 μm in length. The canal was straight and tubular, with a somewhat funnel-shaped opening at the surface of the bladder. As seen in transverse sections, its lumen, from 170 to 190 μm in diameter, was lined by distal cytoplasm 3 to 7 μm in thickness, followed by a layer of perpendicular nuclei 17 to 34 μm in thickness. Outermost was connective tissue up to 35 μm in thickness. At the apex of the canal, the floor was flat and smooth, with no indication of the beginning development of the rostellar cone (cf. Bilqees and Freeman, 1969). In these 10 specimens, the invaginal canal was filled by a mass of leukocytes that sometimes projected as much as 100 μm above the anterior surface of the bladder. The thickness of the bladder walls laterally was 15 to 16 μm, increasing to 36 to 58 μm at the posterior pole, and to as much as 46 μm at the anterior end adjacent to the opening of the invaginal canal. The distal cytoplasm of the tegument showed the same pattern, ranging from about 2 μm laterally to 7 to 10 μm in thickness at the poles. The tegument, rugose when thick, was covered by microtriches about 1 μm in length. The 11 larvae found in the second animal were less advanced developmentally and did not exhibit any unusual features.

13 DAYS POSTEXPOSURE (2 ANIMALS). The 15 and 18 bladders present in these voles were of greater average size than the foregoing, with the largest from 3 to

3.5 mm in length. The invaginated forebody was 700 to 850 μm long and 220 to 280 μm in greatest diameter. The invaginal canal, no longer straight, was often narrower anteriorly. The greatest diameter of the lumen, near the apex, was about 150 μm. As seen in sections stained for reticulum by the Gomori method, reticular fibers were abundant, and tended to be aligned perpendicular to the tegument. The beginning rostellar cone was as much as 60 μm in diameter and 40 μm in greatest height *(fig. 4)*. The distal cytoplasm lining the invaginal canal distally was about 5 μm in thickness, whereas that covering the cone was slightly thicker. In sections stained for reticulum, the well defined basal membrane underlying the tegument was not visible in the cone.

14 DAYS POSTEXPOSURE (2 ANIMALS). Leukocytes coated the surfaces of the bladders and filled the invaginal canals of the two and six larvae obtained. The development of the rostellar cone was less advanced than in larvae on the 13th day.

16 DAYS POSTEXPOSURE (2 ANIMALS). The peritoneal cavity of one vole contained five larvae and 4 ml of turbid ascitic fluid. The liver had adhered to the right kidney and to adjacent loops of the small intestine. In the second vole were 13 bladders and several small, amorphous masses which apparently were vestiges of dead larvae. The specimens from the first vole, mounted permanently and consequently flattened, ranged from 2.2 to 3.6 mm in length by 1.6 to 2.5 mm in greatest width. The length of the invaginated forebody ranged from 861 μm to 1.1 mm, and maximal diameter was about 350 μm. Proximally, for about half its length, the invaginal canal was sinuous, its lumen containing a mass of leukocytes. The lumen of the relatively straight distal half was as much as 97 μm in diameter, and after narrowing somewhat distad, dilated slightly at the apex. The distal cytoplasm lining the canal was about 12 μm in thickness near the orifice, decreasing to about 5 μm distally. Beneath the tegument throughout the length of the canal was a dense layer of nuclei, about 20 μm in thickness, oriented perpendicularly, which merged with a second layer, 20 to 40 μm in thickness, also containing abundant nuclei. An outer, parenchymal layer, thinnest (ca. 20 μm) at the apex of the forebody and from 24 to 85 μm in thickness elsewhere, extended beneath the tegument of the bladder at the orifice of the canal, becoming gradually thinner posteriad until the wall of the bladder attained a uniform thickness of 12 to 22 μm. As seen in serial sections, the tegument of the bladder was underlain by muscle fibers about 1 μm thick, followed by the nuclear layer and a layer of loose parenchyma containing a network of excretory canals up to 9 μm in diameter. The inner wall of the bladder, 5 to 8 μm in thickness, consisted of parallel fibers. Calcareous corpuscles were numerous in the bladder wall. The tegument of the bladder was thickest at the anterior and posterior poles.

The rostellar cone arose centrally from the apical floor of the canal, apparently derived from the innermost layer of nuclei, with which it was continuous. In the least developed among the live bladders from the first vole, the cone consisted only of a slight convexity of the apical floor. In two others, the cones were 85 and 97 μm in diameter at the base and 49 and 46 μm in height. In the two specimens

most advanced in development, the cone was less pointed at its apex, and the base was enclosed by a ring of tissue identified as the prebulb (*cf.* Bilqees and Freeman, 1969, *figs. 15 and 16*). A ring-like channel surrounding the prebulb contained abundant slender spines about 9 μm long, of no discernible pattern in distribution.

Of the 13 larvae from the second vole, 11 were mounted permanently after partial dissection in order to study the developing scolex, and two were sectioned serially. Seven ranged from 2 to 3 mm in length by 2.3 to 3.1 mm in width. The invaginated forebody in these preparations ranged from 880 μm to 1 mm in length by 400 to 500 μm in greatest diameter. Some variation was evident in the state of development of the scolex.

The proximal part of the invaginal canal was usually somewhat dilated, with a diameter of 280 to 350 μm, and was filled with leukocytes. The lumen then narrowed, but expanded abruptly at the distal end. In specimens developmentally least advanced, the distal cavity was nearly spherical, ranging from 290 to 430 μm in transverse diameter by 330 to 390 μm, and often contained leukocytes. Its apical floor was flat and circular in outline. As seen *en face* in one specimen, the diameter of the apical floor was 330 μm. The rostellar cone was broad-based, its flat distal surface contiguous with the underlying layer of perpendicular nuclei. The cone was 85 to 102 μm in diameter and 83 to 92 μm in height. Its base was surrounded by a band-like prebulb, about 20 μm thick, arising from the floor at the same level as the rostellar cone. The prebulb was circular, 134 to 139 μm in diameter, and about 36 μm in height *(fig. 5)*. Peripherally, that structure was surrounded by a double row of slender, spine-like hooks, arching outward, in length (straight line from tip to base) ranging from 49 to 51 μm. As seen *en face*, the hooks alternated in two concentric circles *(fig. 6)*. The inner circle, with 27 hooks, had a diameter of 117 μm; the outer, with 26 hooks, had a diameter of 134 μm. Peripheral to the circles of larger hooks, the floor of the apical cavity was lined by numerous, minute hooks. In the specimen most advanced in development, constricting tissues arising laterally in the floor of the cavity led to formation of a deep groove around the rostellar bulb, within which the rows of large hooks were enclosed. In this specimen, the hooks ranged from 56 to 65 μm in length, and their tips protruded anteriad into the lumen of the apical cavity. In these, some was evident at the basal end.

18 DAYS POSTEXPOSURE (1 ANIMAL). Twenty-five bladders and numerous nodules of amorphous substance were present in the peritoneal cavity of this vole, with little or no excess fluid. Two specimens were sectioned serially. In the largest bladders, 3.7 to 7 mm in length, the forebody was invaginated 900 μm to 1.2 mm. The anterior portion of the invaginal canals had narrowed, because of protrusion of tegumental tissue mediad from their walls. Near the orifices of the canals, the tegument was rugose, and its distal cytoplasm had a thickness of about 12 μm, decreasing posteriad to about 5 μm. Microtriches, 2 to 3 μm long, stained orange by Gomori's trichrome, densely covered the distal cytoplasm of the posterior half

of the canal *(fig. 7)*. In th e wall of the invaginal canal, the suckers now appeare as well defined outpocketings about 130 μm in greater diameter. They, too, were lined with distal cytoplasm covered by orange-staining microtriches. Their thin outer walls contained a thick layer of subtegumental nuclei arranged perpendicularly. At the apex of each invaginal canal, four layers of tissue were discernible: the innermost hook organ, the rostellar pad with perpendicular nuclei, a granular layer, and the external fibrous covering. In a specimen stained in acetic carmine and partially dissected, the inner surface of the apex could be viewed *en face (fig. 8)*. At the center, the hook organ appeared as a rounded, somewhat lobed structure, 85 μm in diameter, from which two rows of hooks projected outward. Straight-line lengths of the hooks *in situ* were about 86 and 170 μm for those of the inner and outer rows, respectively; they were about 5 μm in greatest thickness. Dispersed among the hooks proximally were globules 5 to 15 μm in diameter, consisting of tissue of the hook organ. In an unstained preparation of apical tissues, compressed so that the hooks lay flat, the lengths of the large and small hooks ranged from 178 to 188 μm and from 129 to 134 μm, respectively. The hooks were colorless, translucent, and without handles. In sections stained in hematoxylin-eosin and in Gomori's trichrome, the hooks were purple; the hook organ was colored pink and blue, respectively, by these stains.

30 DAYS POSTEXPOSURE (7 ANIMALS). In these voles, each of which had received five eggs, numbers of larvae in the peritoneal cavity ranged from 16 to 54 ($\bar{x} = 35$). The larvae were piriform, larger at the anterior end and somewhat pointed posteriorly. The anterior pole, around the orifice of the invaginal canal, was somewhat flattened. At this stage, the larvae appeared as typical cysticerci. Undistorted, formalin-fixed bladders ranged from 4 to 6.5 mm in length by 1.5 to 2 mm in diameter ($\bar{x} = 5.1$ by 1.9 mm). Externally, the surface had shallow, transverse, parallel grooves, 36 to 85 μm apart. The opening of the invaginal canal was now slit-like and apparently oriented transversely. Staining in Ehrlich's hematoxylin revealed in the wall of the bladder abundant calcareous corpuscles, typically oval in outline and usually from about 14 to 18 μm in greater diameter. The thickness of the walls of the bladder, about 50 to 95 μm laterally, increased anteriad, attaining a maximum at the anterior end around the forebody; numerous excretory canals were present. The distal cytoplasm of the bladder wall was about 10 μm in thickness. With van Gieson's stain, the external membrane of the distal cytoplasm, about 1 μm in thickness, was pink, as were the microtriches, about 1 μm in length, while the remainder of the distal cytoplasm was yellow. In sections, the basement or cytoplasmic membrane of the distal cytoplasm appeared as a black line about 1 μm in thickness with application of Gomori's reticulum stain. In surfacial view, it was found to consist of a delicate network of fibers. Immediately below the cytoplasmic membrane was a layer of circular muscle fibers, 1 to 2 μm in thickness, followed by a somewhat thinner layer of longitudinal fibers. Subtegumental nuclei, arranged perpendicularly, were rather sparse. The remainder of the bladder wall consisted of parenchyma containing nuclei and calcareous corpuscles.

As seen in specimens mounted entire, the forebody was still straight, but usually had deviated somewhat laterad within the bladder. In its apex three well defined layers of tissue were identified as the external fibrous layer, the rostellar pad, and the prebulb, against which the handles of the rostellar hooks rested. The cytoplasmic membrane enclosing the prebulb stained blue in Masson's trichrome. At 30 days postexposure, numerous, thick, fold-like projections filled most of the lumen of the invaginal canal *(fig. 9)*. The suckers were well developed, and now were about 195 μm in greater diameter. The distal cytoplasm of the invaginal canal, about 10 to 12 μm in thickness, was underlain by thin layers of circular and longitudinal muscle fibers. The layer of subtegumental cells, stained red by Masson's trichrome, was very dense and ranged from 40 to 50 μm in thickness in some areas. Leukocytes and mesothelial cells usually were present in the lumen of the canal, frequently to its distal end. The rostellar hooks were fully developed and embedded in homogeneous tissue of the hook organ, which was confluent laterally with the adjacent distal cytoplasm. The hook organ and the distal cytoplasm took the same blue color when stained in Masson's trichrome. Lengths of the large and small rostellar hooks ranged from 202 to 210 μm and 149 to 151 μm, respectively ($\bar{x}$ = 207 and 149 μm). These measurements were within the range recorded from the strobilar stage of *Taenia polyacantha* from naturally infected arctic foxes: 200 to 214 μm and 142 to 157 μm, respectively (Rausch, 1959).

34 DAYS POSTEXPOSURE (1 ANIMAL). The six larvae studied were similar to the foregoing. The transverse grooves on the bladder surface were more regular and were only 24 to 49 μm apart. The lengths of the rostellar hooks fell within the range given above.

41 DAYS POSTEXPOSURE (1 ANIMAL). All but two of about 35 larvae obtained from this vole were fed to an arctic fox, in which developing strobilae were present when examined 14 days later. The two specimens studied, stained in acetic carmine, were very similar to those at 30 and 34 days postexposure, except that the forebody had reflexed, so that the scolex was directed anterolaterad.

57 DAYS POSTEXPOSURE (1 ANIMAL). Sixty-eight larvae were present, of which six were stained in acetic carmine and mounted entire, and eight were sectioned. The larvae were typical cysticerci, variable in shape but widest near the anterior end and somewhat pointed posteriorly. Fifty-four undistorted specimens in formalin ranged from 4 to 7 mm in length by 2.1 to 2.4 mm in greatest diameter ($\bar{x}$ = 5.2 by 2.3 mm). The forebody was invaginated into the anterior third of the bladder and was reflexed, with the scolex lying near the bladder wall anteriorly or anterolaterally. The slit-like opening of the invaginal canal on the anterior surface of the bladder was perpendicular to the plane of the reflexed forebody.

In microscopic details, these larvae did not appear to differ from those obtained 30 to 41 days postexposure. Vestiges of the prebulb were discernible in sections of the scolex, and the rostellar hooks were still enclosed within the hook organ. The posterior margin of the rostellar pad was very dense in some specimens, forming

a distinct boundary with the surrounding fibrous tissue of the rostellar sheath. Microtriches 1 to 2 μm in length were present on the distal cytoplasm of the bladder and on the upper part of that of the invaginal canal.

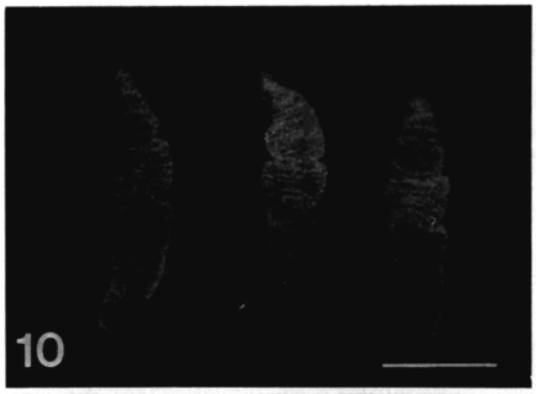
78 DAYS POSTEXPOSURE (1 ANIMAL). Thirty-six larvae and numerous nodules of amorphous tissue were present in the peritoneal cavity. The infection had evoked a severe inflammatory response in the vole, resulting in extensive adhesions of the viscera. The larvae were somewhat more elongate, compared with those obtained on the 57th day, and ranged up to 8.5 mm in length by 2 mm in greatest diameter. The walls of the bladder were transversely wrinkled anteriorly. In most of the specimens, the scolex had evaginated at the apex of the invaginal canal, so that the hooks were directed anteriad. In one, the forebody was almost completely evaginated, so that the scolex lay near the anterior surface of the bladder. The rostellar hooks often were retracted to the extent that only their tips extended beyond the anterior surface of the scolex. None of these specimens was sectioned.

103 DAYS POSTEXPOSURE (1 ANIMAL). Thirty-eight larvae were present. Serial, longitudinal sections were prepared of five, and nine were stained in acetic carmine and mounted entire. Twenty-four undistorted specimens in formalin ranged from 9 to 12.1 mm in length by 2.3 to 3 mm in greatest diameter ($\bar{x}$ = 11 by 2.6 mm). These appeared more or less tripartite : the anterior end, containing the invaginal canal, was usually somewhat smaller in diameter; next, making up less than half of the total length, was a zone greatest in diameter, with a much wrinkled surface; the posterior half of the body was more slender and comparatively smooth, with parallel, transverse grooves *(fig. 10)*. The body of the larva was now somewhat flattened dorsoventrally.

In sections, the fully everted scolex was seen to lie at the apex of the invaginal canal, and the rostellar hooks were directed anteriad. The canal had straightened, projections from its walls were no longer present, and long folds of tissue covered its orifice *(fig. 11)*. Its lumen was relatively wide and somewhat expanded distally,

FIGS. 10-15 and 17-19. *Taenia polyacantha:* Developmental characteristics and structure.

Fig. 10. Larval cestode, 103 days postexposure. Formalin preserved. Scale 5 mm. *Fig. 11.* Everted scolex and short invaginal canal in sagittal section of larval cestode 103 days postexposure. Gomori's reticulum stain. Scale 250 μm. *Fig. 12.* Fibers arising from the handle of the rostellar hook and fusing with those of the rostellar sac, 103 days postexposure. Gomori's reticulum stain. Scale 30 μm. *Fig. 13.* Fibers extending from the cytoplasmic membrane of the distal cytoplasm continuous with the reticulum of the parenchyma, 103 days postexposure. Gomori's reticulum stain. Scale 20 μm. *Fig. 14.* Degenerating eosinophils (arrow) in the invaginal canal, 14 days postexposure. Hematoxylin-eosin. Scale 50 μm. *Fig. 15.* Larval cestode 122 days after surgical implantation of 103-day-old specimens into a second rodent. Formalin preserved. Scale 10 mm. *Fig. 17.* Well developed larvae from a naturally infected northern vole. Formalin preserved. Scale 5 mm. *Fig. 18.* Larval cestode from a naturally infected northern vole, showing degeneration of the posterior part of the body, as compared with a normal specimen from the same animal. Formalin preserved. Scale 5 mm. *Fig. 19.* Rostellar hooks of *T. polyacantha* from a corsac fox collected near Hulunbeiheel, Inner Mongolia. Scale 400 μm.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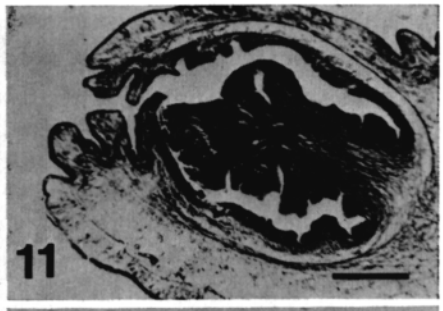
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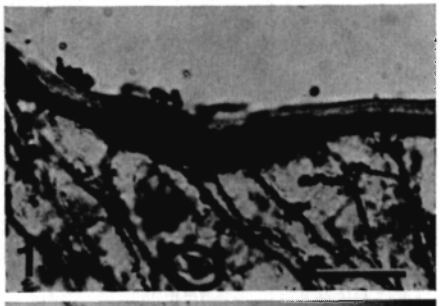
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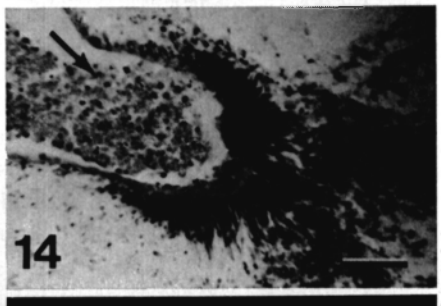
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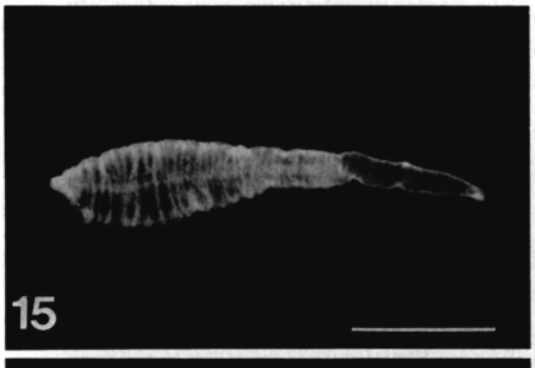
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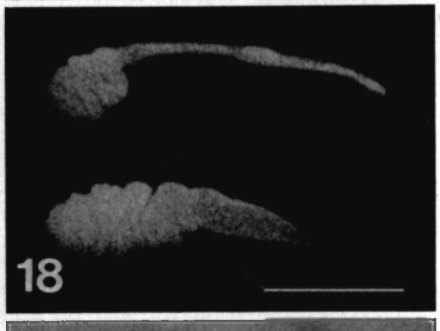
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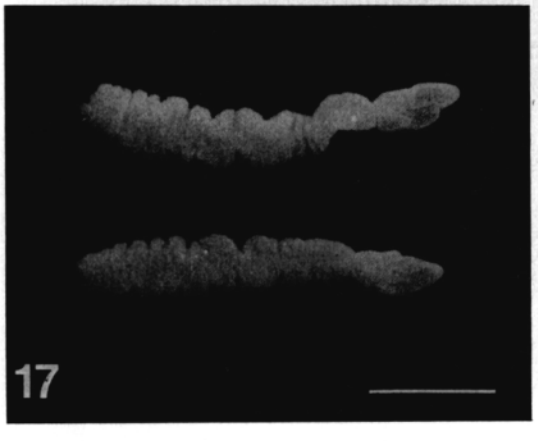
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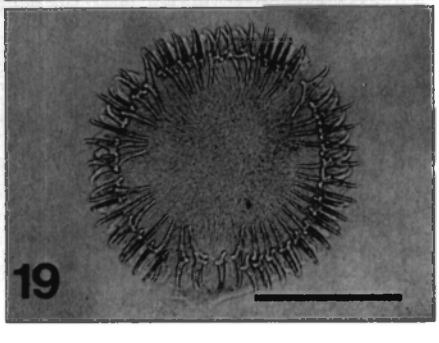
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corresponding to the position of the scolex; there, approximately at the level of the suckers, its maximal diameter was around 600 μm. The thicker, anterior portion of the larva was solid as a result of fusion of the forebody with the former wall of the bladder. At the juncture of the two types of tissue was a layer of longitudinal muscle fibers, adjacent medially to transverse fibers. The tissue enclosed by these muscle layers was fibrous, most dense at the central axis of the body, and lacking calcareous corpuscles. The posterior surface of the fibrous tissue, making up the anterior extent of the lumen of the bladder, was concave or funnel-shaped, with the apex directed anteriad. The posterior half of the body consisted of a true bladder, with thin walls composed of structures described above.

In the scolex, vestiges of the prebulb persisted, and the rostellar hooks remained enclosed at their base by the hook organ. With Gomori's reticulum stain, the rostellar pad was found to be bounded posteriorly by a cytoplasmic membrane. A distinct strand of parallel fibers, stained positively for reticulum, extended posteriad from the lateral root of the handle of each rostellar hook and fused with fibers of the rostellar sac *(fig. 12)*. The distal cytoplasm of the invaginal canal was only 4 to 6 μm in thickness. The subtegumental fibrous zone (Morseth, 1966), about 1 μm thick, was well defined and underlain by a thin circular layer of muscle; a subtegumental longitudinal muscle layer was not certainly identified. Gomori's reticulum stain revealed that the cytoplasmic membrane of the distal cytoplasm gave off fibers that were continuous with the reticulum of the parenchyma *(fig. 13)*. Calcareous corpuscles were numerous peripherally, in the subtegumental parenchyma that corresponded to the bladder wall in larvae at earlier phases of development, but were absent in the tissue enclosed by the deeper muscle layers. The

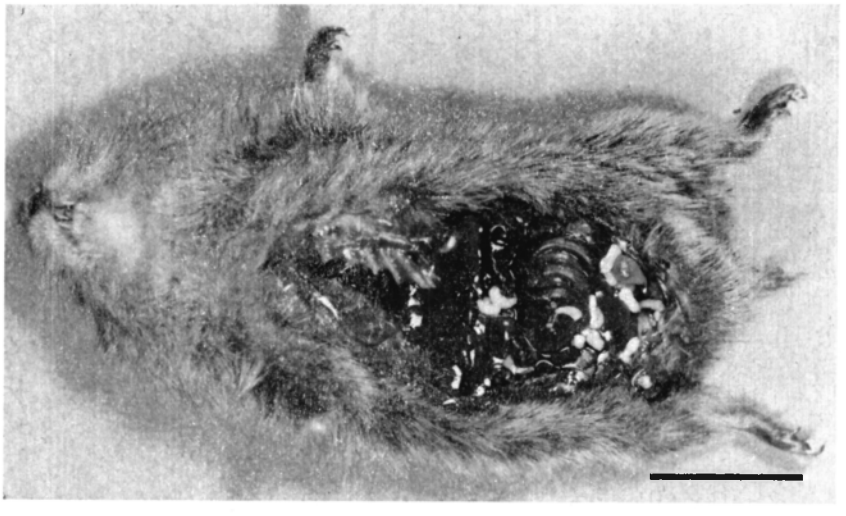

FIG. 16. — *Taenia polyacantha:* Fully developed larvae *in situ* in the peritonea cavity of a brown lemming collected VIII 53 at Point Barrow. Scale 30 mm.

posterior half of the body consisted of a true bladder, the structure of which was identical with that observed in younger specimens. The distal cytoplasm ranged from about 5 to 8 μm in thickness; its external membrane was examined in sections stained by various methods, but the presence of microtriches was not confirmed. The subtegumental nuclei were rounded and sparse immediately below the tegument. The bladder wall also contained abundant calcareous corpuscles. In thickness, the wall ranged from about 58 to 100 μm laterally, and increased to as much as 124 μm near the posterior end of the body. The inner surface of the bladder was lined by a limiting membrane less than 1 μm in thickness, best demonstrated by Gomori's reticulum stain.

108 DAYS POSTEXPOSURE (2 ANIMALS). In one vole, 11 larvae were present in the peritoneal cavity; in the second animal were 22 larvae as well as several plaque-like nodules of amorphous material. These specimens were similar to those obtained at 103 days postexposure.

La deuxième partie de cet article ainsi que la bibliographie paraîtront dans un prochain numéro des *Annales de Parasitologie*.