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

## Second part

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### Tissue Response in the Intermediate Host

When first observed in hepatic tissue, on the 5th day postexposure, the larvae were surrounded by accumulations of eosinophils. Sections of liver showed some degree of focal hepatitis, characterized by infiltration by neutrophils. Emergence of larvae into the peritoneal cavity on the 6th day postexposure was correlated with the presence of ascitic fluid and acute to diffuse peritonitis, indicated by a thin layer of neutrophils and small amounts of fibrin covering Glisson's capsule. Diffuse subcapsular hepatitis, probably related to the migration of the larvae, also was evident. In some animals that received large numbers of eggs, peritonitis was usually more generalized, and sometimes led to extensive adhesions of the abdominal viscera.

In appearance, the ascitic fluid was serous to turbid, and often was colored pinkish by the presence of erythrocytes. Smears stained by the Wright-Giemsa method exhibited numerous eosinophils, along with a few segmented granulocytes and numerous large, vacuolated mesothelial cells. The mesothelial cells occasionally had phagocytized eosinophilic or basophilic material, and some contained markedly degenerated eosinophils; degenerative changes also were evident in some mesothelial cells. Differential counts of leukocytes in stained smears of ascitic fluid, from the first to the 16th day postexposure, showed increased numbers of neutrophils from the 5th day onward and marked eosinophilia from the 9th day onward *(table I)*. The highest observed proportions of eosinophils (59 % and 69 %) were recorded respectively on the 14th and 16th days postexposure. In the cir-

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TABLE I. — Examples of differential counts of leukocytes in the blood and ascitic fluid of nine northern voles at intervals following experimental infection with 10 to 20 eggs each of *Taenia polyacantha* of St. Lawrence Island origin, compared with the means for five non-infected controls (C).

| Days post-exposure | Types of cells (%) | | | | | |
|---|---|---|---|---|---|---|
| | Baso-phil | Éosino-phil | Stab | Neutro-phil | Lympho-cyte | Monocyte |
| Blood: | | | | | | |
| C | 0 | 5 | 4 | 16 | 76 | 2 |
| 1 | 0 | 1 | 0 | 7 | 90 | 2 |
| 3 | 0 | 0 | 0 | 0 | 99 | 1 |
| 5 | 0 | 1 | 0 | 59 | 39 | 1 |
| 7 | 0 | 2 | 4 | 37 | 56 | 1 |
| 9 | 0 | 1 | 1 | 5 | 92 | 1 |
| 11 | 1 | 17 | 0 | 33 | 49 | 0 |
| 12 | 1 | 19 | 12 | 40 | 24 | 4 |
| 14 | 0 | 8 | 3 | 33 | 56 | 0 |
| 16 | 5 | 18 | 0 | 12 | 61 | 4 |
| Ascitic fluid: | | | | | | |
| C | (Mainly mesothelial cells; occasional neutrophils, lymphocytes) | | | | | |
| 1-3 | (Mainly mesothelial cells; occasional neutrophils, lymphocytes) | | | | | |
| 5 | 0 | 1 | 0 | 82 | 18 | 0 |
| 7 | 0 | 2 | 4 | 64 | 17 | 9 |
| 9 | 6 | 29 | 2 | 60 | 3 | 0 |
| 11 | 1 | 43 | 20 | 22 | 7 | 5 |
| 12 | 0 | 15 | 1 | 72 | 11 | 1 |
| 14 | 5 | 52 | 3 | 30 | 5 | 5 |
| 16 | 1 | 69 | 0 | 13 | 6 | 11 |

culating blood of the same animals, eosinophils as a proportion of total leukocytes showed a marked increase by the 11th day postexposure and persisted at a high level at least to the 16th day.

The bladders within the peritoneal cavity were covered by a thin, uniform layer of eosinophils by the 9th day postexposure. As the invaginal canal developed, its lumen was filled by eosinophils. These, by the 14th day postexposure, usually appeared to have degenerated *(fig. 14)*, and they often formed an adherent mass that protruded from the orifice of the canal, beyond the anterior surface of the bladder. After about the 16th day postexposure, eosinophils were not numerous within the lumen, and by the 18th day, plasma cells and mesothelial cells were intermixed. By the time the larvae were fully grown, mesothelial cells predominated within the invaginal canal.

Ascitic fluid and blood serum from experimentally infected voles examined on the 7th and 14th days postexposure were compared for protein content by means of acrylamide gel electrophoresis. Both the fluid and the serum gave identical patterns of bands, and differed from serum of non-infected voles in the apparent absence of alpha and gamma globulins.

### Surgical Implantation of Larvae

When fully developed larvae were transferred surgically from the original intermediate host to the peritoneal cavity of another rodent, whether or not conspecific, typically the larvae not only survived but increased in size and underwent morphological modifications as well. In one case, three of thirty-eight larvae removed from a northern vole 103 days postexposure were implanted into a 36-day-old vole, which was examined 122 days later. The two larvae then recovered were 30 and 31 mm in length by 5 mm in width, were distinctly flattened, and exhibited well defined pseudosegmentation and reduction in size of bladder. They had attained a size approximately twice that of any recorded from primary infections in the laboratory or any from natural infections. The relationships of the scolex and invaginal canal appeared to be unchanged *(fig. 15)*.

Degeneration of the posterior part of the body eventually occurred in implanted larvae. In specimens from a brown lemming 45 days following transfer from a naturally infected northern vole, the posterior part of the body was necrotic, with focal areas of calcification. The affected part was enclosed by a layer of loose connective tissue 40 to 100 μm in thickness, of host origin. Fibroblasts were abundant in that tissue, but leukocytes were not observed. The area containing the scolex was not affected. Such larvae usually survived and grew when the necrotic tissue was amputated and they were implanted a second time. We observed comparable degeneration rarely in specimens from naturally infected rodents.

### Natural Infections in the Intermediate Host

Well developed larvae, apparently infective, were obtained from numerous northern voles collected on St. Lawrence Island and brown lemmings collected near Point Barrow *(fig. 16)*. The prevalence in both was generally low and variable *(table II)*. For more than six thousand northern voles examined on St. Lawrence Island between 1950 and 1987, the overall rate of infection was less than one per cent. In at least one-fourth of these cases, some larvae had degenerated at an early phase of development. The larval *T. polyacantha* was found in the brown lemming only in 1953 (ten infected of 196); none was found in two other years of sampling (1949, 139 animals examined; 1957, 86 examined). That rodent undergoes high-amplitude fluctuations in numerical density, with a periodicity of three to four years (Pitelka, 1973). In the year when the larvae were present in the lemmings, the density of the population had remained relatively high since the preceding summer (Thompson, 1955 *a*, 1955 *b*).

Of the 33 voles found to be infected during the period 1980-1987, numbers of larvae were recorded for 25. The range in individual animals was 2 to 65 ($\bar{x} = 26$). Similarly, in the ten brown lemmings collected in 1953, numbers of larvae ranged from 2 to 63 ($\bar{x} = 31$). In 12 experimentally infected northern voles that had received five eggs each, numbers of larvae ranged from 16 to 68 ($\bar{x} = 35$). These findings indicate that numbers of normal larvae derived from single embryos

TABLE II. — Numbers of northern voles on St. Lawrence Island and brown lemmings on the arctic coast of Alaska naturally infected by *Taenia polyacantha*, 1949 to 1987.

| Host and Locality | 1949-1960 | | | 1961-1970 | | | 1980-1987 | | |
|---|---|---|---|---|---|---|---|---|---|
| | *n* | Infected | (%) | *n* | Infected | (%) | *n* | Infected | (%) |
| Northern voles- | | | | | | | | | |
| St. Lawrence Island: | | | | | | | | | |
| Gambell and vicinity | 2,366 | 2 | (0.1) | 1,467 | 3 | (0.1) | — | — | — |
| Savoonga and vicinity | 534 | 3 | (0.6) | — | — | — | 1,164 | 33 | (2.8) |
| Other areas | 821 | 12 | (1.5) | 156 | 6 | (3.8) | — | — | — |
| Brown lemmings- | | | | | | | | | |
| arctic coast: | | | | | | | | | |
| Barrow and vicinity | 421 | 10 | (2.4) | — | — | — | — | — | — |

ranged from 3 to 14 ($\bar{x} = 7$). Based on numerical similarities, we judge that the naturally infected animals had ingested one to five eggs each.

CHARACTERISTICS OF LARVAE FROM NATURALLY INFECTED RODENTS. All of the normally developed larvae of *T. polyacantha* that we found in naturally infected voles and lemmings had attained the size and conformation of those not less than 30 to 40 days old, as compared with results obtained in experimentally infected rodents, but early infections might have been overlooked. In infections judged to have been more than 100 days in duration, the larvae were markedly flattened and pseudosegmentation was strongly defined. The size of the bladder decreased with age. Fifty-three larvae from the peritoneal cavity of a brown lemming collected near Point Barrow on 15 VIII 53 exemplified age-related modifications. In these specimens, which were about 15 mm in length, the bladder made up the posterior one-third of the body-length, and the diameter of its lumen was reduced. The distinctly flattened body exhibited well defined pseudosegmentation anteriorly, but the surface of the bladder was smooth. As seen in median sagittal sections, the relationships of the scolex and invaginal canal did not differ from those observed in larvae at 103 days postexposure. The pseudosegments appeared as extensions from the dorsal and ventral surfaces, usually 100 to 200 μm in length, with rounded tips. The distal cytoplasm was about 7 μm in thickness anteriorly, increasing to 12 to 22 μm posteriad. Microtriches were not discerned. The combined subtegumental layers of circular and longitudinal muscle fibers were only 2 to 3 μm in thickness. The subtegumental parenchyma was thin anteriorly at the level of the invaginal canal, but ranged from about 300 to 350 μm in thickness over the greater part of the body; from about the level of the anterior end of the bladder, its thickness decreased posteriad to about 50 μm. The parenchyma contained numerous calcareous corpuscles. In transverse section, the body exhibited a central core of

fibrous tissue, more or less rectangular in transverse section, which was separated from the parenchyma dorsally and ventrally by a layer of longitudinal muscle fibers up to about 70 μm in thickness, and immediately below, a layer of transverse fibers of similar thickness. The layers of longitudinal fibers arose near the apex of the invaginal canal, diverged and took a nearly parallel course through most of the length of the body. Near the level of the anterior end of the bladder, they converged and extended posteriad along its luminal surface. The layers of transverse fibers took a similar course, but decreased in thickness posteriad, disappearing near the anterior end of the bladder. The dorsal and ventral layers of muscle fibers did not extend around the lateral margins of the body, where longitudinal excretory canals were present. The tissue enclosed within the muscle layers contained abundant fibers which, as seen in transverse section, had a concentric arrangement and were most dense at the center of the body. Calcareous corpuscles were not present within this fibrous tissue.

No further age-related modifications were noted in the naturally infected animals, except for increased size of the larvae. In the most advanced infections, judged to have been of near-maximum duration (as limited by the life-span of the host), the larvae were larger than those obtained experimentally at 103 days postexposure. As an example, an adult female northern vole collected at Savoonga on 7 VI 82 had 41 larvae in the peritoneal cavity. Her large size (total length 194 mm) indicated that this animal probably had survived two winters and was approaching an age of two years. The larvae were comparatively long and slender *(fig. 17)*, from 15 to 18.5 mm in length by 2 to 3 mm in maximal width ($\bar{x}$ = 16.6 by 2.5 mm). They were dorsoventrally flattened throughout, pseudosegmentation extended over about the anterior two-thirds of the body, and the bladder made up somewhat less than one-third of the total length. In infections of possibly greater duration, the larvae were no larger, but exhibited further reduction in the size of the bladder.

Rounded nodules of an amorphous, eosinophilic material representing larvae that had degenerated at a comparatively early point in development often were found in the peritoneal cavity of naturally infected rodents. In 12 voles for which numbers were recorded, four contained one to four degenerative larvae only; three had 11 to 47 infective larvae with eight to 11 nodules; and five harbored two to 52 infective larvae only. In infections of long duration, degenerative changes affected the posterior end of the body of some larvae. Such degeneration was exemplified in four of 16 specimens from a vole collected near Savoonga on 9 VI 87, wherein necrosis involved up to 13 mm of their length, with shrinkage in width to less than 1 mm *(fig. 18)*. Similar changes occurred in infective larvae that had been transferred surgically.

### The Strobilar Stage of « Taenia polyacantha »

The time required for the larval cestode to become infective for the final host was not determined precisely, but we judge that infectivity may coincide

with full development of the rostellar hooks, about 30 days postexposure. Larvae 41 days old, from a vole, were infective for a captive-reared arctic fox. The oldest known-age larvae used to infect a canid were obtained from a brown lemming 103 days postexposure.

We found that *T. polyacantha* typically localized anteriorly in the small intestine of the definitive host. The time required for the cestodes to produce infective eggs was approximately two months. In cestodes from an experimentally infected fox at 45 days postexposure, the uterus was well developed but did not yet contain eggs. A 20-day-old dog that received five larvae from a naturally infected vole harbored four fully developed cestodes when autopsied on the 66th day postexposure. Eggs from the gravid segments were infective for rodents. In that dog, the cestodes were attached between 82 cm and 119 cm below the pylorus.

The maximal survival-time of the strobilar stage is certainly greater than two years. One captive-reared arctic fox that had received six larvae from a naturally infected vole still had a single cestode when autopsied 22.1 months later. Another, which died of natural causes 24.1 months after infection with 12 larvae from an experimentally infected vole, still harbored three destrobilate cestodes at the time of death. The longest duration known to us was in a naturally infected arctic fox captured as a recently weaned pup at a den on St. Lawrence Island in August 1955 and held in captivity for 34 months. At autopsy, its intestine contained several strobilae of *T. polyacantha* that had been acquired naturally sometime prior to its capture.

Our findings in naturally infected foxes trapped during winter have indicated that most of the cestodes shed the greater part of the strobila in autumn, perhaps coincident with the seasonal change in diet from living prey to stored food and carrion (see Fay and Stephenson, 1988). Destrobilate specimens were usually 10 to 15 mm long by 2 to 2.5 mm in width posteriorly, often appearing wedge-shaped, with a flat strobila consisting of 50 to 70 short segments. Destrobilate specimens were not usually observed in captive foxes that received a standard daily ration, but in the case mentioned above, of the fox that had died of natural causes, the cestodes had destrobilated spontaneously, not more than 24 hours before the death of the host. Cestodes acquired by foxes in spring were readily distinguishable by a more slender, rounded strobila consisting of few segments; the presence of the rounded, terminal segment indicated that destrobilization had not taken place.

The occurrence of *T. polyacantha* in canids other than foxes is rare. In Alaska, we found it in four (6 %) of 58 dogs autopsied within the known geographic range of the cestode. Infected dogs were found on St. Lawrence Island, where the northern vole is the only known intermediate host, and on Nunivak Island, where the brown lemming is the only arvicolid present. In each of two dogs, three cestodes were present. *T. polyacantha* also occurs rarely in the wolf, *Canis lupus* L., in Eurasia (Savel'ev, 1972; Panin and Lavrov, 1962).

INFRASPECIFIC TAXA OF « T. POLYACANTHA »

*T. polyacantha* is a characteristic cestode of the arctic fox in the tundra of North America, on the mainland and adjacent islands, wherever suitable intermediate hosts (northern vole, brown lemming) are present. Less commonly, it is found in the red fox in the continental tundra and on Nunivak Island, but its natural occurrence has not been recorded in any host south of the zone of tundra in North America. In Eurasia, published records from numerous surveys indicate that the geographic range of *T. polyacantha* encompasses much of the continent, from Europe to Bering Strait in the north, and southward into Middle Asia. As in North America, the life cycle in the Eurasian tundra involves mainly the arctic fox and arvicoline rodents (*Microtus* spp. and brown lemming). To the south, the cestode occurs commonly in the red fox, and the corsac fox, *Vulpes corsac* (L.), serves as final host in the arid regions of Middle Asia, at least as far as the Nei Mongol Autonomous Region in northern China. In Europe and elsewhere at latitudes south of the zone of tundra, rodents of the families Sciuridae, Cricetidae, and Muridae, as well as Arvicolidae, serve as intermediate hosts (Wandeler and Hörning, 1972; Wiger *et al.*, 1974; Murai, 1982).

In the Nearctic, the larval stage of *T. polyacantha* has been found only in the peritoneal cavity of the intermediate host; in Europe, it often develops in the pleural cavities of rodents and sometimes attains remarkably large size as compared with any specimens observed in North America (see Šlais, 1973). In addition to apparent biological distinctions between the European and North American cestodes, corresponding differences are obvious in the numbers and dimensions of the rostellar hooks. In the original description of *T. polyacantha*, Leuckart (1856) stated that 62 rostellar hooks were present. Subsequently, ranges in numbers have been reported from various geographic regions: Germany, 58 to 66 (Schmidt, 1961); Norway, 58 to 62 (Wiger *et al.*, 1974); Hungary, 55 to 66 (Murai, 1982); Bulgaria, 58 to 68 (Genov, 1984); and Kazakhstan, Middle Asia, and the Caucasus, 60 to 64 (Voronina, 1971). We have a single specimen from a corsac fox captured near Hulunbeiheel, Nei Mongol Autonomous Region (leg. Dr Tang Chong-ti), that has 74 hooks *(fig. 19)*. Cestodes from the Eurasian tundra, like those in the Nearctic, have a smaller number of rostellar hooks: specimens from three brown lemmings and a narrow-skulled vole, *Microtus gregalis major* Ognev, collected in the Nenets National Region, to the west of the Iamal Peninsula, USSR, had 46 to 49 hooks (Voronina, 1971); from a brown lemming trapped on the southern shore of Chaunsk Gulf, near the arctic coast of northeastern Siberia (leg. Dr L. V. Smirnova), 50 hooks. Arctic foxes collected on the Chaunsk River and in the valley of the Anadyr', farther to the east, harbored cestodes on which the description of *Monordotaenia alopexi* Obushenkov, 1983 was based; the form and size of the hooks of the single row present indicate that the cestodes were specimens of *T. polyacantha* from which the row of large hooks had been lost. As observed already by Leuckart (1856, footnote, p. 68) and by Voronina (1971), the large hooks often become detached from the rostellum after the death of the host. The specimens described

by Obushenkov (1983) had 20 to 24 small hooks, indicating a range of 40 to 48 in total. In Alaskan specimens, the range in numbers of hooks has been reported as 44 to 48 and 44 to 50 (Schiller, 1953; Rausch, 1959).

The lengths of the rostellar hooks of *T. polyacantha* vary within limits typical of cestodes of the genus *Taenia*, but in specimens from the zone of tundra, hooks are of greater average length than are those to the south *(table III)*. The small hooks of the southern form appear to be both relatively and absolutely shorter than those of the form from the holarctic tundra. Probably, mean lengths of both the large and small hooks will be found to differ significantly between the two forms. Two morphological types of *T. polyacantha*, distinguished primarily by differences in numbers and lengths of rostellar hooks, are thus recognizable. The data further indicate that dissimilarities exist in localization in the intermediate host and in host-specificity.

TABLE III. — Lengths of rostellar hooks of *Taenia polyacantha*, in relation to geographical distribution.

| Geographical location | Large hooks (μm) | | Small hooks (μm) | | Source |
|---|---|---|---|---|---|
| | Range | Mean | Range | Mean | |
| Holarctic tundra | | | | | |
| | 200-212 | — | 175-182 | — | Voronina, 1971 |
| | - | — | 144-160 | 153 | Obushenkov, 1983 |
| | 200-217 | 211 | 144-151 | 147 | Chaunsk Gulf (orig.) |
| | 210 | — | 140-155 | — | Schiller, 1953 |
| | 200-214 | 210 | [1]142-157 | 147 | Rausch, 1959 |
| | 207-234* | 223 | 151-163 | 154 | St. Lawrence Island (orig.) |
| Eurasia: south of zone of tundra | | | | | |
| | 184-196 | — | 122-133 | — | Schmidt, 1961 |
| | 186-198 | — | 124-148 | — | Wiger *et al.*, 1974 |
| | 178-221 | — | 120-143 | — | Murai, 1982 |
| | 196-218 | — | 120-138 | — | Genov, 1984 |
| | 180-183 | — | 112-114 | — | Inner Mongolia (orig.) |

* Based on 100 each of large and small hooks.

We propose that the taxon having a mean number of rostellar hooks greater than 55 and a geographic distribution south of the Eurasian tundra be recognized at the infraspecific level as *Taenia polyacantha polyacantha*, Leuckart, 1856, and that the taxon having a mean number of hooks less than 50, occurring throughout the holarctic tundra (excluding Greenland and some of the high-arctic islands, where an intermediate host apparently is not present), be designated *T. polyacantha arctica* ssp. nov. Representative specimens of the latter have been deposited in the Helminthological Collection of the United States National Museum: Holotype,

No. 38398, from an arctic fox, *Alopex lagopus* (L.), collected on St. Lawrence Island (leg. R. L. Rausch); Paratype, No. 79864, from a northern vole, *Microtus oeconomus* (Pallas), collected near Savoonga, St. Lawrence Island (leg. R. L. Rausch). We herewith place *Monordolaenia alopexi*, Obushenkov, 1983 in synonymy with *Taenia polyacantha arctica*.

## Discussion

Shortly after the oncosphere of *T. polyacantha arctica* localizes in the liver of the intermediate host, the primary vesicle develops, and its passage to the peritoneal cavity by the sixth day postexposure coincides with the production of secondary vesicles that soon become detached and develop independently. In *T. polyacantha polyacantha*, the locus of initial development includes the lungs as well as the liver. Asexual multiplication in *T. polyacantha* involves a process of early proliferation that has not been described in any other species of the genus *Taenia*. In other species in which asexual multiplication occurs, a single vesicle arising from the oncosphere ultimately becomes polycephalic or, as in *T. crassiceps* (Zeder, 1800), new vesicles are produced by budding from the bladder wall.

After the dissociation of the secondary vesicles on the ninth or tenth day postexposure, the pattern of development of *T. polyacantha*, leading to the formation of a typical cysticercus, is essentially like that described by Gläser (1909) and Bilqees and Freeman (1969) for *T. crassiceps*. The cysticercus of *T. p. arctica* seems to become infective coincident with or soon following attainment of full development of the rostellar hooks, approximately 30 days postexposure. At an age about 60 days, the cysticercus begins a process of secondary growth and reorganization that results in a more complex type of larva. We were able to enhance those changes by surgically transferring fully developed larvae from the original host to the peritoneal cavity of a second animal.

Initially, we considered that the marked changes occurring in the transferred larvae might be related to a lack of immunity in the recipient animal, but a greater degree of modification in some from naturally infected rodents has been reported. Šlais (1973) described a specimen of the larval *T. p. polyacantha* 70 mm in length and 10 mm in width from the pleural cavity of a squirrel, *Sciurus vulgaris* L. A second specimen, from a wood mouse, *Apodemus sylvaticus* L., a rodent smaller than either the northern vole or the brown lemming, was longer than any of those observed by us (see Šlais, 1973, *fig. 30*). Specimens of *T. p. arctica* obtained by us from experimentally infected muskrats did not differ in size or form from those in voles. The physical size of the intermediate host did not appear to influence the ultimate size of the larval cestode. Šlais (1973) considered that the modifications in the form of the larval *T. polyacantha* represented abnormal growth in over-age specimens. Sections of our material showed that the post-cysticercal modifications led to acquisition of a strobila-like structure by the forebody. Whereas the ingestion of unmodified larvae (cysticerci) of *T. p. arctica* results in the deve-

lopment of strobilae with infective eggs after about 60 days, those that exhibit late modification may develop more quickly in the final host. Possibly, modified larvae ingested by foxes in late autumn lose the vestigial bladder and persist unchanged until the following spring, resembling specimens that have destrobilated. Further investigation is required to define more adequately the adaptive significance of the postoncospheral peculiarities of *T. polyacantha*.

As Šlais (1973), Murai (1982), and others have noted, the most extremely modified larvae of *T. polyacantha* are practically indistinguishable (except for characteristics of rostellar hooks) from those of *Taenia martis martis*, which occurs widely in western Eurasia. Rodents of several species serve as intermediate hosts of *T. m. martis*, and the larvae develop only in their pleural cavities. From the findings of Shakhmatova (1963, 1964) in experimentally infected rodents, we consider that the sequence of changes in form, beginning a few days postexposure in the larval *T. intermedia* Rud., 1810 (= *T. m. martis*) and leading initially to the formation of a typical cysticercus, closely parallels that of the larval *T. p. arctica* as described herein. Shakhmatova saw no indication of early budding, but did not examine any animals before seven days postexposure. By the 100th day postexposure, marked changes had taken place in the form of the larval *T. m. martis* (Shakhmatova, 1964, *fig. 2*). As we determined from study of material from the taiga vole, *Microtus xanthognathus* (Leach), the larval stage of *T. m. americana* Wahl, 1967 also attains the form of a cysticercus before undergoing late modification. We have a single specimen from the pleural cavity of a red squirrel, *Tamiasciurus hudsonicus* (Erxleben), collected at Fairview, Alberta (leg. K. Dies), that exhibits the large size (ca. 65 mm in length) and marginal folding like those figured for the larval *T. m. martis*.

Since we never found two or more cohorts of the larval *T. p. arctica* in a single rodent, we presume that the primary infection induces an immune response that prevents suprainfection. We observed in naturally and experimentally infected rodents that the larval stage of *T. p. arctica* frequently co-occurs with that of other taeniids. In the 1,164 voles examined during 1980-1987 on St. Lawrence Island, both *T. p. arctica* and *Echinococcus multilocularis*, Leuckart, 1863, were found together in twelve (1 % of total animals or 36 % of those harboring *T. p. arctica*). A single lemming was infected concurrently with *T. p. arctica* and *T. crassiceps*. In muskrats infected in the laboratory, we obtained concurrent infections of *T. p. arctica*, *E. multilocularis*, and *T. crassiceps* in two. The findings suggest that cross-immunity does not exist among those larval cestodes.

Judging from the relationship of numbers of larvae to numbers of eggs administered to experimentally infected rodents, we consider that natural infections in voles and lemmings by *T. p. arctica* usually result from ingestion of five eggs or less. More severe infections may be debilitating or even fatal in such rodents, because of the inflammatory response evoked by migration of larvae from the liver to the peritoneal cavity. We have observed that infections involving around 100 larvae in northern voles are characterized by severe ascites and formation of extensive adhesions of the viscera, which may be sufficient to hamper locomotion.

Individuals so affected are likely to be more vulnerable to predation than are animals with few or no larvae. Wiger *et al.* (1974) reported the finding of 224 larvae of *T. polyacantha* in a red-backed vole, *Clethrionomys glareolus* (Schreber), in Norway, 218 of which were in the peritoneal cavity and six in the pleural cavities. With reference to the same animal, Tenora *et al.* (1979, p. 179) stated that « ...the liver and diaphragm were completely adhered, and the stomach, duodenum and spleen were enveloped in connective tissue. » They also remarked that other animals of the same series, with numbers of larvae ranging from only five to 26 each, exhibited ascites and some degree of adhesions. That we did not observe residual effects of peritonitis in any of the infected voles examined on St. Lawrence Island suggests either that the larval *T. p. polyacantha* is more pathogenic, or that voles that ingested larger numbers of eggs of *T. p. arctica* did not survive.

The different geographic distributions of the two forms of *Taenia polyacantha* have come about through factors that have influenced dispersals, and ultimately, host-specificities. Published records and our observations indicate that few species of rodents serve as intermediate host of *T. p. arctica*. On St. Lawrence Island, the mammalian fauna includes the northern vole, the northern red-backed vole, a varying lemming, *Dicrostonyx exsul* Allen, and the arctic ground squirrel, *Spermophilus (Citellus) parryi* (Richardson). All but the varying lemming have been numerically well represented in our surveys there (Rausch, 1953; Fay, 1973), but only the northern vole has been found to be infected. On the mainland, the larval cestode has been found only in the northern vole and the brown lemming. In North America, the geographic range of *T. p. arctica* evidently coincides with that of another cestode, *Echinococcus multilocularis*, which in Eurasia has a distribution encompassing both that of *T. p. arctica* in the north and that of *T. p. polyacantha* south of the zone of tundra. The typical intermediate hosts of *E. multilocularis*, as well, are the northern vole and the brown lemming. We have established experimentally that rodents of several species that have extensive geographic ranges to the south of the tundra also can serve as intermediate hosts of *E. multilocularis*; yet that cestode until very recently occurred only in the zone of tundra. Its dispersal to and establishment in central North America obviously have depended on the involvement of rodents of species not present in the arctic regions from which it spread. The same result might be expected if *T. p. arctica* were introduced to the south of the zone of taiga. By analogy, we consider that *T. p. arctica* and *E. multilocularis* must have had similar distributional histories in the Nearctic, whereas the extensive ranges of *T. p. polyacantha* and *E. multilocularis* in Eurasia are attributable to different factors.

In the tundra, the numerical density of rodents appears to influence the transmission of taeniid cestodes, in that carnivores serving as final hosts depend on the most available prey, and a high frequency of predator-prey interaction favors completion of the cycles of the cestodes. In the vicinity of Point Barrow, where our data on the occurrence of *T. polyacantha* were obtained, we collected rodents of only two species, the brown lemming and a varying lemming, *Dicrostonyx rubricatus* (Richardson), which was uncommon during the time of our work. The

brown lemming alone was found to be infected, and it was the primary prey of foxes in that region. The frequency of occurrence of the larval *T. polyacantha* in the brown lemming was comparatively high (5 %) in the summer of 1953, a peak year in the population cycle, following a high pre-peak density in 1952 (Thompson, 1955*a*, 1955*b*). We consider that the greater duration of interaction between predator and prey in 1952-1953 contributed to the relatively high prevalence of the cestode as compared with the peak year 1949 and the post-peak year of 1957, when no infected lemmings were obtained (see Rausch, 1950; Pitelka, 1973). The pattern was identical for two other taeniid cestodes: *Taenia crassiceps*, which has the same hosts as *T. polyacantha*, and *Taenia mustelae* (Gmelin, 1790), of which the mouse weasel, *Mustela nivalis* L., serves as final host. *T. crassiceps* and *T. mustelae* were found in nine (4.6 %) and eight (4 %), respectively, of lemmings examined in 1953. The larval *T. mustelae* was recorded from a single lemming (1 %) in 1949; neither was recorded in 1957.

The range in rates of infection by the larval *T. p. polyacantha* was somewhat greater than that recorded for *T. p. arctica* in Alaska, as exemplified by the following data from surveys in Europe: in Hungary, 0.03 % of 298 muskrats, 0.36 % of 561 *Clethrionomys glareolus*, and 0.07 % of 2610 *Microtus arvalis* Pallas (Murai, 1982); in Czechoslovakia, 1.8 % of *Pitymys subterraneus* Selys-Longchamps (Murai and Mészáros, 1984); in Germany, 1.9 % of 105 *M. arvalis* (Schmidt, 1961); in Bulgaria, 3.1 % of *C. glareolus* and 1.43 % of *M. arvalis* (Genov, 1984); and in Norway, 12.3 % of 65 *C. glareolus* (Wiger *et al.*, 1974).

Reported rates of infection in the red fox in western Eurasia were: in Mordovia, 35 % of 51 foxes (Machinskii and Semov, 1966); in Austria, 22 % of 100 (Hinaidy, 1971); in Germany, 7.7 % of 3,573 foxes examined between 1975 and 1980 (Loos-Frank and Zeyle, 1982); and in France, 27 % of 19 animals (Petavy and Deblock, 1980). The rates are low, compared to those of *T. p. arctica* (80-90 %) typical of the arctic fox in Alaska. The intensity of infection in the red fox in Europe also appears to be low. Machinskii and Semov (1966), for example, found only one to eight cestodes in foxes in Mordovia. Infections consisting of more than 100 strobilae of *T. p. arctica* were not unusual on St. Lawrence Island, where the maximum number recorded was 642 identified specimens plus 80 *Taenia* sp. not identified because the rostellar hooks had been lost. The apparent disparities in rates and intensities of infection in foxes are difficult to explain. The much greater diversity of prey-species in Europe, and their relatively low numerical densities, may be important factors. The prolonged survival of the strobilar stage of *T. p. arctica*, by its cumulative effect, should result in an increased rate of infection with increased age of the final host; hence, the time of year of sampling could influence observed rates. On St. Lawrence Island, we found that the rate of infection in young foxes nearly doubled from August to December of their first year of life, and low-amplitude seasonal changes occurred thereafter, with a trough in spring and a peak in autumn (Rausch, Fay, and Williamson, manuscript), which suggests that the cestodes are mainly acquired by foxes during summer and the snow-free months of autumn.

Since *T. p. arctica* destrobilates in autumn or early winter, the dispersal of eggs must take place mainly during the warmer months. The eggs probably remain infective for some time beneath the snow, where they would be available for ingestion by voles and lemmings. Because we have not found any newly acquired infections in spring, however, we suspect that the eggs are not so cold-resistant as are those of *E. multilocularis* (see Schiller, 1955). Newly acquired infections of that cestode are frequent in voles collected as the snow disappears on St. Lawrence Island at the end of May. The arctic foxes begin to prey on voles as soon as much of the snow has melted in the lowlands. For example, numerous, recently acquired strobilae of *T. polyacantha*, up to about 15 mm in length, were found in the intestine of two arctic foxes collected on 27 V 86. If, as experimental infections of foxes indicate, 50 to 60 days are required for the cestodes to produce gravid segments, the dispersal of eggs would begin by early August, when the population of voles consists mainly of young-of-the-year. Such young animals would contain infective larvae after about 30-40 days postinfection, and would provide a source of cestodes for foxes the following spring.

The high degree of phenotypic uniformity of *T. p. arctica* throughout its holarctic range is indicative of gene-flow that probably is mediated by the long survival-time of the strobilar stage, coupled with extensive wandering of arctic foxes during the colder months of the year. Winter movements of individual foxes, presumably in search of food, can amount to more than 1,000 km from land on the pack-ice, or southward into the taiga (Ognev, 1931; Braestrup, 1941; Chapskii, 1946; Rutilevskii and Uspenskii, 1957; MacPherson, 1968; Rausch, 1968; Wrigley and Hatch, 1976). We found *T. polyacantha* in two arctic foxes that were killed on the ice island T-3 when it was drifting in the Arctic Ocean at about lat. 73°39′ N by long. 161°40′ W and lat. 74°32′ N by long. 162°50′ W. The primary stimulus for long migrations by foxes seems to be the unavailability of arvicoline rodents in winter, but even in years when rodents are moderately abundant, some foxes move hundreds of kilometers from their summer habitat (Eberhardt and Hanson, 1978). Further information concerning the strobilar stage of *T. polyacantha* and other helminths in arctic foxes will be reported in a subsequent publication.

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