THE BIOLOGY, PATHOGENICITY AND OCCURRENCE OF *ECHINURIA UNCINATA* (RUDOLPHI, 1819), SOLOVIEV, 1912 (SPIRURIDA, NEMATODA) AT DELTA, MANITOBA

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ABSTRACT

Infective, third stage E. uncinata juveniles were found in Daphnia pulex, D. magna and Simocephalus vetulus collected from the Field Station Pond at Delta. The parasites were present in the pond from late May to early November, and reached a peak abundance of 108 parasites per 100 D. magna in early August.

Laboratory experiments with Daphnia pulex, D. magna, Simocephalus vetulus, Ceriodaphnia reticulata, C. acanthina, Moina macrocopa, Eurycercus lamellatus, Gammarus lacustris, Hyalella azteca, Lynceus brachyurus and Chirocephalopsis bundyi demonstrated that these Delta crustaceans become infected when exposed to E. uncinata eggs. Insect larvae, ostracods, copepods and the cladocerans Alona sp. and Scapholeberis sp. did not become infected.

E. uncinata developed to third stage in Daphnia pulex and D. magna in 30 days at 15°C. and in 10 days at 20 - 24°C.

Eggs of E. uncinata perished when frozen for 85 days but survived the same period when dried on filter paper at 20 - 24°C.

In penned Delta Mallards, E. uncinata moulted from fourth stage juveniles to adults after 20 days; male worms were sexually mature after 30 days and females were ovipositing after 40 days.

E. uncinata grew faster and were more successful in one-week old Delta Mallards than in two and three-month old birds. This nematode easily infected mallards, pintails, gadwalls, lesser scaup, common eiders and domestic geese, but not shovellers, blue-winged teal, redheads, ruddy ducks and coots.

In the definitive host, E. uncinata burrowed under the mucosa of the isthmus, the junction of the proventriculus and gizzard, where granulomas were formed. The number of granulomas was correlated with the number of parasites. E. uncinata survived all winter in mallards kept at the Delta Waterfowl Research Station.

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INTRODUCTION

The biology of the parasite nematode, Echinuria uncinata (Rudolphi, 1819), Soloviev, 1912, and its effects on waterfowl populations have been studied in the old world by several European and Russian researchers. Little information on this nematode appears in North American literature. Unpublished data of the late Dr. R. Connell of the University of Saskatchewan indicated a heavy infestation of mallards from western Canada with this nematode. Cornwell (1963) described an outbreak of echinuriasis in wild ducks and trumpeter swans at Delta, Manitoba.

The large Delta Marsh is situated at the southern tip of Lake Manitoba and supports large populations of the hosts required for the development of E. uncinata. Excellent research facilities are available at the Delta Waterfowl Research Station. These factors make this location ideal for a study of the biology, occurrence and pathogenicity of E. uncinata.

The objectives of this study are to obtain information on the biology, pathogenicity and importance of E. uncinata at Delta, Manitoba. This information will help towards a better understanding of the ecology of this parasite and its influences on a valuable resource, waterfowl. To achieve these objectives, we examined the following hypotheses and aspects of the ecology of E. uncinata at Delta: 1) its occurrence in the crustaceans of the Delta Marsh, 2) can E. uncinata infect invertebrates other than Daphnia pulex and D. magna, 3) its development in D. pulex and D. magna, 4) the tolerance of

E. uncinata ova to freezing and dessication, 5) its development in the Delta Mallard, 6) the infections of E. uncinata in Delta Mallards of different ages, 7) E. uncinata infections in different species of waterfowl, 8) E. uncinata infection of different intensities in Delta Mallards and 9) the duration of natural infections of E. uncinata in Delta Mallards.

All field surveys and experiments requiring waterfowl were carried out at the Delta Waterfowl Research Station during the summers of 1968 and 1969. Other experiments and the analysis of data were conducted at the University of Manitoba.

REVIEW OF LITERATURE

Published reports on Echinuria uncinata deal with its taxonomy, occurrence, morphology and pathogenicity with few notes on its biology.

SYSTEMATICS

The order Spirurida was reviewed by Cram (1927), Chitwood and Chitwood (1950), Osche (1955), and Skrjabin et al.(1965). In Spirurida, the superfamily Spiruroidea Raillet and Henry, 1915, contains the family Acuariidae Raillet, Henry et Sisov, 1912. Genera of Acuariidae have pseudolabia and cuticular ornaments on the cephalic region. The subfamily Acuariinae Raillet, Henry and Sisov, 1912, contains genera with cordons. Sobolev (1943) split Acuariinae by establishing the new subfamily Echinuriinae, which contains genera with cordons and body spines, the latter being absent from genera of Acuariinae.

The genus Echinuria Soloviev, 1912 has the following synonymys according to Cram, (1927); Filaria Mueller, 1787, pro parte; Acuaria Bremser, 1811, pro parte; Spiroptera Rudolphi, 1819, pro parte; Dispharagus Dujardin, 1845, pro parte; Histiocephalus Diesing, 1851, pro parte; Dispharynx Raillet, Henry and Sisov, 1912, pro parte and Hamannia Raillet, Henry and Sisov, 1912.

Occasionally, the name Acuaria is still used instead of

Echinuria in recent papers (e.g. Marotel and Pierron, 1947; Moynihan and Stovell, 1955).

The number of species of Echinuria is uncertain. Ryzhikov (1961a) listed 11 species, Yamaguti (1961) 19 and Ali (1968) 16. Echinuria cygni Morini, Colombo and Martin, 1960 was not included in any of these listings.

Species of Echinuria have been found in Anseriformes, Ciconiformes, Phoenicopteriformes, Lariformes, Charadriformes (after Ryzhikov, 1961a) and Ralliformes (Pavlov and Sergeeva, 1961). Echinuria uncinata (Rudolphi, 1819) Soloviev, 1912, is a parasite of Anseriformes with one reported infection in the coot, a ralliform (Colbo, 1965).

MORPHOLOGY

Echinuria uncinata is the type species of the genus and Echinuria is the type genus of the subfamily Echinuriinae. E. uncinata possesses four cordons which anastomoze and are non recurrent. Four rows of spines run nearly the entire length of the body (Cram, 1927). The cordons are a series of double pointed ridges (Czaplinski, 1962) and not glandular structures as described by Marotel and Pierron (1947). Two prominent pseudolabia surround the mouth opening which leads into the buccal capsule or stoma. The oesophagus has two parts, an anterior muscular and a posterior, glandular section. Measurements of body parts are given in Table I & II.

TABLE I

Recorded ranges for body portions of adult E. uncinata in millimeters

	Females		Males	
	Measurement	Reference*	Measurement	Reference*
Body length	6.7 - 20.0	(1)	4.6 - 11.6	(1)
Max. Body width	0.50 - 1.02	(1)	0.280 - 0.382	(1)
Cordon length	0.528 - 1.02	(1)	0.392 - 0.772	(1)
Buccal length	0.112 - 0.212	(1)	0.110 - 0.170	(1)
Musc. Oes. length	0.630 - 1.06	(1)	0.520 - 0.892	(1)
Gland. Oes. length	2.29 - 2.53 1.254 - 2.210	(2) (1)	1.05 - 2.55	(1)
Tail length	0.20 - 0.24 0.212 - 0.297	(3) (1)	0.330 0.360 - 0.430	(4) (2)
Left Spicule length			0.515 - 0.730 0.580 - 0.840	(2) (5)
Right Spicule length			0.140 - 0.208 0.204 - 0.246	(5) (1)
Vulva to tip of tail	0.680 - 1.70	(1)		
Ova width	0.018 - 0.020 0.0212- 0.0255	(3) (1)		
Ova length	0.033 - 0.037 0.034 - 0.042	(2) (1)		

* (1) Potekhina, 1963; (2) Czaplinski, 1962; (3) Bezubik, 1956; (4) Cram, 1927; and (5) Rhyzikov, 1961.

TABLE II

Measurements of E. uncinata collected in Manitoba and Saskatchewan ‡

in millimeters

	Females	Males
Body length	3.0* - 20.95	3.4* - 13.9
Max. Body width	0.13*- 0.87	0.11*- 0.60
Cordon length	0.25*- 1.10	0.25*- 0.93
Buccal length	0.13 - 0.20	0.09 - 0.19
Musc. Oes. length	0.64 - 1.22	0.41 - 1.05
Gland. Oes. length	1.25 - 3.25	1.00 - 3.04
Tail length	0.08*- 0.38	0.17*- 0.43
Left Spicule length		0.19*- 0.94
Right Spicule length		0.11*- 0.26
Vulva to tip of tail	0.43*- 1.82	

‡ Collected for Dr. R. Connell.
* Measurements taken from sexually immature adults.

Gravid females are didelphic with the anterior portion of the uteri nearly reaching the stoma. The vagina and muscular sphincter (Cram, 1927) make up the ovijector. Males possess two unequal and differently structured spicules. The left is long and thin, the right is short and heavy (Cram, 1927). Caudal alae are supported by four pairs of pedunculate precloacal papillae. The exact number of postcloacal papillae is in question. Bezubik (1956), Cram (1927), Czaplinski (1962) and Ryzhikov (1961a) claimed that five pairs are present while Potekhina (1963) observed only four pairs.

The cuticle of E. uncinata has no fibrillar layer and consists of a thin cortex, external lamella, homogenous layer, internal lamella, basal layer and membrane (Bogoyavlenski, 1961). Bogoyavlenski (1962) also studied the hypodermis of this nematode.

The eggs of E. uncinata are thick shelled, ovate, embryonated and have a specific gravity of 1.2 (Shakhnazarova, 1946). Monné (1958) found that the egg shells contained quinone - tanned, gram negative proteins.

First stage E. uncinata juveniles are 0.126 - 0.175 mm. in length soon after hatching (Kauker, 1941 and Romanova, 1947). Koteľnikov (1961) observed a slight bulb in the oesophagus of first stage juveniles. Second stage juveniles are 0.636 - 0.640 mm. in length (Romanova, 1947) and have a cylindrical oesophagus and a well defined intestine. Koteľnikov (1961) observed a thin sheath which extended beyond the head of second stage juveniles. Third

stage juveniles are infective and generally measure 1.2 to 1.6mm. in length (Romanova, 1947). Bezubik (1956) reported that third stage juveniles were 1.7 to 2.0 mm. in length, while Garkavi (1960) found some of these juveniles to be only 0.86 mm long. Short cuticular ridges are found near the extreme anterior tip of third stage juveniles. These might be primordial cordons, and Seurat (1919), Chabaud (1954) and Osche (1955) suggested that juveniles of acuariid nematodes possess the cordons of more primitive genera. This hypothesis was supported with examples by Chabaud and Petter (1959). Fourth stage juveniles of E. uncinata are not described in the literature.

No reports on variations in adult morphology of E. uncinata are available, but according to Ryzhikov (1961a), the best and presumably least variable generic characteristics of Echinuria are the extension of the cordons, absolute and relative spicule length, shape of spicules, and the number and arrangement of caudal papillae. In the related genus Acuaria, Williams (1929) found that relative cordon length and body organ ratios were constant but that body length and width were variable. Akhmedova (1954) reported that Amidostomum anseris infected both ducks and geese, but smaller worms occurred in the ducks. Chitwood (1957) found intraspecific variations in parasitic nematodes and Anderson (1968) found that tail, lip and gonad morphology and nerve ring, excretory pore and phasmid position were variable in species of Acrobeloides, depending on culture media.

Echinuria species described from only a few specimens should be reviewed in the light of possible variation in morphological characteristics. Echinuria parva Cram, 1928, E. querquedulae Johnston and Mawson, 1942, E. cygni Morini, Colombo and Martin, 1959 and possibly E. borealis Mawson, 1956 are a few examples.

BIOLOGY

In The Intermediate Host

Host list: Echinuria uncinata is a typical acuariid, requiring both a definitive and intermediate host to complete development (Ivashkin, 1961). Hamann (1893) suspected that Daphnia pulex was the intermediate host for E. uncinata. Romanova (1938, 1947 and 1948), Kauker (1941), Srilkov (1963) and Radin (1959) showed experimentally that D. pulex and D. magna serve as intermediate hosts. Kotel'nikov (1961) experimentally infected Gammarus sp., Ceriodaphnia sp., Asellus aquaticus, and an unidentified cyprid with E. uncinata. Development of this parasite in copepods was not observed (Romanova, 1938).

Seasonal abundance, occurrence and intensity of infection: The peak abundance of E. uncinata in Daphnia is in summer and autumn. Movsesian (1962b) found 15.6 % of Daphnia infected with juvenile acuariids and tetramerids in a pond in August. In a river bay, only 2.1 % were infected in June and only 0.6 % in August. Kotel'nikov (1961) observed that 2.0 % of Daphnia were infected with E. uncinata

juveniles in a pond which supported a flock of ducklings, all of which were infected with this nematode. Marotel and Pierron (1947) found a high percentage of Daphnia infected in a pond frequented by many ducks. Usually only one infective E. uncinata juvenile was found per Daphnia even though three juveniles were found in some (Kauker, 1941).

It is not known if E. uncinata can survive the winter in a marsh or pond. Garkavi (1960) believed it could not over-winter in ponds which freeze, because the intermediate hosts perish. However, Daphnia can survive all winter under ice (Pennak, 1953) and Klesov and Kovalenko (1967) found that Tetrameres sp. and Streptocara sp. juveniles could survive the winter in Gammarus sp. Romanova (1948) and Radin (1959) showed that eggs and juveniles of E. uncinata cannot survive low temperatures or dessication, though the chemistry of the egg shells suggests resistance to these environmental factors (Monné, 1958).

Development and pathogenicity: Daphnia become infected with E. uncinata by eating viable eggs which are passed with the definitive host's faeces (Hamann, 1893). Lubimov and Alf (1934) disagreed because the eggs appeared to be too large (after Radin, 1959), but the experimental results of Romanova (1938) and others corroborated Hamann's views.

Eggs of E. uncinata will hatch free of Daphnia in water. Akhtar (1936) observed this fifteen minutes after the eggs were removed from female worms and Kauker (1941) saw the same after

two days.

Once inside the Daphnia, the parasites penetrate through the intestinal wall into the haemocoel, usually within 3 days (Radin, 1959). Here, they grow and moult twice before becoming infective. Romanova (1938) thought a month was needed for the juvenile worms to complete development, but later (1947 and 1948) she found that only 12 days at 25 to 29°C. or 14 days at 17 to 23°C. were required. She found that the first moult occurred at 6 days and the second at 12 to 14 days. Kotel'nikov (1969) found completely developed juveniles in 11 days at 18 to 20°C. while Kauker (1941) found 11 to 12 days were sufficient. Radin (1959) believed 12 to 16 days were required, while Garkavi (1959) stated that 5 days at 26 to 30°C. or 6 days at 16 to 20°C. were adequate.

The effects of this parasite on Daphnia are not well understood but a high rate of mortality was recorded by Kauker (1941).

In The Definitive Host

Distribution: E. uncinata has been reported from many parts of the world by many researchers - from the Soviet Union (Shabaev, 1961; Markov, 1941; Potekhina, 1963; Gerasimova, 1964; Maksimova, 1964), Poland (Czaplinski, 1962; Bezubik, 1956), Germany (Hamann, 1893; Kauker, 1941; Hill, 1941), England (Buxton, Ford and Munro, 1952; Venn, 1954; Gibson and Barnes, 1957; Avery, 1966), France (Marotel and Pierron, 1947), Denmark (Knudsen, 1966), Africa (Cram, 1927), Afghanistan (Akhtar, 1936), India (Maplestone, 1939; Lalitha and Alwar, 1960), United States (Cram, 1927;

Cheatum, 1952), and Canada (Swales, 1934; Moynihan and Stovell, 1955; Cornwell, 1963; Crichton, 1969; Connell, unpublished). E. uncinata may also be present in Argentina and Australia. E. cygni Morini, Colombo and Martin, 1959, found in Argentina does not differ from E. uncinata. E. querquedulae Johnston and Mawson, 1942, found in Australia, also appears to be E. uncinata (Mawson, 1968).

Recent surveys of helminth parasites of birds (including waterfowl) in Central America (Hatherill, 1968), Pakistan (Hassan, 1966) and Mongolia (Danzan, 1964) did not reveal this parasite in these regions.

Host list: E. uncinata is a parasite of most species of waterfowl (see Table III). Gower (1939), Lepage (1961), Czaplinski (1962) and others listed over forty hosts in Anseriformes and Colbo (1965) has found this parasite in a member of Ralliformes (Fulica americana).

Seasonal abundance: E. uncinata is most prevalent in late summer. In ducks sampled in Russia, Shevtsov and Zabello (1965) found 14% infected in August and September, 3.3% in February, and none in March through May. Potemkina (1956) and Kotel'nikov (1961) also noted a high occurrence in July. In England, Venn (1954) found most Echinuria late in the waterfowl breeding season. In Germany, Kauker (1941) observed the heaviest losses of ducks from echinuriasis in July, August and September. Cornwell (1963) noticed a peak mortality in Canadian wild ducks in August. Similar

TABLE III

Recorded Waterfowl Hosts of *E. uncinata*

	Hosts*	Reference
1.	*Aix galericulata*	Cornwell, 1963
2.	*A. sponsa*	Cornwell, 1963
3.	*Anas acuta acuta*	Bezubik, 1956
4.	*A. americana*	Wickware, 1941
5.	*A. bahauensis bahauensis*	Cornwell, 1963
6.	*A. capensis*	Cornwell, 1963
7.	*A. castanea*	Cornwell, 1963
8.	*A. carolinensis*	Bezubik, 1956
9.	*A. crecca crecca*	Bezubik, 1956
10.	*A. discors*	Buscher, 1966
11.	*A. penelope*	Bezubik, 1956
12.	*A. platyrhynchos platyrhynchos*	Bezubik, 1956
13.	*A. platyrhynchos domesticus*	Cornwell, 1963
14.	*A. querquedula*	Bezubik, 1956
15.	*A. rubripes*	Bezubik, 1956
16.	*A. sibilatrix*	Cornwell, 1963
17.	*A. sprasa leucostigma*	Cornwell, 1963
18.	*A. sprasa sparsa*	Cornwell, 1963
19.	*A. strepera strepera*	Bezubik, 1956
20.	*A. undulata undulata*	Cornwell, 1963
21.	*Anser anser anser*	Bezubik, 1956
22.	*A. domesticus*	Bezubik, 1956
23.	*A. cinereus*	Bezubik, 1956
24.	*Aythya affinis*	Cornwell, 1963
25.	*A. americana*	Cornwell, 1963
26.	*A. ferina*	Bezubik, 1956
27.	*A. valisinera*	Cornwell and Cowan, 1963
28.	*Branta canadensis canadensis*	Cornwell, 1963
29.	*Cairina hartlaubi hartlaubi*	Cornwell, 1963
30.	*Cygnus buccinator*	Cornwell, 1963
31.	*C. olor*	Cornwell, 1963
32.	*C. olor domesticus*	Bezubik, 1956
33.	*Dendrocygna viduata*	Cornwell, 1963
34.	*Fulica americana*	Colbo, 1965
35.	*Lophonetta specularoides s.*	Cornwell, 1963
36.	*Mergus albellus*	Bezubik, 1956
37.	*Neochen jubatus*	Cornwell, 1963
38.	*Netta rufina*	Cornwell, 1963
39.	*Oxyura leucocephala*	Gerasimova, 1964
40.	*Philomachus pugnax*	Bezubik, 1956
41.	*Somateria mollissima m.*	Bezubik, 1956
42.	*S. spectabilis*	Cornwell, 1963
43.	*Spatula clypeata*	Czaplinski, 1962
44.	*Tadorna ferruginea*	Cornwell, 1963
45.	*T. tadorna*	Bezubik, 1956

* Scientific names taken from references cited.

observations were made by Buxton, Ford and Munro (1952); Gibson and Barnes (1957); Marotel and Pierron (1947) and Hill (1941).

The fate of these parasites in winter is not clear. Garkavi (1960) believed they wintered in ducks, to be reestablished in ponds in spring with the return of infected birds. However, Crichton (1969) found few of these parasites in mallards and pintails in April and May of 1968, though heavier infections were noted in the previous autumn.

Occurrence: In England, Buxton, Ford and Munro (1952) reported the deaths of 200 of 250 Aylesbury ducks were caused by echinuriasis. Thirty - nine ducks of six species perished in Langford, England (Venn, 1954). Thirty - seven of them were juveniles. Marotel and Pierron (1947) reported a mortality exceeding 40% in French ducks while in Germany losses ranged from 34% (Grafner et al. 1967) to 100% (Kauker, 1941; Hill, 1941). Kauker explained that such losses did not occur every year.

In large duck farms of the Soviet Union, local outbreaks of echinuriasis were often serious (Potemkina, 1956). Sulimov (1966) stated that Echinuria is the most dangerous helminth of ducks in the Tuva Region. Movsesian (1962a) observed such outbreaks in domestic ducks and geese of Moldavia from July to November. Egizbaeva (1964) noted that 56 to 100% of the ducks of the Tselin area were infected with average intensities of 250 to 400 E. uncinata per bird. Garkavi (1958) found that over 300 ducks of the Krasnovadsk Region perished from echinuriasis (after

Radin, 1959). Kotel'nikov (1961) claimed that all the ducks on one pond in Krasnodar were infected with E. uncinata. In a larger survey, Shevtsov and Zabello (1965) recorded the occurrence of E. uncinata in domestic ducks to be 10.1% in birds up to 6.5 months old, 7.2% in birds 7 to 12 months old and 0% in birds over 12 months. Kovalenko and Kalchenko (1966) indicated that over 12,000 ducks of 2 to 3 months age were infected with E. uncinata with an average intensity of 600 worms per bird. Petrochenko and Kotel'nikov (1963) found that chemical treatment prevented high mortality. Over 25,800 ducks in the Omsk region were treated (Selivanova, 1960).

Wild birds can serve as reservoirs for parasites of domestic birds (Kotel'nikov, 1962). Markov (1941) found 40% of Somatilis spectabilis (King eider duck) from Bezymiannay Bay in Northeastern U.S.S.R. parasitized by E. uncinata. In Manitoba, Cornwell (1963) observed heavy infections with E. uncinata in wild ducks. He estimated that 30% of 400 ducks perished in one summer. Cornwell and Cowan (1963) found that 20% of the canvasback (Aythya valisineria) ducklings from Manitoba and the lower Detroit River were infected with E. uncinata. Connell (unpublished) stated that 75% of the wild mallards sampled in Saskatchewan were infected.

In Poland, Czaplinski (1962) found that many species of birds were infected with E. uncinata; the highest occurrence was 3% in domestic mallards. Knudsen (1966) and Marotel and Pierron (1947) believed that echinuriasis was rare in Denmark and France

respectively. A survey by Buscher (1965) in the United States revealed that less than 1% of the wild ducks examined were infected with this nematode.

Intensity: The intensity of infection varies depending on age, sex, species and/or stress of the host, and on the exposure to infective juvenile parasites.

Younger birds are more heavily infected than older birds. Kauker (1941) and Knudsen (1966) noted that 6 to 14 week old birds were most frequently infected, and in Russia, Shevtsov and Zabello (1965) and Potemkina (1956) reported similar findings. It is not clear why the youngest birds are more frequently infected, but one reason may be that they feed more heavily on invertebrates and become more exposed to the parasites than do the adults (Buscher, 1965, and others). Collias and Collias (1963) noticed that young ducklings selected invertebrates in their diet and generally consumed more than did adults. Bartonek (1968) found the same in young redheads, canvasback and scaup ducks. Moyle (1961) believed that younger birds have higher protein requirements and select animal foods to meet this requirement. Because freshwater invertebrates are vectors of E. uncinata, the younger birds probably ingest more parasites than do adults.

Young birds may also be more susceptible to parasitic invasion. This higher susceptibility may be influenced by the production of antibodies from the bursa of Fabricius, a lymphatic tissue sac near the cloaca (Olson, 1965). Glick, Chang and Jaap

(1955) found that the ability to produce antibodies depended on the size of the bursa of Fabricius, reaching a peak in chicks 4 to 10 weeks old. Chang, Rheins and Winter (1957) corroborated these findings.

The intensity of infection may also depend on the sex of the host. Schad (1962) found a higher intensity and extensity of Notocutylus attenuatus infections in male domestic geese. Todd and Hollingsworth (1952) found a higher intensity of Ascaridia galli in male chickens experimentally infected. Dobson (1961) suggested that hormones may govern susceptibility.

Host-specificity may also influence intensity of infection. Ryzhikov (1961 a & b) stated that E. uncinata is limited to Anseriformes, especially those in the mid-temperate regions. Ducks of the genus Anas, especially the domestic and wild mallards, appear to be more frequently infected with this parasite (Crichton, unpublished; Czaplinski, 1962).

Stress can also influence the intensity of infection with helminths in waterfowl. Cornwell (1966) stated;

> " Parasitic disease tend to prevail in unstable situations, marginal habitats, and under competitive conditions. Whatever the cause, stress imposed upon the host is likely to influence the host - parasite association, often resulting in an increase in the helminths."

Reports on the intensity of E. uncinata infections vary.

Cornwell (1963) observed over 2,000 worms in one trumpeter swan cygnet and usually 1 to 100 worms in ducks. Connell (unpublished) found 1 to 650 E. uncinata in wild mallards examined in Saskatchewan, mostly 10 - 100 per host. Kovalenko and Kalchenko (1966) found an average of 600 E. uncinata in Russian domestic ducks. As many as 300 worms were found in a Aylesbury duck in England by Buxton, Ford and Munro (1952).

Development: The definitive host becomes infected by ingesting third stage E. uncinata juveniles with the intermediate host, e.g. Daphnia (Hamann, 1893). Romanova (1938, 1947 and 1948) found eggs of the parasite in the duckling's faeces 52 days after infection. Radin (1959) claimed that 48 to 52 days were sufficient, while Kotel'nikov (1961) observed parasite eggs in the faeces after only 40 days. After 30 days, the parasites were sexually mature, but not ovipositing. Garkavi (1960) found gravid female E. uncinata with unembryonated ova 34 days after infection.

Symptomatology: The symptoms associated with severe echinuriasis differ slightly in the ducks, geese and swans, and are well studied.

In ducks, the most obvious manifestation of echinuriasis is a retardation of growth and emaciation. A prominent keel is often seen (Cornwell, 1963). Potemkina (1956) found that infected birds weighed only 200 to 500 grams, while healthy birds of the same age weighed 1,300 to 1,500 grams. Marotel and Pierron (1947) and Potemkina (1956) thought that the malnutrition and emaciation resulted

from the occlusion of the proventriculus, interfering with digestion and absorption of food. Jarrett (1966) observed that secretions of enzymes and HCL decreased in cattle infected with Ostertagia sp. Potemkina (1956) referred to work by Tsvetaev who observed disorders in protein metabolism in birds infected with E. uncinata. Deposits of amyloid were seen in various organs, e.g. the kidneys, and the liver was grayish - pink, hardened and enlarged 2 to 3 times.

Other symptoms of echinuriasis in ducks are dullness and lethargy. Buxton, Ford and Munro (1952) noted an inability to fly properly, absence of awareness, atrophy of visceral organs, and faded, discoloured and poorly groomed plumage in infected birds. Gibson and Barnes (1957) and Knudsen (1966) observed vomiting. Other symptoms include fatigue, uncertain movements, diminished appetite, running of eye and nasal fluids, increased uptake of fluids resulting in liquid faeces and difficulty in breathing associated with a gaping bill (Kauker, 1941). Kauker also witnessed partial paralysis in some birds who balanced their heads on their bills or held them back over their bodies. Death occurred in this position. Buxton, Ford and Munro (1952) and Marotel and Pierron (1947) observed mortality starting 3 weeks after infection and continuing up to 2 months.

Knudsen (1966), Gibson and Barnes (1957) and Kauker (1941) pointed out that many symptoms of E. uncinata infections in ducks do not occur in geese, and that these hosts die suddenly after a short period of increased appetite.

Moynihan and Stovell (1955) noticed cachexia, emaciation

and ruffled feathers in swans infected with E. uncinata. Cornwell (1963) found that the infected trumpeter swan cygnet was considerably smaller than its clutch mates. It died 7 weeks later with its proventriculus occluded by granulomas.

Pathology: After ingestion by the duck, the worms burrow into the mucosa usually at the boundary of the proventriculus and gizzard (Romanova, 1938). Here, hard nodules from 5 to 15 mm. in diameter form (Romanova, 1947). Garkavi (1958) found up to 60 nodules in one duck (according to Radin, 1959).

Radin (1959) stated that Skrjabin (1915) found nodules at the junction of the gizzard and proventriculus, while Henry and Sisov (1912) saw them only in the proventriculus. Radin (1959) stated that in heavy infections the gizzard also becomes affected. Cram (1927) claimed that E. uncinata settled in the glandular and muscular stomach and in the small intestine. She also reported an infection of the air sacs, though Kauker (1941) questioned this finding.

In describing the nodules, Buxton, Ford and Munro (1952) used the term "lesions"; Cornwell (1963) called them "ulcerative cysts"; Kauker (1941) and Marotel and Pierron (1947) used "cysts", and Shevtsov and Zabello (1965) called them "granulomas". The term lesion and ulcer refer only to open sores (Pennak, 1964) whereas the term "cyst" simply implies a sac or capsule containing a liquid or semisolid substance (Dorland, 1965). According to Boyd (1961), granulomas are the result of a chronic inflammation, characterized

by the preponderance of histiocytic rather than hematocytic infiltration. Granulomas are highly specific reactions of the reticuloendothelial system almost without exudate and vasodilatation. Necrosis and caseation may be observed in the center of the lesion and collogen may form at its periphery. The nodules produced by echinuriasis must be regarded as granulomas.

Kauker (1941) stated that in early stages of severe echinuriasis the proventriculus has a swollen mucous membrane overlying a gray or brown gelatinous mucosa. This layer contains isolated parasites. Cavities of the subserosa were crossed by many fibers which divided them into niches filled with nematodes and bloody fluid. In older lesions containing mature parasites, the granulomatous reactions were well expressed.

Shevtsov and Zabello (1965) described the granuloma formation in E. uncinata infections. The juvenile worms entered the muscular layer of the stomach. In infected areas, infiltration by hystiocytes was noticed. Muscular fibers underwent cloudy swelling. Soon, the hystiocytes and the fibroblasts produced a dense connective tissue capsule which later became hyalinized. The capsule formation was completed when the parasites attained sexual maturity. Necrosis of the mucosa developed at this stage.

Caseous detrital yellow material often containing both dead and living parasites were often found in larger nodules. Later, this mass became green - gray and the parasites were absent. Scars often occur in the proventriculus of adult ducks. Crichton (personal

communication) believed these to be old, degenerated nodules caused by E. uncinata infections.

Granulomas are often infiltrated by eosinophils and lymphocytes (Knudsen, 1966). Potemkina (1956), reported that the infected proventriculus also increased in size.

The histopathology in geese and swans is similar to that in ducks (Cornwell, 1963; Moynihan and Stovell, 1953). However, the nodules in geese are more prominent and project well into the lumen of the proventriculus (Kauker, 1941).

Chemotherapy: The importance of echinuriasis in the U.S.S.R. is reflected by the numerous papers dealing with chemical treatment of infected birds. Compounds such as carbon tetrachloride, phenothiozine, piperazine adipate and Lugol's solution have been given at different concentrations to ducks infected with E. uncinata with varying degrees of success (Garkavi, 1960; Kovalenko, Kalchenko and Mikhailenko, 1965; Kovalenko and Kalchenko, 1966; Petrochenko and Kotel'nikov, 1966; Selivanova, 1966 and Vorontsov, 1962).

METHODS

COLLECTION OF PARASITIC MATERIAL

Infective Juveniles

Infective third stage E. uncinata juveniles were collected with the help of Baermann funnels (Baermann, 1917). Large numbers of Daphnia pulex and D. magna were collected from Site 1 (Table IV). These were broken up in a Petri dish by applying pressure with an inverted glass stopper. The resulting "mulch" was placed into Baermann funnels and allowed to stand for 1 to 4 hours. Small aliquots of water were then drawn from the bottom of the funnel and examined in a Petri dish under 10X magnification. Individual nematodes were picked out with an eye-lash brush, counted and transferred to a small dish containing water. All nematodes were used within several hours of collection.

Adult Parasites

Adult or developing parasites were removed from the nodules of infected birds. The nodules were gently slashed with a razor until the worms were visible. These were then removed with forceps and transferred to a small dish containing water.

Viable Parasite Ova

Eggs of E. uncinata were collected from the uteri of worms placed in a small dish with water, held at the anterior end with forceps and opened with a needle.

TABLE IV

Primary sampling sites of

invertebrate - parasite survey

Site	Description
1. Field Station Pond	- 7.6 acre pond - 5 yards south of the D. W. R. S.* library - sampled along north shore at water depth of 6" to 18" - with many birds (Fig. 11).
2. Bain's Pen and Swan Pond.	- Two small, man-made enclosures west of Site 1 - received water from Field Station Pond - birds supported in both enclosures.
3. Delta Road Slough	- Slough, half mile long - 10 feet wide - four feet deep - running north/south along west edge of Delta Road - sampled 100 yards south of turn off to D. W. R. S.* frequented by wild birds (Fig. 12).
4. Blind Channel	- 200 foot wide channel running south of Lake Manitoba - half mile west of D. W. R. S.* - frequented by many wild ducks in spring and autumn (Fig. 13).

* Delta Waterfowl Research Station.

In most cases, gravid females were stored up to 10 days in small covered dishes containing water at room temperature.

PROCESSING OF PARASITIC MATERIAL

Parasites were killed in boiling 0.5% acetic acid before being fixed and stored in 4% formaldehyde for at least 24 hours. Worms were then transferred to a mixture of 90 parts ethanol (70%) and 10 parts glycerine. The alcohol was allowed to evaporate over a 5 to 6 day period. Worms were mounted in pure glycerine on slides which were sealed with nail varnish (mod. Seinhorst).

Measurements of the parasites were taken from cammera lucida drawings and from images projected by a Bausch and Lomb projector (Model Try - Simplex). Photographs were taken with a Pentax Spotmatic using Kodak Plus X 35 mm. film. Negatives were developed in D - 76 and prints made on Kodak polycontrast paper developed in Dektol.

Drawings were made from both permanent and temporary mounts. The latter were made by placing specimens on a cavity slide with a few drops of fixative and covering them with a large coverslip. Temporary slides of living specimens were made by placing a few drops of water with the worms on a slide. A coverslip, ringed with glycerine jelly, was then applied.

COLLECTION OF INVERTEBRATES

Sites for the qualitative sampling of invertebrates were chosen near the Delta Waterfowl Research Station (Tables IV and V). Samples were taken with a dip net near the shore in areas frequented by waterfowl.

The invertebrates, principally crustaceans, were examined under 10x magnification in the field laboratory and identified with the aid of keys in Pennak (1953) and Ward and Whipple (1966) and the check list of Delta Marsh crustaceans by Smith (1968).

To determine the presence of E. uncinata at each site, a large sample of crustaceans was placed in a Baermann funnel. When parasites were found, a more detailed, quantitative examination was carried out on each species of crustacean. The larger individuals, (i.e. Gammarus, Lynceus, etc.) were dissected with forceps in a Petri dish. The smaller crustaceans (i.e. Cladocera) were counted and ruptured under a microscope slide in a Petri dish. The ratio of worms per host was recorded for each species of invertebrate.

CULTURE OF CRUSTACEANS

Certain crustaceans from Delta were cultured in five and ten gallon aquaria. "Pure" cultures proved difficult to maintain,

TABLE V

Invertebrate survey sample sites

Site	Primary invertebrates	Date sampled (1969)
Site 1 (Table IV)*	Daphnia, Simocephalus, Moina, Cyclops, Diaptomus	May - November
Site 2 (Table IV)*	Daphnia, Moina	May - July
Site 3 (Table IV)*	Daphnia, Simocephalus, Ceriodaphnia, Lynceus Diaptomus, Eurycercus	May - August
Site 4 (Table IV)*	Daphnia, Gammarus, Hyalella, Simocephalus Lynceus	March - July
Chadam Bay	Daphnia, Gammarus, Hyalella	June 10
School Bay	Daphnia pulex and Daphnia magna	June 10 and August 20
Lake Manitoba	Daphnia magna	July 17
Minnedosa Potholes	Daphnia, Hyalella	June 24
Dugouts in Back Marsh*	Daphnia pulex and Daphnia magna	May - June

* Sites where infective E. uncinata juveniles were found.

so "mixed" or "balanced" cultures were established. The latter had species ratios in proportion to those present at the site of collection. Water and vegetation were collected from the same site. Aeration was supplied by an electric pump at a rate of 50 cc/min. for each five gallons of water. Algae and/or yeasts were occasionally added.

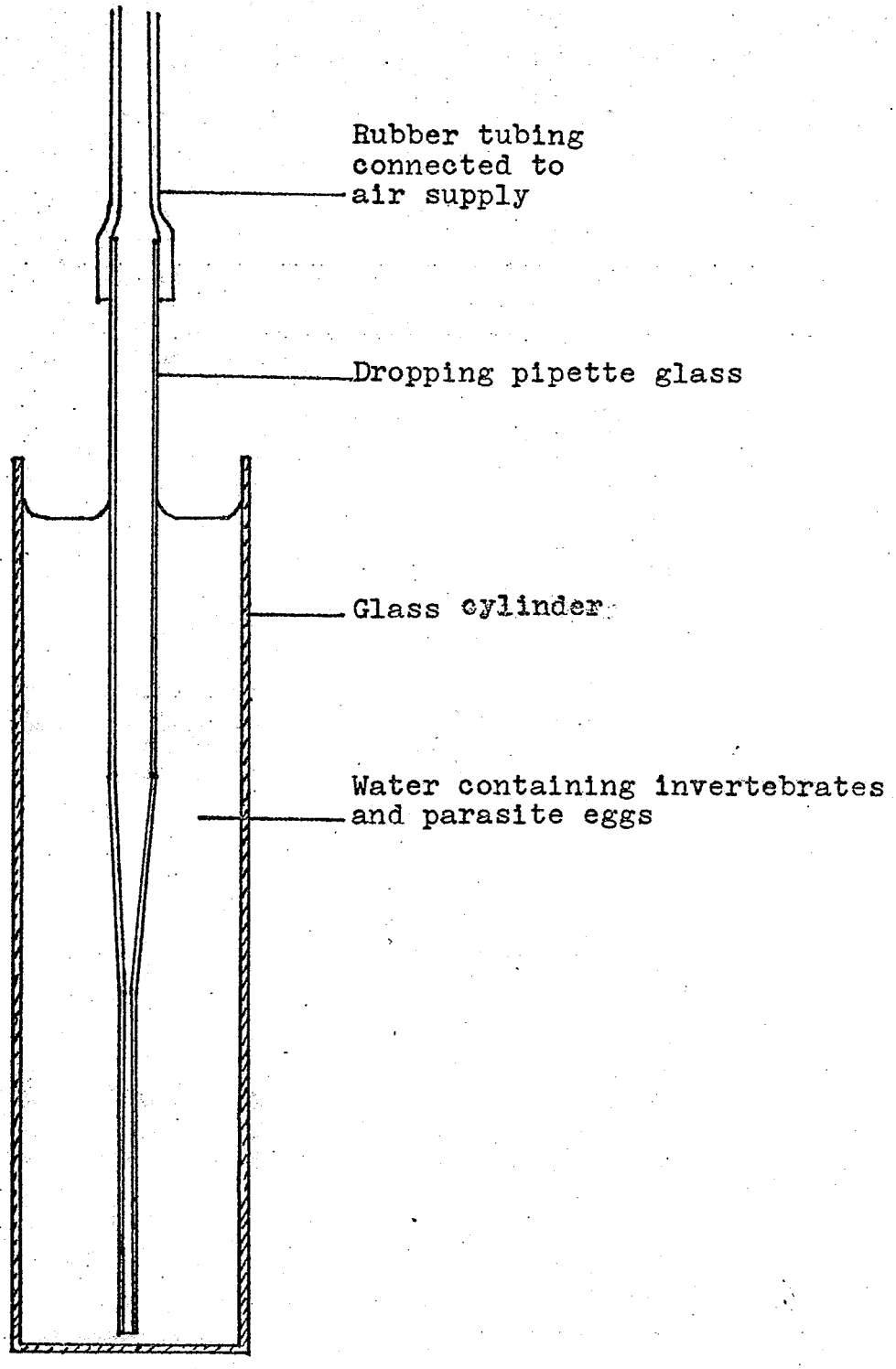
Daphnia pulex and D. magna were maintained for seven months in the winter in a hundred gallon, soapstone aquarium at the University of Manitoba. The temperature was kept at 15°C. and yeasts were added twice weekly.

INFECTION OF CRUSTACEANS

Crustaceans were exposed to viable E. uncinata ova to determine which species were potential intermediate hosts. The infection chamber (Fig. I), a test tube 8" by 1", was filled with water containing 20 - 50 crustaceans. Eggs from one or two gravid female parasites were added to the tube. A dropping pipette connected to an air supply was then inserted into the tube. This produced a continuous flow of bubbles keeping the eggs in suspension.

After 15 minutes to 3 hours, the crustaceans were removed and their intestines and hemocoel were examined for parasites under 100x magnification.

FIGURE 1



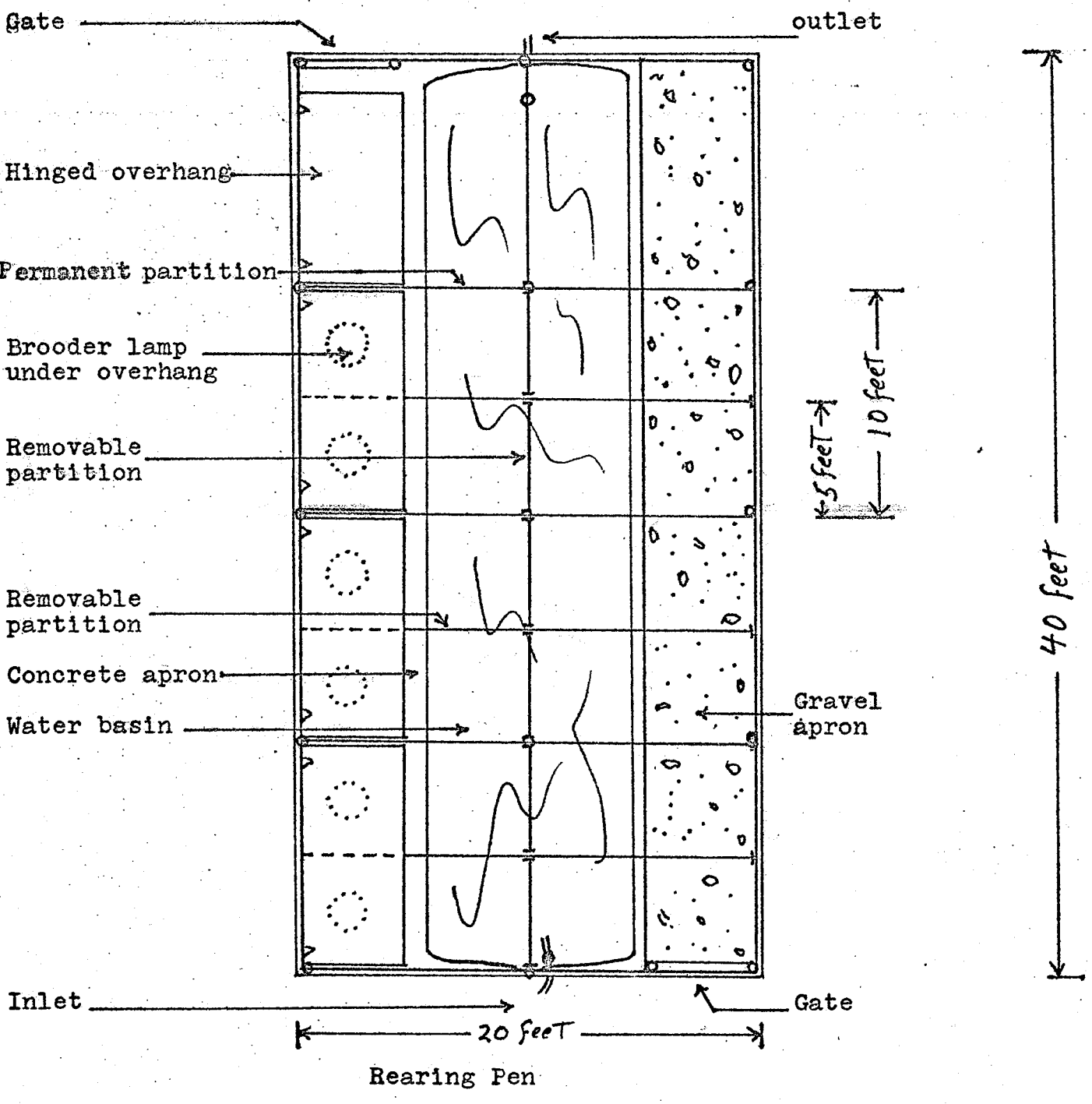
"INFECTION CHAMBER"

REARING OF BIRDS

All birds used in this study were reared at the Delta Waterfowl Research Station from artificially incubated eggs. Wild ducks were hatched from eggs collected by Mr. Louis Ducharme. Delta Mallards were reared from eggs of an inbred population of birds maintained at the Field Station. Domestic mallard eggs were purchased from the Sunnyside Hutterite Colony situated on the Assiniboine River, west of Winnipeg. These birds have wild mallard plumage but are heavier and "dumpier" than wild mallards. Domestic geese eggs were purchased from another Hutterite Colony. All these birds were white. All eggs of the domestic birds were washed in a disinfectant at 46°C. prior to incubation at 99°C.

Day - old birds were transferred from the incubators to brooders in a pen built especially for this study (Fig. 2). This enclosure (Fig. 14) was supplied with water from a covered well, free of invertebrates. Birds were kept under brooder bulbs until four weeks old. The pen was cleaned daily and feed supplied twice daily. Birds under four weeks received a mixture of an unmedicated commercial poultry grower (16% min. protein), soybean meal (44% min. protein) and fish meal (60% min. protein). Older birds were fed rolled oats and soybean meal mixed with water, and whole wheat added to dry poultry grower.

FIGURE 2



Rearing Pen

INFECTION OF BIRDS

Two methods were used to infect experimental birds with E. uncinata. In the first method, birds were exposed to the infected Daphnia pulex and D. magna at site one where they were enclosed and allowed to feed and drink water. This supplied data on naturally acquired infections. Unfortunately, infection intensity depended on the feeding and drinking behavior of each bird.

The second method was designed to overcome the disadvantages of the first. This time, birds of known age were given a known number of infective third stage E. uncinata juveniles introduced into the oesophagus with a small eye dropper. Some water was administered to wash down the worms. Birds were banded for identification.

AUTOPSY OF BIRDS

An incision was made along the breast, to the left of the keel and the body cavity was opened with bone cutters to reveal the gizzard, proventriculus and liver. The gizzard and proventriculus were cut open, washed under running water, and their inner surface examined under a 7x dissection microscope. Each nodule was opened and its contents examined. Some organs were fixed and stored in

FAA for subsequent examination. The following data were recorded for each bird: weight, sex and condition of each bird; condition of viscera; number, size and position of nodules; presence of blood, mucus and necrotic tissues in the gut lumen; presence of detritus and/or fluid in the nodules and number of parasites from each nodule. See data sheet (Appendix I).

Scientific names were taken from P. Scott's "A Coloured Key to the Waterfowl of the World" (1957).

OBSERVATIONS

1. INVERTEBRATE SURVEY

During the spring and summer of 1968, invertebrates, primarily crustaceans, were collected from various sites in the Delta Marsh (Table IV). Third stage juveniles of E. uncinata were found from July to late October in Daphnia pulex and D. magna from site one only. On July 21, six and nine infective juvenile worms were found for each 100 D. pulex and D. magna respectively. One week later, 7.5 nematodes were found per 100 individuals for both Daphnia species.

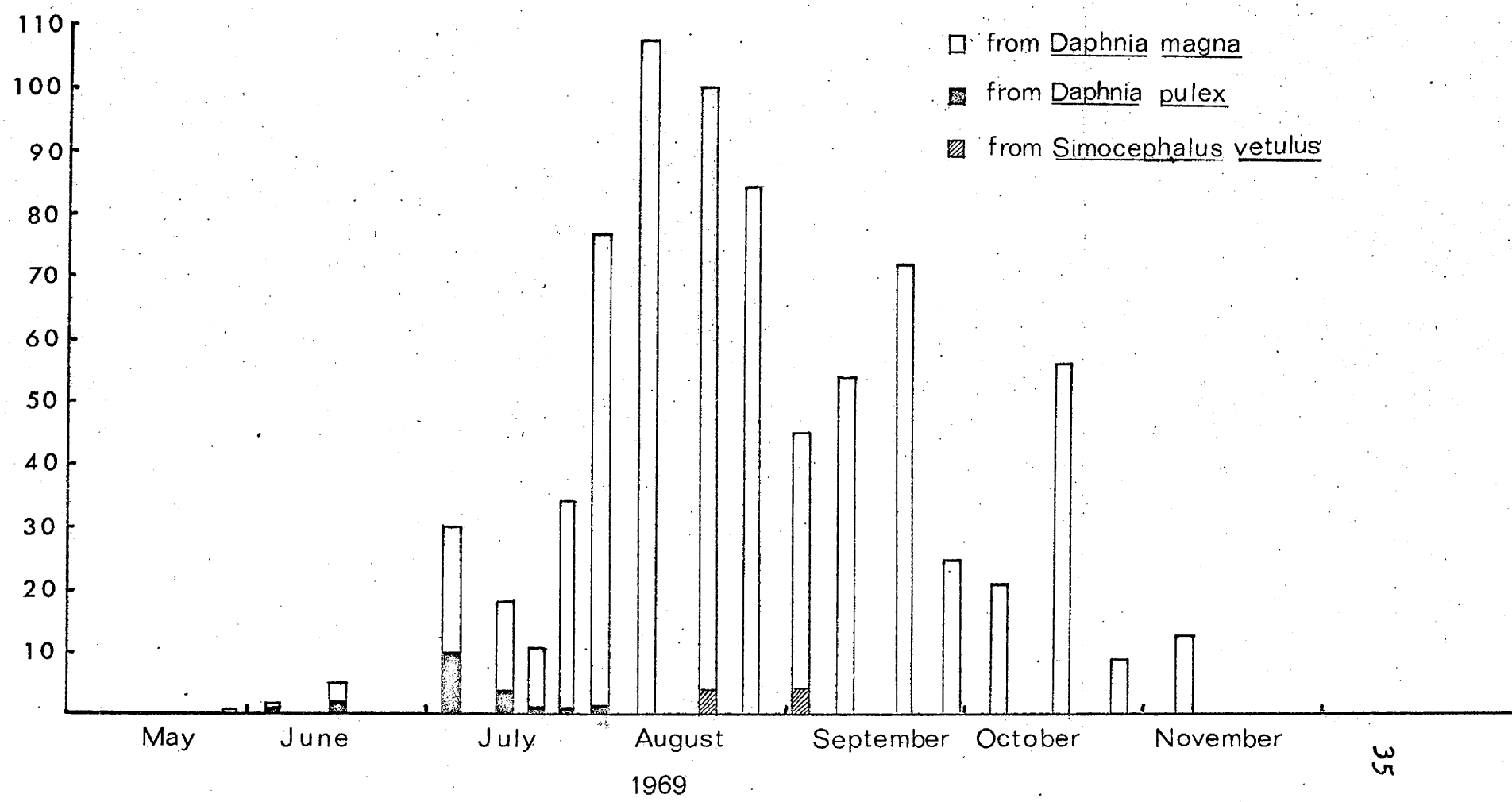
Crustaceans were sampled from sites one through four at 7 to 10 day intervals from April to October, 1969. Other sites (Table V) were also examined occasionally throughout the summer. The numbers of infective juveniles of E. uncinata per 100 crustaceans collected from site one between April and November, 1969 are given in Figure III.

2. INVERTEBRATE INFECTION EXPERIMENTS

Various invertebrates from Delta were exposed to E. uncinata ova to determine if they would become infected and thus

FIGURE 3

Numbers of 3rd. stage E. uncinata juveniles per 100 crustaceans from Site One



serve as potential intermediate hosts. Each host species was maintained in culture and examined for developing parasites.

Seven species of Cladocera, two species of Amphipoda, one species of Anostraca and one species of Conchostraca (Table VI) became infected with first stage juveniles of E. uncinata within 3 hours after exposure to the eggs. Juvenile parasites were observed in the hemocoel and in the gut tube. Only D. pulex Leydig 1860 emend. Richard 1896, D. magna Straus, 1820, Simocephalus vetulus Schødler 1858, and Lynceus brachyurus O. F. Müller 1785, cultures survived long enough to allow the parasites to develop to third stage juveniles. The following is a detailed account on each species examined.

Cladocera

Daphnia pulex: from all sites, readily became infected with E. uncinata. Many Echinuria eggs were noticed in the intestines (Fig. 15) of individuals minutes after exposure, and as many as 30 first stage juveniles were found in some after one hour (Fig. 16). Most juvenile parasites were observed in the dorsal hemocoel near the heart, but many were found in the gill filaments, abdomen, antennae, head and ventral carapace as well.

Most second stage juveniles were dorsal to the gut and anterior to the heart. They were coiled and inactive (Fig. 19).

TABLE VI

Intermediate hosts of E. uncinata

Invertebrate	Extent of observed parasite development
- Cladocera -	
Daphnia pulex	- to third stage, found naturally infected
Daphnia magna	- to third stage, found naturally infected
Ceriodaphnia reticulata	- to first stage juvenile in hemocoel
Ceriodaphnia acanthina	- to first stage juvenile in hemocoel
Ceriodaphnia sp.	- to third stage juvenile*
Simocephalus vetulus	- to third stage, found naturally infected
Moina macrocopa	- to first stage in hemocoel
Eurycercus lamellatus	- to first stage in hemocoel
- Amphipoda -	
Gammarus lacustris	- to third stage, found naturally infected
Hyalella azteca	- to second stage juvenile in hemocoel
- Anostraca -	
Chirocephalopsis bundyi	- to first stage juvenile in hemocoel
- Conchostraca -	
Lynceus brachyurus	- to third stage juvenile
- Ostracoda -	
cypridae	- to first stage juvenile*
- Isopoda -	
Asellus aquaticus	- to first stage juvenile*

* After Kotel'nikov, 1961

Up to 20 third stage juveniles were recovered from 3 artificially infected D. pulex after 11 days at room temperature (Fig. 20). Most worms were situated in the dorsal hemocoel, but a few were extended into the gill filaments and antennae.

Daphnia magna: from all sites, became infected as readily as D. pulex. This host was also tolerant to heavy infections. Development of the parasite to third stage was complete in 11 days at room temperature. Most third stage juveniles were found in the region of the gill filaments (Fig. 21).

Simocephalus vetulus: from sites one, three and four, became infected after one hour in the "infection chamber". Eight first stage juveniles were seen in one individual, three in the hemocoel and five in the intestine. Development to third stage was complete in 11 days at room temperature.

Ceriodaphnia reticulata Jurine, 1820: from site four did not readily become infected with Echinuria. Only two of these small crustaceans were found with a single, first stage worm each. One parasite was coiled in the dorsal hemocoel anterior to the cervical sinus. The other parasite was moving about in the hemocoel two days after exposure.

Ceriodaphnia acanthina Ross 1897: from site four, became infected with first stage E. uncinata which were noticed in the hemocoel of the head and antennae one day after exposure to

the parasite's eggs.

Moina macrocopa Straus 1820: from site one in early May, 1969, became infected with first stage Echinuria two hours after exposure to the eggs. As many as five juveniles were observed in some individuals.

Eurycercus lamellatus O. F. Müller, 1785: from site four became infected with first stage juveniles two hours after exposure. The juveniles were noticed in the hemocoel of the head and abdomen.

Alona sp.: from site four, never became infected with E. uncinata after several, prolonged exposures to the parasite's eggs.

Scapholeberis sp.: from site four were never found nor observed with juveniles or eggs of E. uncinata after prolonged exposure in the "infection chamber".

Amphipoda

Gammarus lacustris Sars, 1865: from site three became infected with first stage E. uncinata within four hours after exposure to the parasite's eggs. Both Echinuria eggs and juveniles were in the mid intestine. Juveniles were also observed in the hemocoel.

Hyalella azteca Saussure 1858: from site three repeatedly became infected with first stage juveniles of this nematode. Juveniles were found in both the intestine and hemocoel within two hours after exposure to Echinuria eggs. After six days, juveniles were counted in the head, appendages, tail, and intestine of some individuals.

Conchostraca

Lynceus brachyurus: from sites three and four became infected with first stage E. uncinata juveniles two hours after exposure. Juvenile worms were seen in the hemocoel of the head and near the dorsal margin. Fully developed third stage juveniles were observed in the dorsal hemocoel after 11 days at room temperature (22°C.). Some individuals contained two or three third stage juveniles.

Copepoda

Diaptomus sp.: from all sites were never found with first stage E. uncinata after repeated and prolonged exposures to the parasite's ova. An Echinuria egg was seen once in the anterior gut of an individual.

Cyclops sp.: from sites one and two were never seen with either E. uncinata ova or juveniles after repeated and prolonged exposures to the eggs.

Miscellaneous Aquatic Invertebrates

Mosquito, chironomid, hemipteran and coleopteran larvae, as well as water mites and ostracods were never found with ingested eggs of E. uncinata after exposure in the "infection chamber".

3. GROWTH AND DEVELOPMENT OF E. UNCINATA IN DAPHNIA PULEX AND D. MAGNA

In order to observe the growth and development of E. uncinata in its intermediate hosts, D. pulex and D. magna, these crustaceans were exposed to the parasite's ova, and maintained in aquaria. Prior to culturing, individuals were selected at random and examined under 40x magnification to determine if they had become infected.

E. uncinata eggs were readily engulfed by the Daphnia and were often seen in the host's intestines (Fig. 15) after only 15 minutes in the "infection chamber". In the intestine, some eggs hatched, releasing active juvenile nematodes. Other eggs were passed before hatching in the Daphnia and some eggs hatched outside of the crustacean, though it is not known whether these eggs had been previously ingested. After hatching, the small first stage juveniles actively thrashed about in the gut lumen, and were often seen oriented at steep angles to the gut wall. In the posterior gut region, near the post abdominal process, these worms were observed to penetrate the intestinal wall into

the hemocoel. In Daphnia with many parasites the gut wall in this region was dark brown, irregular and strongly contracted. Once in the hemocoel, the parasites moved about with the body fluids, until they became lodged in some tissues, mostly near the heart. Worms were less frequently seen in the head, antennae, gill region and in the posterior abdomen.

To follow the subsequent growth of these parasites, separate cultures of D. pulex and D. magna were maintained at room temperature (20 - 24°C.) during August of 1968 at the Delta Waterfowl Research Station. The worms were removed from the Daphnia after known periods of development and examined microscopically. The increase in body length over time is given in Figure IV. It was difficult to determine when the first moult occurred, probably prior to 100 hours. At seven days (170 hours) 0.8 - 1.4 mm. long worms with a hyaline cap at the head end were observed. This cap is believed to be the loosened cuticle, just prior to the second moult. Third stage juveniles were present after 10 days (240 hours). These were 1.0 - 1.9 mm. (averaging 1.5 - 1.7 mm.) long, and possessed clearly defined, chevron shaped primodial cordons at the extreme anterior end (Fig. 21). Development appeared similar in both Daphnia species.

This experiment was repeated at the University of Manitoba with a large mixed culture of infected D. pulex and D. magna. The aquarium was kept at 15°C., and all worms were

observed *in situ*. The few third stage juveniles appeared after 28 days (670 hours), but second stage juveniles were still found after 39 days (940 hours) (see Fig. 4).

After two weeks at 15°C., some *Daphnia* were removed and recultured at 24°C. in order to determine if the *Echinuria* juveniles would repond to an increased temperature and develop more rapidly. After only four days at 24°C., completely developed third stage juveniles 1.2 - 1.35 mm. long were found (see Fig. 4).

4. FREEZING AND DESICCATION OF *E. UNCINATA* OVA

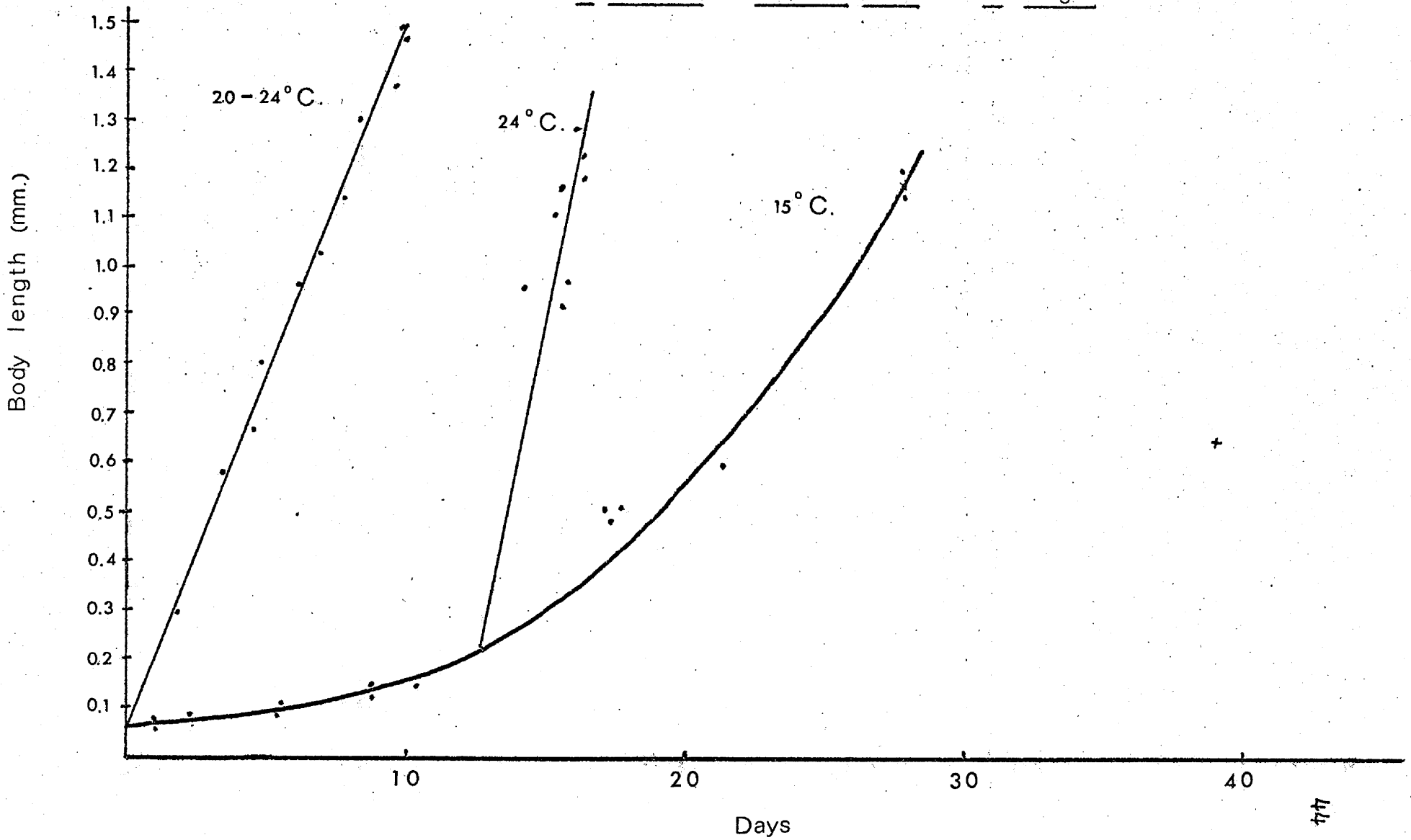
We investigated the effects of freezing and drying on the viability of *E. uncinata* ova to ascertain if these eggs could survive the winter in the marsh.

Eggs frozen for 85 days were distorted and ruptured. When eaten by *Daphnia*, they failed to hatch, suggesting that they were not viable after treatment.

Eggs that had been dried and stored on filter paper for 85 days (relative humidity above 80%) were normal in appearance. Many of these eggs hatched when eaten by *Daphnia* and released active first stage juveniles. The hatchability was about half that of untreated eggs.

FIGURE 4

Growth of E. uncinata in Daphnia pulex and D. magna



5. GROWTH, DEVELOPMENT AND PATHOGENICITY OF E. UNCINATA IN THE DELTA MALLARD

To study the growth and development of E. uncinata in its definitive host, 20 one month old Delta Mallards were each inoculated with 50 third stage E. uncinata juveniles. Four birds were taken at random every ten days and autopsied. This procedure yielded material from birds that had been infected 10 to 50 days. The proventriculus and gizzard of one bird from each set was kept for histological examination except when no or a few worms were recovered from the other three birds.

Growth

Male worms from 10 day old infections averaged 2.05 mm. in length and females 2.07 mm. (see Table VII). This represents a 25% increase in length from the time of infection. All worms recovered were fourth stage juveniles.

Nematodes recovered from 20 day old infections averaged 3.56 mm. and 3.43 mm. long for males and females respectively. This represents a 75% increase in length from 10 day old infections. The parasites from two of the birds were mostly adults while those from the third bird were all fourth stage juveniles.

Worms recovered from the 30 day old infections averaged 4.88 mm. and 5.95 mm. long for males and females respectively.

TABLE VII

Body lengths of E. uncinata from infections of different age

	Male E. uncinata		Female E. uncinata	
	$\bar{X}$ ± 95 % C. I.*	Range	$\bar{X}$ ± 95 % C. I.*	Range
At time of infection	1.63 ± 0.07	1.45 - 1.72	1.63 ± 0.07	1.45 - 1.72
10 day infection	2.05 ± 0.05	1.52 - 2.37	2.07 ± 0.05	1.54 - 2.37
20 day infection	3.56 ± 0.16	2.24 - 4.27	3.43 ± 0.16	2.26 - 4.43
30 day infection	4.88 ± 1.39	2.77 - 6.37	5.95 ± 0.77	4.60 - 6.64
40 day infection	8.67 ± 0.33	6.42 - 9.46	10.44 ± 0.41	8.41 - 12.71
50 day infection	9.40 ± 0.36	8.45 - 12.20	11.37 ± 0.32	11.12 - 11.84

* Mean body length ± 95 % confidence interval, in millimeters.

This represents a 35% increase in male body length and a 75% increase in female body length.

Worms from 40 day infections averaged 8.67 mm. and 10.44 mm. long for males and female respectively. This represents a 75% increase in body length for both males and females.

Worms from 50 day old infections averaged 9.40 mm. and 11.37 mm. in length for males and females respectively. This represents an 8.5% and 9.0% increase in body length over 40 day old worms for males and females respectively.

The most rapid increase in body length occurred between 10 and 40 days after infection. The widest variability of body lengths was recorded for 20 to 40 day old worms. As the rate of growth diminished from 40 to 50 day old infections, the body length values fell into narrower limits (see Figures 5 and 6).

No third stage juveniles were observed after infection; fourth stage juveniles were found in 10, 20 and 30 day old infections and adults were first seen in 20 day infections. Adults were never under 3.00 mm. in length and fourth stage juveniles never over 3.00 mm.

Development and Morphology

All the E. uncinata recovered from the 10 day infections were fourth stage juveniles which have straight, non anastomozing cordons under 0.15 mm. long (Fig. 22) and four rows of body spines.

FIGURE 5

BODY LENGTHS OF E. UNCINATA MALES OF DIFFERENT AGES

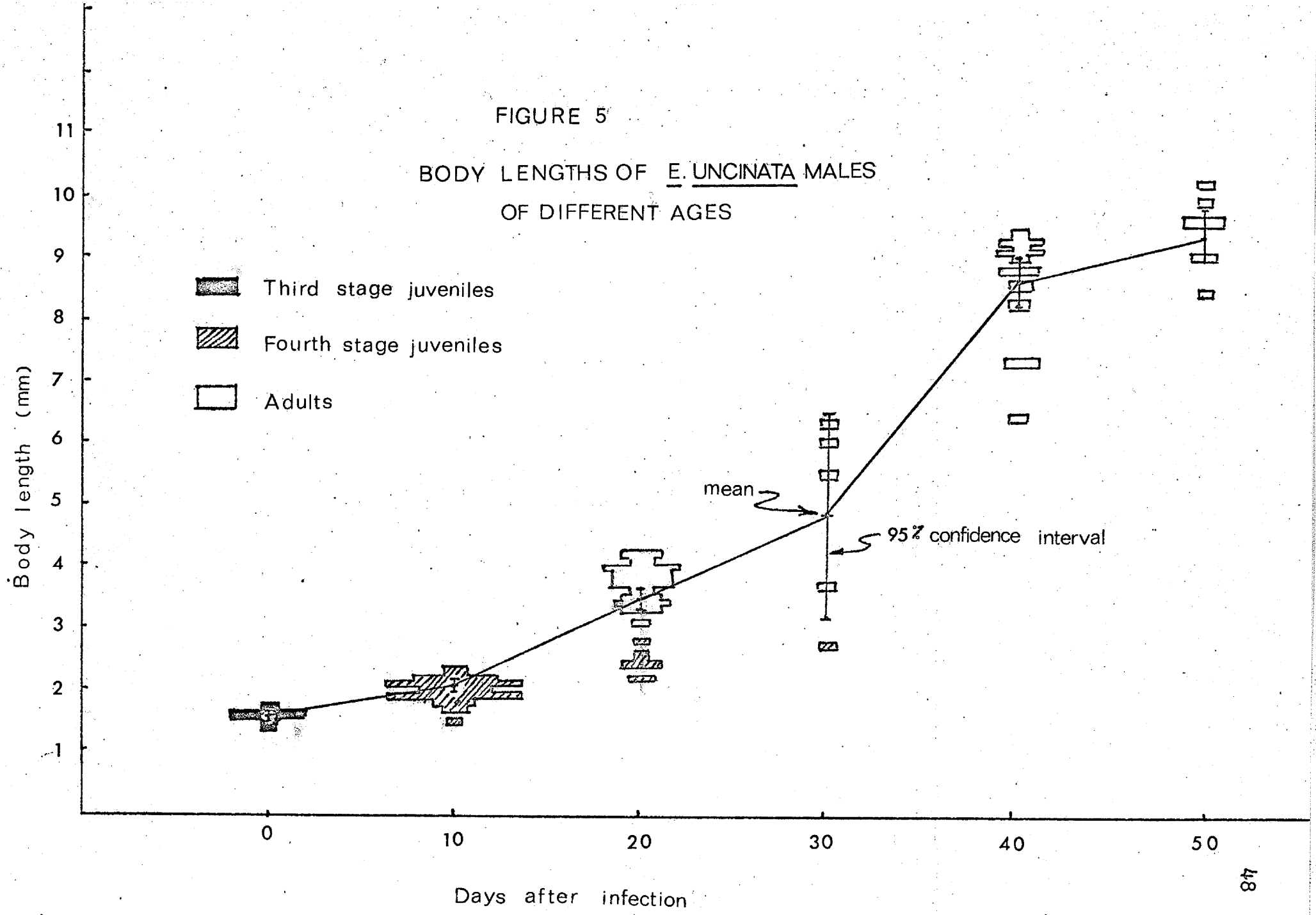


FIGURE 5

BODY LENGTHS OF E. UNCINATA MALES OF DIFFERENT AGES

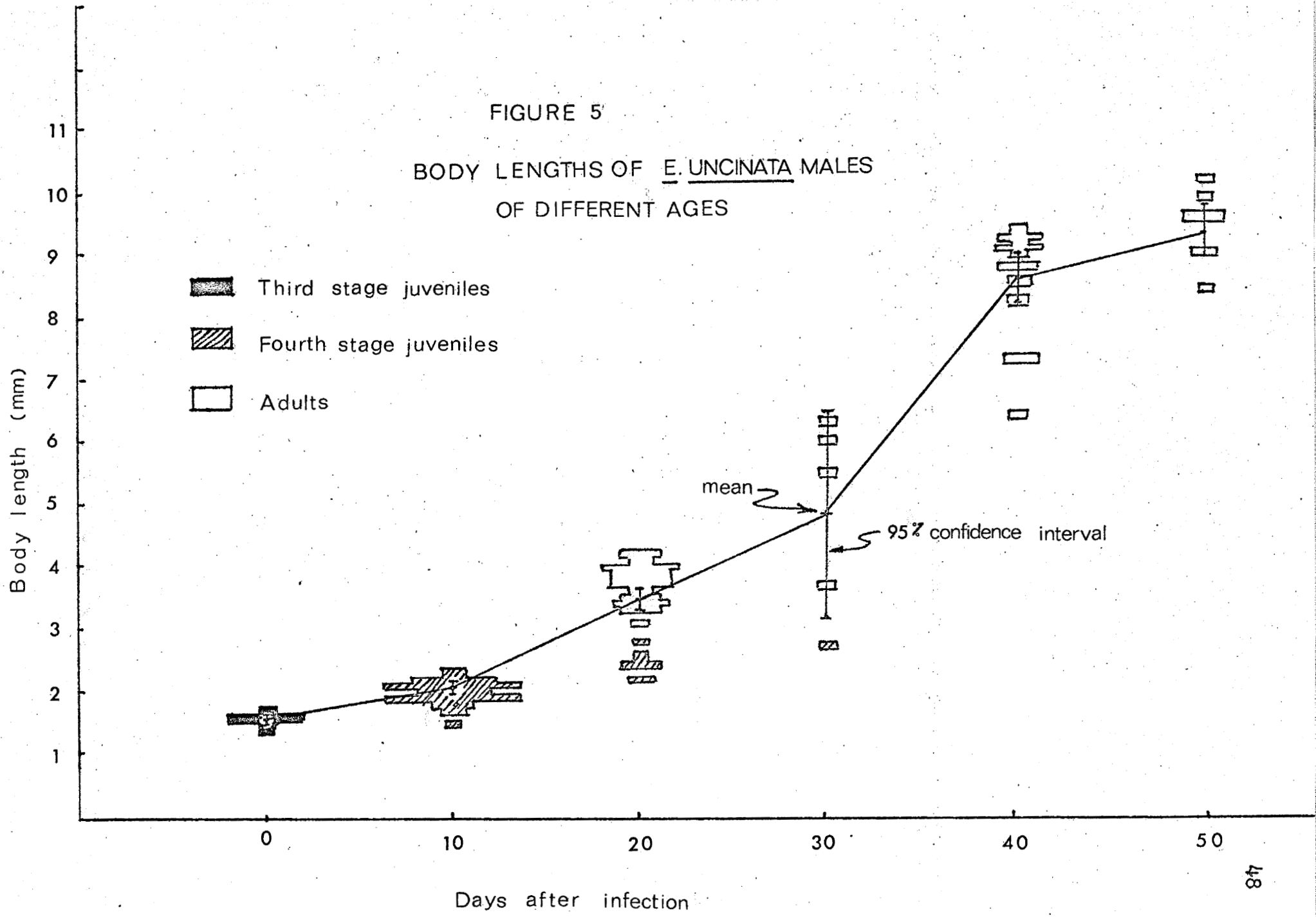
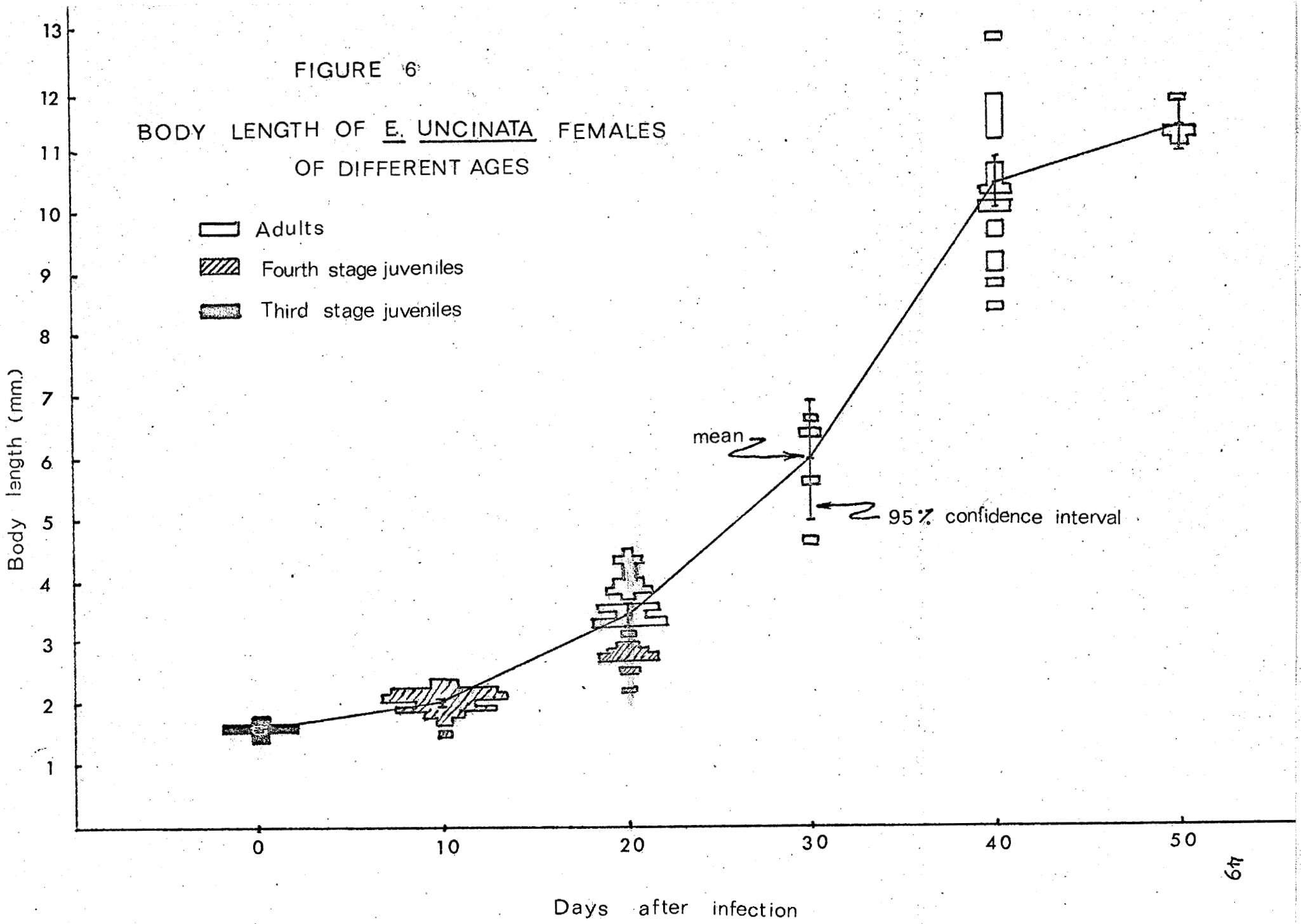


FIGURE 6

BODY LENGTH OF E. UNCINATA FEMALES OF DIFFERENT AGES



Males lacked adult sexual characteristics; tails were straight and lacked alae or papillae, and spicules were absent, although a dense cell formation in this region suggested the spicule anlagen. Females lacked a vulva, but a spherical mass of cells, possibly the vaginal anlage, appeared in this region. A slender, cuticle - like structure connected the developing vagina - ovijector with the cuticle of the animal (Fig. 25 and 26).

Two mallards with 20 day infections had parasites moulting from fourth stage juveniles to adults (Fig. 23). The third mallard had only fourth stage juveniles which resembled worms from 10 day infections. Moulting of the worms in temporary water mounts was observed. The cuticle split longitudinally from the tip of the tail, allowing the parasite to back on itself, as when someone pulls his hand out of a rubber glove. Thus, the completely shed cuticle is inside out. Body spines and cordons are clearly visible on the inside of the shed cuticle.

The emerged adults have long (generally over 0.25 mm.), winding cordons that anastomoze. Males showed most adult characteristics. Tails were strongly coiled ventrad and had well defined, pedunculate papillae and caudal alae. The small right spicule was completely formed but appeared more translucent than that of older adults. The large left spicule was completely formed distally, but not proximally. As a result, it was only slightly longer than the short spicule. The gonad was completely developed,

extending anteriad to about the mid point of the body. The vas deferens was distended with developing sperm but the seminal vesicle was not apparent.

Females had well developed vulva and a vagina lined with cuticle (Fig. 27). The ovijector, which swings posteriad from the vagina, was muscularized and the ovaries appeared ripe. Uteri were filled with developing embryos or unshelled eggs. The long and slender opisthodelphic ovaries were reflexed about mid body.

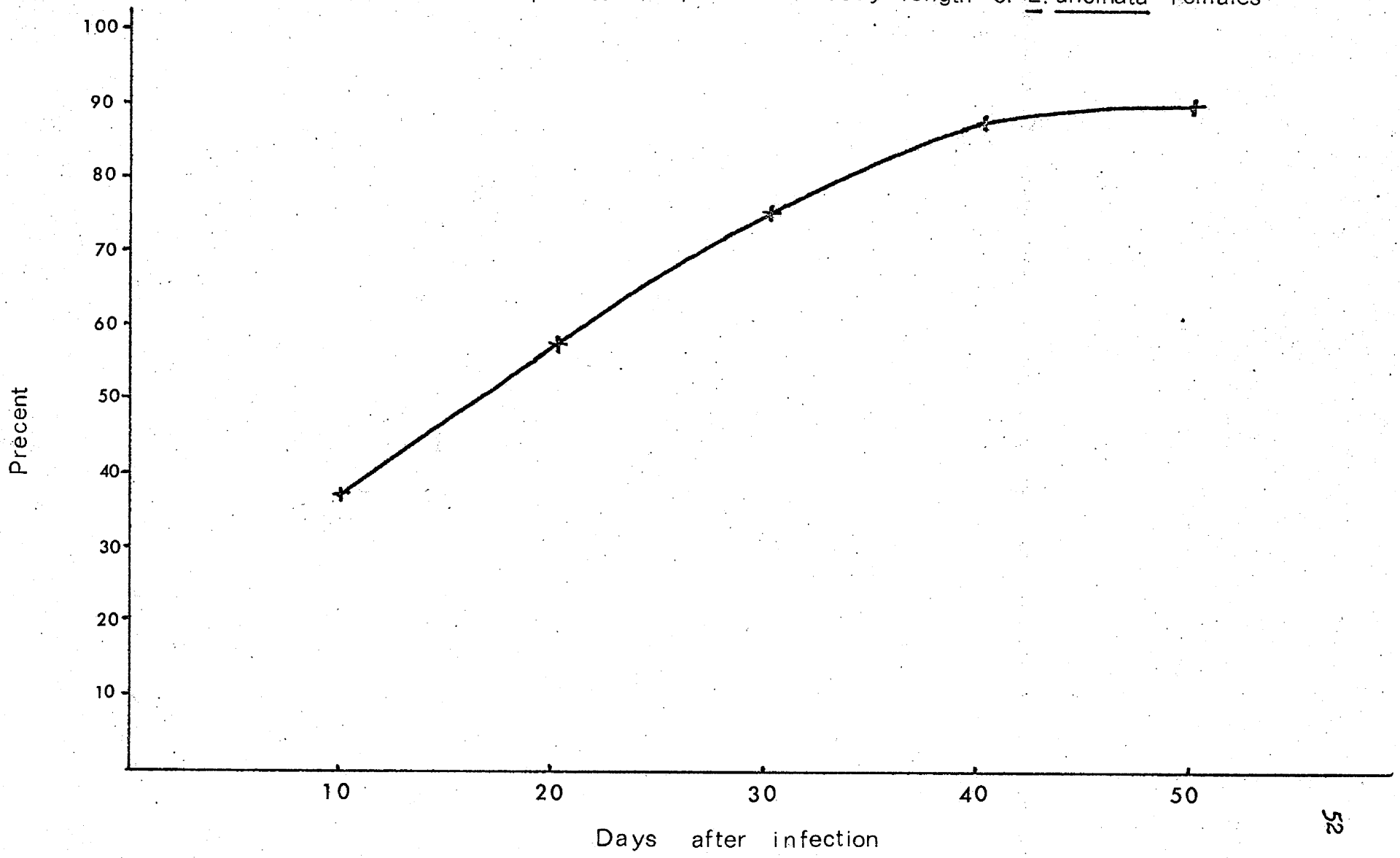
All but one of the worms recovered from 30 day infections were adults. Males were sexually mature and some ejaculated spermatozoa when held in a small dish of water. The large left spicule was completely formed. Uteri of females were distended with shelled ova and extended down 75% of the body (Fig. 7). Ova did not contain completely formed embryos. No females were seen laying eggs.

In 40 day infections, males were as described above (Fig. 29), but larger. Females had completely embryonated ova in their uteri (Fig. 27), which extended nearly 90% of the body length. Some worms laid thin strings of one to two dozen eggs which seemed connected by a fine secretion passed with the ova (Fig. 28).

Both male and female parasites from the 50 day old infections were larger than previously described. The gonads extended to 58% of the body length in males and 93% in females (Fig. 24).

FIGURE 7

Anterior extension of uteri expressed as percent of body length of E. uncinata females



Pathogenicity

In the 10 day infections, small lesions were present on the mucosal lining of the gizzard, isthmus and proventriculus of the host. Small foci of inflammation on the mucosa of the isthmus were also visible (Fig. 8A). These foci were circular, slightly raised and lighter than the surrounding mucosa (Fig. 30). Mucus was sometimes evident in this region.

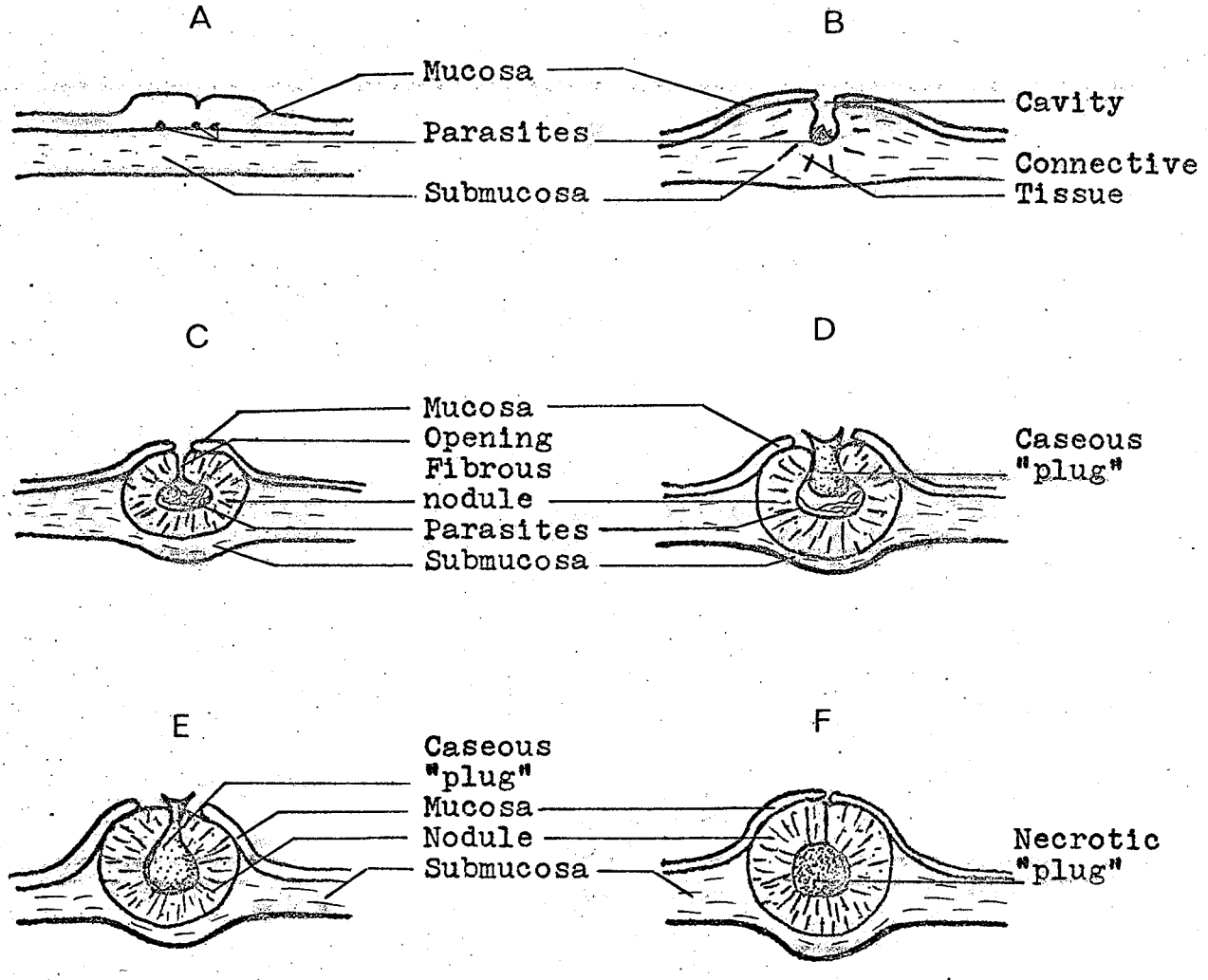
All parasites were found between the yellowish mucosal layer and the whiter, downy, submucosal layer. Most of the worms were recovered from the vicinity of the foci of inflammations, though several were located elsewhere under the mucosa of the proventriculus and gizzard. All of the birds examined with 10 day infections were parasitized.

In 20 day infections, the inflammations on the isthmus were more pronounced than in 10 day infections (Fig. 31). The mucosal layer was eroded about a central opening in each nodule (Figure 8,B). This opening sometimes contained a small, yellowish "plug" of caseous material. The submucosa was swollen about the opening, pink, hardened and fibrous. The parasites were found only in the central cavities of each granuloma. All three birds with 20 day infections were parasitized.

In 30 day infections, the granulomas were prominent and projected well into the gut lumen. Their openings with eroded mucosa, were often plugged with necrotic tissue (Fig. 8,D and 38).

FIGURE 8

Diagrammatic Cross-section* of Mucosa and Submucosa of Isthmus Showing Pathological Reactions to E. uncinata



* Diagrams based on gross observations.

A. Typical reaction observed in 10 day infections.
B. Typical reaction observed in 20 day infections.
C.-F. Typical reactions observed in 30 to 50 day infections. (Fig. 32)
E. and F. These granulomas rarely had living parasites. (Fig. 38)
F. Note - mucosa nearly healed over granuloma.

The walls of the cavities of these granulomas were thick, fibrous, firmer closer to the cavity and softer farther away. Many of the granulomas lacked parasites. Instead, large necrotic irregular masses filled the cavities normally occupied by the worms (Fig. 8,E; 8,F; 33 and 34).

In 40 day infections, granulomas were larger and thicker than those in 30 day infections. All the worms were located in the relatively small cavities at the center of the nodules. Cloudy fluid, presumably lymph, and necrotic debris were common in the cavities both with and without parasites. Only two of the four birds examined had parasites.

Many smaller and less prominent granulomas were found in birds with 50 day infections. Often the mucosal layer had completely healed over the granulomas so that no opening was evident. The central cavities of many were completely filled with a necrotic mass (Fig. 8,F). A few of the granulomas had tiny central cavities without any necrotic material or parasites. Only one of the four birds examined had parasites.

6. GROWTH, SURVIVAL AND PATHOGENICITY OF *E. UNCINATA* IN DELTA MALLARDS OF DIFFERENT AGES

Four groups of five Delta Mallards were administered third stage *E. uncinata*, 50 per bird. The first group was

infected when the birds were one week old, the other three groups when the birds were one, two and three months old respectively. All birds were autopsied 40 days after inoculation.

Growth and Survival

All birds infected at one week had an average of 21 worms per bird when autopsied. Male worms averaged 8.54 mm. long and females 10.57 mm. (Table VIII).

A total of 79 worms were recovered from the mallards infected at the age of one month. Males averaged 7.92 mm. long and females 8.26 mm. One of the five birds had no parasites at the time of autopsy.

Four of the five birds infected at two months were parasitized after 40 days with a total of 34 worms. Male parasites averaged 6.24 mm. long and females 4.68 mm.

Three of the five birds infected at three months had a total of 29 E. uncinata when autopsied. Males averaged 6.36 mm. and females 6.90 mm. long.

Pathogenicity

Granulomas of birds infected at one week were generally large, thick - walled and located on the isthmus. Many contained necrotic debris and worms. Sometimes, when parasites were present, a large green caseous mass was found in the cavity.

TABLE VIII

Body lengths of *E. uncinata* from Delta Mallards of different age

Host age when infected	Male *E. uncinata*		Female *E. uncinata*	
	$\bar{X} \pm$ 95% C. I.*	Range	$\bar{X} \pm$ 95% C. I.*	Range
One week	8.54 ± 0.24	7.65 - 9.75	10.57 ± 0.58	8.40 - 12.95
One month	7.92 ± 0.56	5.02 - 9.19	8.26 ± 0.84	5.02 - 10.55
Two months	6.24 ± 1.20	4.86 - 7.66	4.68 ± 1.49	2.31 - 7.40
Three months	6.36 ± 0.76	4.35 - 7.78	6.90 ± 0.84	5.35 - 8.30

* Mean body length ± 95% confidence interval, in millimeters.

Granulomas of birds infected at one month were thick - walled and contained white or yellow caseous material in their cavities.

Granulomas of birds infected at two months had thick walls, and were sometimes completely solid. Yellow or white necrotic debris was generally found in those granulomas that had a cavity. In one case, some worms were found outside the granuloma, in a mucus overlying it.

Granulomas from birds infected at three months were also thick - walled and contained green or white necrotic debris, sometimes with pink coloration suggesting the presence of blood. Small scars, probably remnants of old, degenerated granulomas were present in several birds.

7. GROWTH, SURVIVAL AND PATHOGENICITY OF E. UNCINATA IN DIFFERENT WATERFOWL SPECIES

Two sparate experiments were carried out, one in 1968 and one in 1969. In the former, 16 birds (8 species, 1 subspecies) were given access to the Field Station Pond (site one), an area with abundant Daphnia infected with E. uncinata. Birds were examined 42 and 43 days after the start of the experiment. The results are summarized in Table IX.

TABLE IX

Waterfowl With Naturally Acquired Infections of E. uncinata

Host	Age*	Sex	Infection Age*	No. Nodules	Parasite No.	Weight
Anas strepera	42	female	21	30+	1,000+	165 gr.
A. platyrhynchos	93	male	43	10	50 - 100	1,307 gr.
A. platyrhynchos	94	male	43	6	-	1,134 gr.
A. p. domesticus	58	male	43	14	100+	2,227 gr.
A. p. domesticus	58	female	43	6	-	1,778 gr.
A. acuta	92	male	42	4	-	791 gr.
A. acuta	92	female	42	2	-	709 gr.
A. clypeata	79	female	43	-	-	490 gr.
A. clypeata	79	female	43	-	-	518 gr.
Aythya americana	76	male	43	-	-	786 gr.
A. valisineria	72	male	42	3	10 - 20	717 gr.
Oxyura jamaicensis	66	female	42	1	-	438 gr.
Oxyura jamaicensis	66	female	42	2	-	425 gr.
Anser domesticus	87	female	43	16+	10+	4,791 gr.

* Days

Pathogenicity in Naturally Acquired Infections

A gadwall, Anas strepera, died 21 days after the start of the experiment. This bird was seriously emaciated and weighed only 165 grams compared to the normal weight of 500 to 550 grams for a healthy gadwall of the same age (Oring, 1968). The proventriculus (45.0 x 30.0 mm.) was remarkably swollen and inflammed. Tall, bloody peaks of proventriculus tissue projected through the thick (25.0 mm.) mucus jelly overlying the entire organ. Over 1,000 parasites were found both in the mucus and stomach tissues.

Two wild mallards, Anas platyrhynchos platyrhynchos, had an average of 8 large granulomas from 5.0 by 5.0 mm. to 11.0 by 15.0 mm., near the isthmus only. Mucus often reddish in colour, possibly evidence of bleeding, accompanied the granulomas.

Two domestic mallards, Anas platyrhynchos domesticus, had an average of 10 large granulomas ranging in size from 7.0 by 9.0 mm. to 11.0 by 15.0 mm., on the isthmus as a continuous band of hyperplastic connective tissue with interconnected cavities. One bird had a granuloma, 7.0 by 7.0 mm., at the junction of the proventriculus and oesophagus. The granulomas, often protruding 6 or 7 mm. into the lumen of the stomach, contained large, yellow necrotic plugs in their central cavities and openings.

Two pintails, Anas acuta, had an average of 3 low profile granulomas ranging from 1.5 by 1.5 mm. to 5.0 by 5.0 mm. in size. Several had yellow, necrotic material in their nodule cavities.

One of the two ruddy ducks, Oxyura jamaicensis, had a small soft nodule 1.0 by 1.0 mm. on the isthmus. The other had two granulomas. One was large (14.0 by 14.0 mm.) and appeared muscularized, with abundant caseous material around the parasites in the central cavity.

A canvasback, Aythya valisineria, had three granulomas, 7.0 by 8.0 mm. to 10.0 by 10.0 mm. located on the isthmus. All the worms (10 - 20) found in this bird were under 3.0 mm. long.

Redheads, Aythya americana, and shovellers, Anas clypeata, had neither parasites nor granulomas. A few small scars were present on the isthmuses of the shovellers.

The domestic goose, Anser domesticus, had sixteen large (up to 8.0 by 10.0 mm.) granulomas. Eight were located at the junction of the oesophagus and proventriculus, four were in the glandular portion of the proventriculus and four along the isthmus which also had other, smaller lesions. The larger granulomas were haemorrhagic.

In 1969, another experiment was carried out with 57 birds (eleven species and one subspecies). Each bird was administered 50 third stage juveniles of E. uncinata when the birds were 15 to 19 days old. The birds were autopsied 40 days after infection.

Growth and Survival

Delta Mallards had a total of 22 worms with only one bird of five parasitized at the time of autopsy. Male worms averaged 6.49 mm. and females 7.61 mm. long (Table X).

Domestic mallards had an average of 26 parasites per bird and all six birds were infected when autopsied. The worms averaged 8.21 mm. and 10.13 mm. in length for males and females respectively.

All gadwalls were parasitized with an average of 23 worms when autopsied. Male worms averaged 7.56 mm. and females 7.96 mm. in length.

Four of five pintails were parasitized when autopsied. The total of 73 worms had mean body length of 6.27 mm. and 6.43 mm. for males and females respectively.

Only three of five blue - winged teal, Anas discors, survived forty days after infection, and were not parasitized when autopsied. The other two teal, killed by other birds 23 and 24 days after infection, had one worm each.

Four parasites were found in a shoveller duckling which was killed 11 days after infection by other birds. Four other shovellers which survived the 40 day experimental period, were not parasitized when autopsied.

None of five redhead ducklings harbored parasites when autopsied.

TABLE X

Different Waterfowl Species Artificially Infected With E. uncinata

Host	Ave. No. Worms	Ave. No. Nodules	$\bar{X}$ Body length Male worms* ± 95% C.I.	$\bar{X}$ Body length Female worms* ± 95% C.I.
Anas platyrhynchos	4.5	3	6.49 ± 1.79	7.61 ± 4.25
A. p. domesticus	26	3.5	8.21 ± 0.62	10.13 ± 0.90
A. strepera	23	3.2	7.56 ± 0.73	7.96 ± 0.37
A. acuta	13.5	3.6	6.27 ± 0.84	6.43 ± 1.75
A. discor	-	-	-	-
A. clypeata	-	-	-	-
Aythya americana	-	1.0	-	-
A. affinis	4	2.6	6.70 ± 0.91	6.33 ± 0.61
Oxyura jamaicensis	0.5	0.5	-	9.34 **
Anser domesticus	3.5	2.3	6.46 ± 1.22	6.26 ± 0.60
Fulica americana	-	-	-	-

* Body length ± 95% confidence interval in mm.

** Body length taken from a single worm.

Lesser scaup ducklings, Aythya affinis, had a total of 20 parasites. Only one of five birds was parasitized. Male worms averaged 6.70 mm. and females 6.33 mm. in length.

All five common eider ducklings, Somateria mollissima dresseri, died before the scheduled autopsy date. Inspection of the air sacs revealed nodules similar to those of aspergillosis. All birds had parasites when they died. The longest surviving bird (33 days after inoculation) had twenty parasites which averaged 8.40 and 10.85 mm. in length for males and females respectively.

Two of four ruddy ducklings were parasitized with one worm each. One worm, a female, was 9.34 mm. long.

When autopsied, two of four domestic geese had a total of 14 E. uncinata which averaged 6.46 mm. and 6.26 mm. long for males and females respectively.

None of four coots, Fulica americana, had parasites 40 days after infection.

Pathogenicity in Artificially Infected Birds

In Delta Mallards, an average of three granulomas per bird was found. All granulomas were located on the isthmus. In one bird, two nodules with small worms (about 4 mm. long) contained yellow necrotic material. A third nodule with large worms (9.00 - 11.00 mm. long) lacked necrotic material. Some of the birds

without parasites had low profile, soft granulomas. In others, harder and more prominent nodules with "glycerine - jelly" like plugs were seen.

Domestic mallards had an average of 3.5 granulomas per bird. All granulomas were located near the isthmus, and most contained white, caseous material in the central cavities which often adhered to the parasites. Some granulomas contained green or brown "glycerine - jelly" like plugs. A few contained a clear fluid with parasites.

Gadwalls had an average of 3.2 granulomas near the isthmus mostly without necrotic material.

Pintails had an average of 3.6 granulomas at the isthmus which usually contained yellow, caseous material. A few had a white, cloudy fluid, and in one the lining of the cavity was reddish. Most nodules had thick fibrous walls and relatively small cavities.

No granulomas were present in the blue - winged teal which survived 40 days after infection. Only small (1.0 mm. by 1.0 mm.) scars were noticed on the isthmus. A different situation existed in the two teal which were killed at 23 and 24 days following inoculation. One bird had 3 nodules, two filled with large yellow "plugs", and the third with a hard, green, necrotic "plug". The other teal had a large, white

caseous plug in its single nodule (Fig. 38).

Two small nodules were present in the shoveller which died 11 days after inoculation, but only small scars were present on the isthmuses of the other shovellers.

The lesser scaups had an average of 2.6 granulomas, usually containing necratic material, either the yellow, caseous type or the green, "glycerine - jelly" type. A few of the nodules were solid connective tissue without a central cavity.

Eider ducklings had granulomas confined to the isthmuses. The nodules lacked openings in the 33 day infection, though worms were present. White and yellow caseous material was present in these nodules.

Two of the four ruddy ducklings had thick - walled granulomas. The other two birds had only inconspicuous scars located on the isthmuses.

A total of nine granulomas were found in four domestic geese. Seven nodules were located at the junction of the oesophagus and proventriculus (Fig. 36); the other two were on the isthmus. All granulomas contained large, irregular plugs of yellow caseous material (Fig. 33 and 34).

No granulomas were present in any of the coots. However, a band of necrotic mucosa was seen at the junction of the proventriculus and gizzard (Fig. 37). I was unable to

determine whether or not this band was the result of echinuriasis.

8. GROWTH, SURVIVAL AND PATHOGENICITY OF E. UNCINATA IN DELTA MALLARDS WITH DIFFERENT INTENSITIES OF INFECTION

Eight Delta Mallards, about one month old, were arranged in four pairs; one pair received 100, another 250, another 500 and the other 750 third stage E. uncinata. All birds were autopsied 40 days later.

Growth and Survival

Of the two birds which received 100 parasites each, one had 13 and the other none at the time of autopsy. The male worms averaged 5.61 mm. and females 5.54 mm. in length (Table XI).

The two birds which received 250 parasites each had 40 and 66 worms when autopsied. Males averaged 7.24 mm. and females 7.76 mm. long.

The two mallards which had received 500 parasites each had 107 and 218 worms averaging 8.68 mm. and 9.56 mm. in length. Often, worms from one granuloma were noticeably larger than those from an adjacent nodule.

One of the two birds which had received 750 parasites each had 179 worms averaging 9.52 mm. and 11.22 mm. long for males and females respectively. The other bird had none.

TABLE XI

E. uncinata infections of different intensities in Delta Mallards

Sex	Weight (grams)	Infection No.	No. Recovered.	Nodule No.	$\bar{X}$ Body length ± 95% C. I.*	
					Male worms	Female worms
Female	1,088	100	13	6	5.61 ± 0.63	5.54 ± 1.16
Male	1,160	100	-	3		
Male	1,025	250	40	10	7.24 ± 1.54	7.76 ± 2.95
Male	1,025	250	66	10		
Female	1,085	500	218	26	8.68 ± 0.30	9.56 ± 0.65
Male	1,169	500	107	15		
Female	1,034	750	-	7	9.52 ± 0.56	11.22 ± 0.88
Female	1,069	750	179	16		

* Confidence interval in mm.

Pathogenicity

All granulomas formed during this experiment were located on the isthmuses of these birds.

The two birds which received 100 parasites had three and six granulomas usually containing caseous material which filled the central cavities and plugged the openings.

The two birds which received 250 parasites had ten granulomas each. Some of the nodules contained yellow caseous material while others were filled with a clear or cloudy fluid.

The two birds which received 500 parasites had sixteen and twenty - six granulomas. These were crowded in a band along the isthmus. The fibrous walls of adjacent nodules were continuous, forming a ridge of connective tissue with a series of cavities filled with parasites and caseous material.

One of the two birds which received 750 parasites had seven granulomas, the other sixteen. The former had no parasites. Its granulomas were heavily walled with barely discernible cavities, three of which contained bits of greenish, necrotic debris. The other bird had numerous parasites in the cavities along the ridge of fibrous tissue. Seven of these cavities also contained some caseous material.

9. OBSERVATIONS ON THE LONGEVITY OF E. UNCINATA IN MALLARD DUCKS

Twelve, juvenile Delta Mallards were captured in late summer (1968) on the Field Station Pond at the Delta Waterfowl Research Station. They were reared here and were thus exposed to E. uncinata which was present in the pond (Site one). During the winter and spring, a few birds were sacrificed at intervals to determine if the parasites persisted. Two wild mallards from the breeding stock maintained at the Field Station were also examined in early summer of 1969 (See Table XII).

Growth and Survival

In one female Delta Mallard with an estimated eight month infection, sixteen reddish E. uncinata were found. The red colour instead of the usual cream, may have been due to bleeding into the nodule cavity. The female parasites were about 8 mm. long.

In a wild mallard with an estimated ten month infection, eighty - two reddish worms were found. Females were between 18 and 20 mm. long. In another wild mallard with an estimated eleven month infection, forty - nine cream coloured worms were found. Males were 10 to 12 mm. long and females 13 to 17 mm. This bird probably died of the E. uncinata infection.

One female Delta Mallard with an estimated twelve

TABLE XII

Observations on Old, Naturally Acquired E. uncinata Infections in Mallard Ducks

Sex	Weight grams	Estimated Age of Infection*	No. Nodules Found	Parasite No.	Remarks
Female	986	6 weeks	7	350 +	Bird in emaciated condition
Female	754	7 months	-	-	Small scar present on isthmus
Male	935	7 months	2	-	Green necrotic material in nodules
Female	1,020	8 months	3	16	Worms reddish, caseous material in nodules with worms.
Male	1,053	8 months	3	-	All nodules closed, necrotic debris present in nodules.
Male	1,032	9 months	2	-	Nodules closed, other scars present
Female	852	9 months	-	-	One small scar on isthmus
Male	1,098	9½ months	-	-	Four small scars on isthmus
Female	878	9½ months	2	-	Caseous material in one nodule
Female	1,203	10 months	1	-	Caseous material in nodule
Male	1,101	11 months	1	-	Caseous material present
Female	1,248	12 months	6	398	Nodules thin-walled, filled with fluid. Bird with deformed liver.
Male**	1,155	10 months	2	82	Nodules thin-walled, filled with bloody fluid. Many parasites dead.
Male**	830	11 months	4	49	Nodules filled with caseous material. Bird believed died of echinuriasis.

* Estimated age of infection equals age of bird. Based on date of first exposure to Field Station Pond - only applies to Delta Mallards.

** These two birds were wild mallards, both adults.

month infection, had 398 parasites. The large, about 20 mm. long, female E. uncinata had reddish anterior ends.

Pathogenicity

The Delta Mallard with the eight month infection had three small granulomas, and one contained a soft, yellow, necrotic "cream" with parasite eggs, spicules and pieces of dead worms.

The wild mallard with the ten month infection had two large granulomas and several smaller ones located on the isthmus. The largest (25 x 20 x 20 mm.) had a spherical shape maintained by turgor pressure of the bloody fluid inside its thin, fleshy walls. Fifty - two dead E. uncinata with white, necrotic debris adhering to their cuticles were found. The worms were only slightly decomposed which suggested recent death. The second granuloma, 12 x 15 mm., also had thin walls and contained grayish fluid and thirty living parasites.

The wild mallard with the eleven month infection had four granulomas averaging 9.5 by 7.0 mm. on the isthmus. These blocked the opening between the proventriculus and gizzard, probably causing the severe emaciation and death of this bird. There was no blood in these granulomas, but bleeding was evident in the overlying mucosa. Each nodule contained worms and yellow caseous material.

The Delta Mallard with the estimated twelve month infection had six granulomas averaging 10 by 12 mm. Their cavities contained fluid and parasites (Fig. 35). No necrotic material or blood was seen. The body cavity of the bird contained a clear fluid and the liver appeared cirrhotic. The left lobe was thick and white and the right lobe red with a yellow mottled pattern. The bird appeared healthy at the time of autopsy.

The other Delta Mallards with estimated seven to eleven and a half month infections, had no E. uncinata when autopsied, but all birds showed evidence of previous infections. Some had well developed granulomas containing hard, green or brown necrotic masses. Others were filled with yellow caseous material. The mucosal layer had healed over the openings of many of the parasite - free nodules. Some birds had small scars on the isthmuses suggesting previous infections with Echinuria.

DISCUSSION

The results of my investigations were statistically analysed and compared to other published data. Proper statistical evaluation was hindered by the fact that in some cases relatively few experimental animals were used due to limitations in time, cost and facilities. Another disadvantage to the statistical approach stemmed from the high morphological and presumably, physiological variability of the Delta Mallard. These ducks originated from the McGraw Mallard, developed from a domestic duck X wild mallard cross. Delta Mallards have therefore inherited considerable gene diversity. The lack of selection pressure on these captive birds may have allowed a higher frequency of unusual phenotypes to appear in the flock. These two facts might account for wide variation in our data.

1. OCCURRENCE OF E. UNCINATA IN THE INVERTEBRATES OF THE DELTA MARSH

The presence of E. uncinata in waterfowl at Delta was first described by Cornwell in 1963. An estimated 30% of the ducks on the Field Station Pond (Site 1) and a valuable trumpeter swan cygnet died of Echinuria infections. Crichton (1969) found E. uncinata in wild mallards and pintail which dwell elsewhere in the marsh.

Infective juveniles of E. uncinata were found in the Field Station Pond in 1968 and 1969. In mid July, 1968, juveniles were first found in Daphnia pulex and D. magna. However, it is probable

that the worms were present in the pond as early as late May. Samples taken in late October still contained parasites.

In 1969, more extensive sampling and more careful examinations revealed the presence of the parasites earlier than in 1968. Ice on the pond melted by mid April, and by late April the first Daphnia appeared. In late May, the first parasites were found in the crustaceans. This is interesting for two reasons; first, the appearance of parasites in late May, 1969 supports the contention that Echinuria juveniles were also present in late May, 1968; second, the appearance of parasites one month after the first occurrence of Daphnia suggests that Daphnia must have become infected immediately after hatching from ephippia. The average water temperature between late April and late May was about 15°C., a temperature at which the parasites require 30 days to mature in Daphnia (Fig. 4).

Figure 3 gives the numbers of third stage E. uncinata juveniles per 100 cladocerans from the Field Station Pond from May to freeze - up. This histogram shows the changes in numbers of parasites in the intermediate hosts from May to November, but does not give an indication of the total numbers of juveniles, as no estimates of the size of the cladoceran populations were made.

In Daphnia pulex, the numbers of juvenile parasites increased sharply from the end of May to early July, when the ratio started declining. At the end of July, only one or two worms per 100 D. pulex were found. In the following months, this host became so uncommon that further examination for parasites was not warranted.

From mid August to early September, Simocephalus vetulus were frequently present in our samples. Five to six parasites per 100 S. vetulus were found during this period.

Daphnia magna, the largest and most numerous cladoceran, had the most parasites. The numbers of E. uncinata juveniles per 100 D. magna increased from late May to early July when it started declining, as it did in D. pulex. The reason for this decline is unknown, but a possible explanation is that a Daphnia bloom might have occurred, as recorded for Daphnia in this pond by Collias and Collias in 1954. A bloom would account for a higher proportion of uninfected Daphnia and result in a lower parasite - host ratio.

The numbers of third stage juveniles increased rapidly in mid July and reached a peak of 108 parasites per 100 D. magna in early August. This period of rapid increase occurred approximately 50 days after the first infective juveniles were found in the pond. Ducklings present at that time might have become infected. Their Echinuria would then have released ova into the pond in early July thus causing a rapid increase in the parasite - host ratio in mid July. After leveling off in August, the number of parasites declined to 14 per 100 D. magna in November.

The ratio of juvenile parasites per Daphnia was much higher in 1969 than in 1968. This apparent difference may be due to the fact that two of the three samples collected in 1968 were taken at a time when the ratio may have been particularily low, as it was during the same period in 1969. Also, all Daphnia, regardless of size,

were examined in 1968, while only the largest were examined in 1969. The smaller Daphnia have predominantly first and second stage juveniles which are not readily detected by the "squash technique". Consequently, many parasites may have been overlooked in 1968 samples. When only the largest Daphnia with predominantly third stage juveniles were examined in 1969, fewer parasites were missed.

In 1968, E. uncinata juveniles were recovered only from Daphnia from the Field Station Pond. In 1969, more extensive examinations revealed that these parasites were more widely spread. On March 22, 1969, a single, third stage juvenile was found in a Gammarus lacustris from the Blind Channel (Site 4). This demonstrated that an amphipod could vector E. uncinata juveniles and probably support them through the winter. Subsequent samples of Gammarus from this site were negative. In early June, third stage juveniles were found in Daphnia from Bain's pen and the Swan Pond (Site 2). Both pens received unfiltered water from the Field Station Pond. Parasites were also found in Daphnia from "dug - outs" excavated north of the new hatchery facilities earlier in the spring. These "dug - outs" received the effluent of a large, wild mallard breeding pen which held over 100 adult birds. One of these birds was later found infected with E. uncinata.

The epizootic of E. uncinata at Delta is similar to those reported from Eurasia. At Delta, this parasite occurred in stagnant pools used by waterfowl. The nematode was most abundant in mid summer and was limited to specific areas. Shevtsov and Zabello (1965);

Potemkina (1956); and others reported that echinuriasis was most serious in small, stagnant ponds intensively used by ducklings. Movsesian (1962) found the highest extensity of acuariid juveniles in Daphnia in mid summer. Kotel'nikov (1961) reported that all ducklings which used a pond with Daphnia 2% of which were infected with juveniles, were parasitized by E. uncinata. Venn (1954) noted that the incidence of echinuriasis was high in birds using stagnant pools but low when birds used flowing water. Potemkina (1956) stated that E. uncinata outbreaks occurred in limited areas or foci.

The focus of this nematode at Delta appears to be the Field Station Pond, an area intensively used by resident and migrant waterfowl. Nest boxes and feeders make this area attractive to many birds which produce many ducklings in the spring and summer. In autumn, migrant birds stop here and take refuge during the hunting season. Consequently, this pond is probably the main source of echinuriasis in the Delta Marsh.

2. E. UNCINATA INFECTIONS IN CRUSTACEANS OTHER THAN DAPHNIA PULEX AND D. MAGNA.

Daphnia pulex and D. magna were the only known intermediate hosts of E. uncinata until Kotel'nikov (1961) investigated other potential crustacean hosts. Experimentally, he was able to infect Gammarus sp., Asellus aquaticus (Isopoda), Ceriodaphnia sp. and a cyprid (Ostracoda) with E. uncinata by exposing these crustaceans

to the parasite's eggs. His findings prompted our investigation.

We found that five species of Cladocera (besides Daphnia), two Amphipoda, one Conchostraca, and one Anostraca became infected after exposure to E. uncinata eggs (Table VI). Two cladocerans, Alona sp. and Scapholeberis sp., did not become infected nor did any copepods, ostracods and insect larvae studied.

Why some crustaceans become infected and others do not is unknown, but host size may be a factor. Alona, Scapholeberis, copepods and ostracods are smaller than the crustaceans which become infected. Eggs of E. uncinata are probably too large for the smaller crustaceans to ingest.

3. GROWTH AND DEVELOPMENT OF E. UNCINATA IN DAPHNIA PULEX AND D. MAGNA.

Disagreements in the literature on the development time of E. uncinata in Daphnia (Table XIII) prompted this study.

As temperature influences the growth rate of this nematode in Daphnia, experiments were conducted at two temperatures, one at 20 - 24°C., and the other at 15°C. The former temperature equaled the water temperatures at Site 1 in August. The latter equaled the early spring and late fall water temperatures.

At 20 - 24°C., E. uncinata matured in ten days to third stage juveniles, 1.5 mm. long. In D. pulex juveniles were usually free in the dorsal hemocoel, whereas in D. magna they were in the

TABLE XIII

Published Development Times For *E. uncinata* in *Daphnia*

Development Time	Temperature	Reference
12 days	25 - 29°C.	Romanova (1947, 1948)
14 - 16 days	17 - 23°C.	Romanova (1947, 1948)
11 days	18 - 20°C.	Kotel'nikov (1961)
11 - 12 days	-	Kauker (1941)
12 - 16 days	-	Radin (1959)
5 days	26 - 30°C.	Garkavi (1960)
6 days	16 - 20°C.	Garkavi (1960)

gill filaments. They were never coiled inthe thoracic muscles. Growth and development of the parasites started soon after infection (Fig. 4).

At 15°C., maturation of E. uncinata took 30 days. Worms were coiled in thoracic muscles (Figs. 17 and 18) and developed little during the first ten days of the infection (Fig. 4). The effect of temperature on the metabolism of parasites and hosts may explain why growth rates differ in the two experiments.

Our observations generally agree with the published times needed for the development of E. uncinata in Daphnia (Table XIII). Slight discrepancies may result from differences in techniques. The major discrepancy between our observations and Garkavi's data may stem from his possible misinterpretation of the juvenile stages of the parasite. He claimed that the third stage juveniles were only 0.86 mm. long, this much smaller than those observed by us and others. He may, therefore, have confused second stage juveniles with third stage infective nematodes.

4. TOLERANCE OF E. UNCINATA OVA TO FREEZING AND DESSICATION.

We found that E. uncinata ova perished when frozen for 85 days, but that many survived for the same period when dried on filter paper. This may contradict Romanova's (1948) observation that eggs of E. uncinata perished in 20 - 26 hours when stored at "low temperature" or a relative humidity of 31 - 45%.

Tolerance to dessication may allow Echinuria eggs to survive in waterfowl faeces deposited on dry land. Rain or flooding could then wash the faeces and eggs into a pond and initiate an infection of intermediate hosts present.

5. GROWTH, ALLOMETRIC GROWTH, TAXONOMIC CONSIDERATION AND PATHOGENICITY OF E. UNCINATA IN THE DELTA MALLARD.

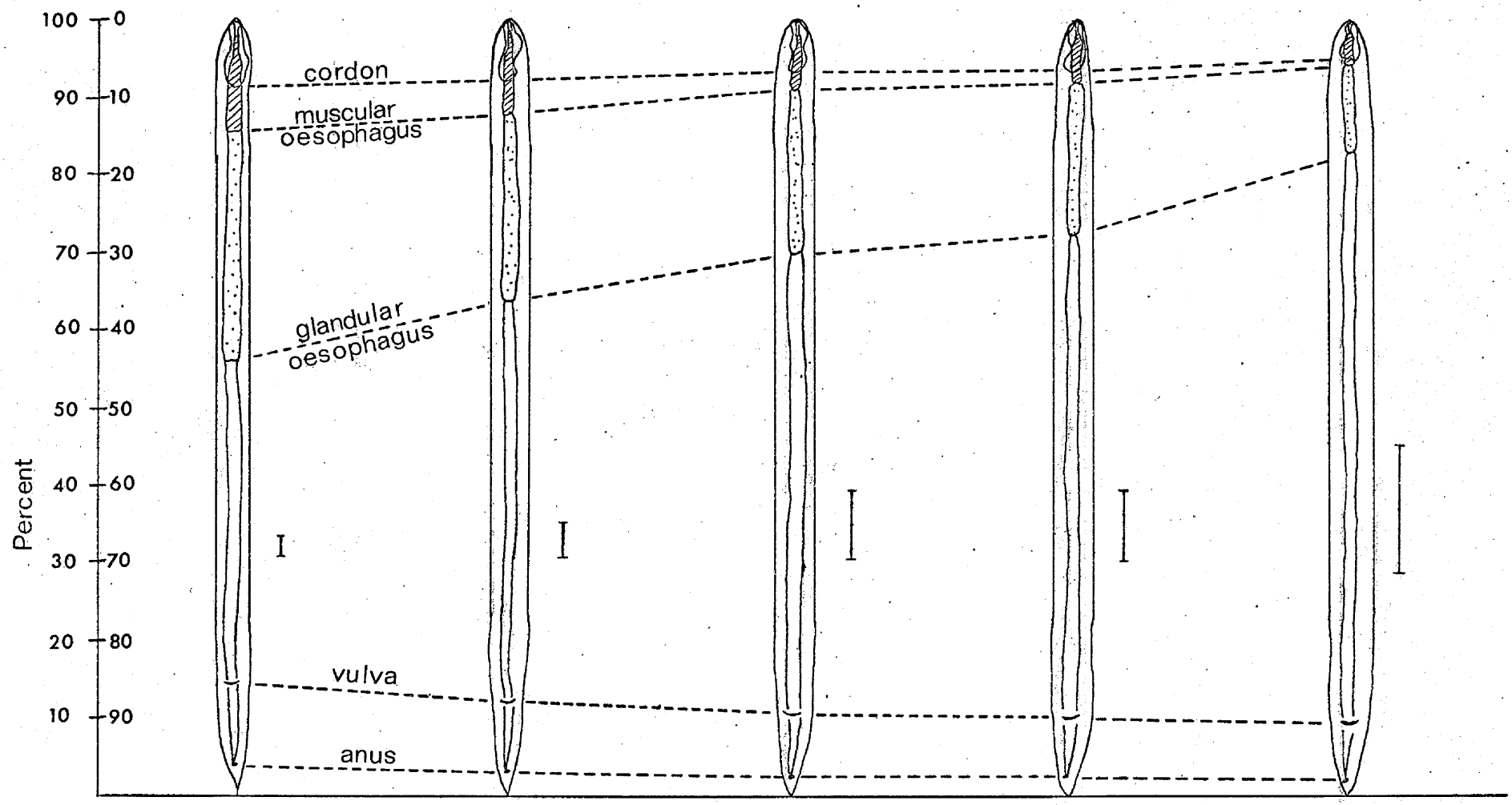
The growth of E. uncinata during the first 50 days of infection was not uniform but was fastest between 20 and 40 days, the period when gonadal development was most rapid (Figs. 5, 6 and 7). The middle portion of these grew faster than the head or tail ends, causing changes in body proportions (Fig. 9). Refer to Thompson (1959) and Medawar (1958) for a detailed discussion of allometric growth.

Chabaud and Petters (1961) and Williams (1929) believed that ratios of body parts and length are good taxonomic characteristics for the genus Acuaria. Their conclusion is probably correct if comparisons are limited to worms of the same stage of development. When Cram (1928) described Echinuria parva principally because its size and body proportions differed from those of large E. uncinata, she was probably unaware of the stage of development of those nematodes. When compared with 30 day E. uncinata, E. parva cannot be distinguished by Cram's characteristics. It seems probable that she described relatively young adults of E. uncinata as a new species.

Rhyzikov (1961) stated that absolute and relative spicule

FIGURE 9

Relative body proportions of E. uncinata adult females of different ages



lengths were good criteria to separate Echinuria species. Here again problems might arise if spicule lengths are used as taxonomic criteria for Echinuria of unknown age. In E. uncinata, the length of the left spicule ranges from 0.19 to 0.70 mm. in adult males from 20 to 50 day infections. The ratio of this spicule to body length ranges from 1 : 14.5 to 1 : 9.5; and the ratio of the right spicule length to the left spicule length ranged from 1 : 1.3 to 1 : 3.6 during the same period.

Cordon structure is another important taxonomic characteristic (Osche, 1955, and Chabaud and Petters, 1959) that varies during the development of E. uncinata. Third stage juveniles possess cordons resembling those of Paracuaria (Fig. 21), and fourth stage juveniles have Acuaria - like cordons (Fig. 22). Chabaud and Petters (op. sit.) indicated that Paracuaria and Acuaria are more primitive than Echinuria. They also discussed the occurrence of primitive cordon structure in juvenile stages of other Acuariidae.

Russian authors generally stated that 48 to 52 days were required for the development of E. uncinata to the egg - laying stage in ducks (Romanova 1938, 1947 and 1948; Radin, 1959). Kotel'nikov (1961) noted that only 40 days were needed before ovipositing commenced. His observations agree with our findings.

Detailed histopathological examinations of granulomas of Delta Mallards with E. uncinata infections were not carried out. Gross examination indicated that the nodules formed were fibrotic granulomas often containing necrotic material. Their location on

the isthmus, between the proventriculus and gizzard, may be explained by the fact that this region is softer and more easily penetrated than either the proventriculus or gizzard. Cram (1931) believed this to be true of Cheilospirura hamulosa (Diesing, 1851) Diesing, 1861, infections in chickens.

6. GROWTH AND SURVIVAL OF E. UNCINATA IN DELTA MALLARDS OF DIFFERENT AGES.

Four groups of Delta Mallards of different ages were infected with third stage juvenile E. uncinata to see if the age influences the resistance of the definitive host to this parasite. After 40 days, the size and numbers of parasites were compared to determine susceptibility of each group of birds. The size and number of parasites gave indications of growth and percent survival of the nematodes respectively. These parameters were correlated (correlation coefficient, P=0.001); the largest worms being found in infections with the highest percent survival of the parasites.

Our results indicate that one-week old Delta Mallards are more susceptible to E. uncinata infection than two and three-month old birds (Table VIII). One way analysis of variance was carried out on male and female body lengths from each of the Delta Mallard age groups. The F ratio was acceptable for both sexes (P=.01)

The frequency of echinuriasis is higher in younger birds than in older birds (Kauker, 1941; Knudsen, 1966; Shevtsov and Zabello

1965). Buscher (1965) stated that the high frequency of parasitism in ducklings may stem from the fact that ducklings feed more extensively on invertebrates (i. e. parasite vectors) than do adults. Other factors may also be important, however, as all of our ducks received identical numbers of parasites and yet had different intensities of infection. These factors may be physical, physiological and immunological. Toughness or thickness of stomach tissues and hormonal changes associated with maturation may effect the parasites growth and survival. Another factor, activity of antibody producing organs such as the bursa of Fabricius, is known to vary with the age of the bird (Olson, 1965).

7. SUSCEPTIBILITY OF DIFFERENT WATERFOWL SPECIES TO E. UNCINATA INFECTIONS.

Susceptibility to E. uncinata (ability of being invaded or infected by it) was determined in different species of waterfowl by comparing the size and number of parasites and number of granulomas in each species. Two experiments were performed, in one, naturally acquired infections were compared (Table IX); and in the second, infections from known numbers of infective juveniles were compared (Table X). Although the results of both experiments differed slightly, they indicated that some species of waterfowl were more susceptible than others. Species that had prominent granulomas which usually contained parasites were regarded as susceptibly. Resistant birds

had few or no granulomas or worms.

Susceptible were the domestic mallards, Delta Mallards, wild mallards, gadwalls, pintails, lesser scaup, common eiders and domestic geese. Mallards, gadwalls and pintails had great numbers of large parasites while the scaup and geese had fewer and smaller worms. The premature death of the eiders prevented the comparison of their parasites with those of other species, but they were heavily infected and parasites were large for their age.

Blue-winged teal, shovellers, redheads, ruddy ducks and coots seemed to be more resistant. Neither teal nor shovellers had parasites or granulomas at the end of the experimental period. The ducklings (two teal and one shoveller) which died prematurely had small granulomas and a single, 2 mm. long worm each. No redheads were parasitized when autopsied and only one of the six ducklings had granulomas. Ruddy ducks had few granulomas and very few worms. It is uncertain whether ruddy ducks are as resistant as the above birds. More birds should have been examined. Coots had neither granulomas nor parasites.

There are probably many reasons why the susceptibliliy to E. uncinata infection of different hosts varies. For example, shovellers, by nature of their feeding behavior, have probably been frequently exposed to Echinuria in the past. Perhaps, as the result of natural selection, shovellers have evolved a high resistance to this parasite. Blue-winged teal is closely related to the shoveller (Delacour and Mayr, 1945) and may share this resistance. Mallards

and pintails are closely related and are both susceptible. The high susceptibility of the domestic mallards may be the result of artificial selection to which these birds were exposed.

The size and physical properties of the birds may also influence their susceptibility. Of the dabbling ducks examined, the largest (mallards, pintails and gadwalls) were most susceptible and the smallest (teal and shovellers), the most resistant. The large domestic mallards and geese had the largest granulomas which probably provided more space for the parasites.

Bezubik (1956), Cornwell (1963) and Czaplinsky (1962) listed over 40 species of waterfowl serving as definitive hosts of E. uncinata (Table III). Unfortunately, these authors did not provide data on the extensity of infection in these birds.

8. GROWTH, SURVIVAL AND PATHOGENICITY OF E. UNCINATA IN INFECTIONS OF DIFFERENT INTENSITIES.

To see if growth, survival and pathogenicity of E. uncinata are influenced by intensity of infection, eight Delta Mallards were infected with large numbers of third stage juveniles and examined 40 days later (Table XI).

The examination showed that the growth of the parasites was fastest in birds which received the greatest numbers of juveniles and slowest in those which received the smallest numbers (single-factor Anovar P=.01). No correlation (reject below P=.01) existed

between the size of the inoculum (infection dose) and the survival of the nematodes; E. uncinata body length and percent survival; and parasite body length and number of worms. The lack of correlation in the latter three tests suggests that the existence of a relationship between inoculum size and parasite length is uncertain. Numbers of granulomas from each host correlated (corr. coef. P=.001) with numbers of parasites present (Fig. 10) but not with the inoculum size.

The fact that one statistical test was significant whereas the others were not may stem from the high variability in the data. For example, one mallard received 500 juvenile worms and retained 218 after 40 days. Another bird received 750 juveniles but was free of infection when autopsied. The use of more birds might have given more consistant results.

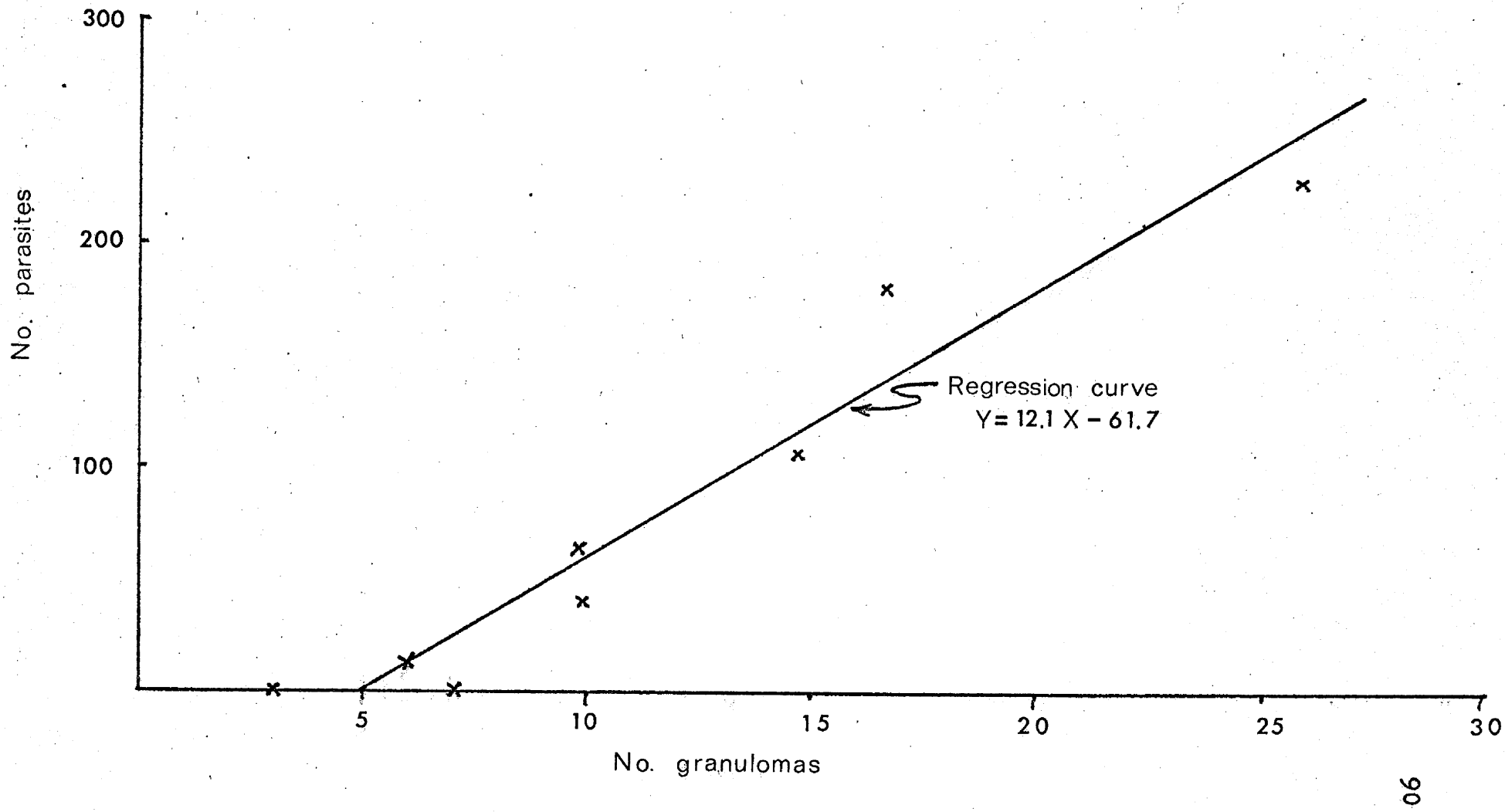
9. THE FATE OF E. UNCINATA IN WINTER AT DELTA.

At Delta, two conditions exist which permit this nematode to over-winter. First, certain areas of the marsh do not freeze to the bottom (e. g. Site 4); and second, many waterfowl are kept through the winter at the Delta Waterfowl Research Station.

By not freezing to the bottom, certain areas could provide a refuge for E. uncinata eggs, if these eggs can survive long periods of near freezing temperatures. The tolerance of Echinuria eggs to environmental stresses is not known, but Monné (1958) thought that the quinone-tanned proteins of E. uncinata egg shells may protect

FIGURE 10

Correlation between No. parasites and No. granulomas



the ova against cold, dessication and ultra violet light. Our observation, that eggs can survive dessication for 85 days corroborates his views.

Suitable crustacean hosts might also harbor E. uncinata through the winter in the water basins which do not freeze to the bottom. Gammarus sp. is known to harbor Streptocara sp. and Tetrameres sp. juveniles all winter (Klesov and Kovalenko, 1967). At Delta, Gammarus lacustris survives under the Blind Channel ice all winter and one individual with a juvenile E. uncinata was found on March 22, 1969. Daphnia can also survive all winter under ice (Pennak, 1953).

We cannot be certain if and how eggs and/or juveniles of E. uncinata over-winter at Delta, but we are certain that adult parasites survived in some of the birds kept at Delta in winter. Of twelve Delta Mallards reared on the Field Station Pond in the summer of 1968, one retained ovipositing worms to January, 1969 and one had nearly 400 worms in June, 1969 (Table XII). Crichton (1969) and Connell (unpublished) observed this nematode in wild ducks returning to the prairies in early spring, which suggests that this parasite might survive all winter in wild ducks as well.

Russian workers stated that most waterfowl parasites, including Echinuria, can not over-winter in a marsh. Gerasimova (1962) stated that helminths could not survive the winter in a marsh that freezes solid. Garkavi (1960) thought that E. uncinata must return each spring with the migrating birds. Romanova (1948) and

Radin (1959) supported this premise with their observations that both eggs and juveniles of *E. uncinata* died when frozen or dessicated.

CONCLUSION

Information obtained in the course of this study clarifies and expands our knowledge of E. uncinata, its biology, pathogenicity, and its occurrence at Delta, Manitoba. Although our investigations were limited, they provide a foundation for more detailed research on this pathogen of waterfowl.

The follwoing are the conclusions derived from this investigation:

1. Juvenile E. uncinata were found in Daphnia pulex, D. magna and Simocephalus vetulus collected from the Field Station Pond in the summer months.

2. E. uncinata can infect at least eleven species of Delta crustaceans; namely seven Cladocera including Daphnia pulex, D. magna, Simocephalus vetulus, Ceriodaphnia reticulata, C. acanthina, Moina macrocopa and Eurycercus lamellatus; two Amphipoda, Gammarus lacustris and Hyalella azteca; one Conchostraca, Lynceus brachyurus, and one Anostraca, Chirocephalopsis bundyi.

3. E. uncinata developed to third stage juveniles in Daphnia pulex and D. magna in 10 days at 20 - 24°C. and in 30 days at 15°C.

4. Eggs of E. uncinata died when frozen for 85 days but survived dessication for the same period.

5. In Delta Mallards, E. uncinata moulted from fourth stage juveniles to adults 20 days after the infection and females

were ovipositing 40 days after infection.

6. E. uncinata grew faster and the survival rate was higher in one-week old Delta Mallards than in two and three month old birds.

7. E. uncinata readily infected the follwoing waterfowl; Anas platyrhynchos domesticus, A. p. (Delta Mallard), A. p. platyrhynchos, A. strepera, A. acuta, Somateria mollissima, Aythya affinis and Anser domesticus. This parasite did not readily infect Anas clypeata, A. discor, Aythya americana, Oxyura jamaicensis and Fulica americana (Rallidae).

8. Most granulomas were found in birds with the highest intensities of infection.

9. E. uncinata is known to overwinter in the definitive host where it can survive for one year.

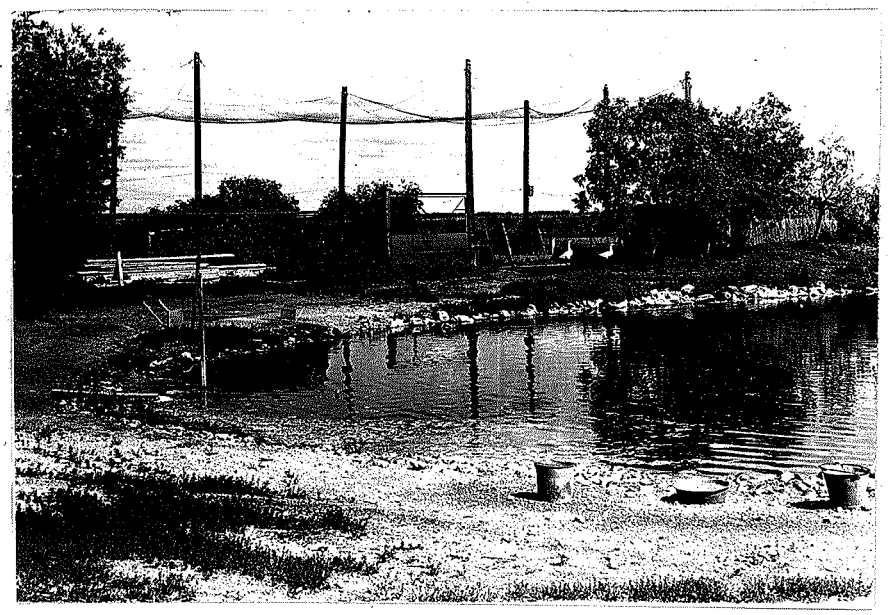


FIGURE 11
Field Station Pond - Site one

FIGURE 12
Delta Road Slough - Site three

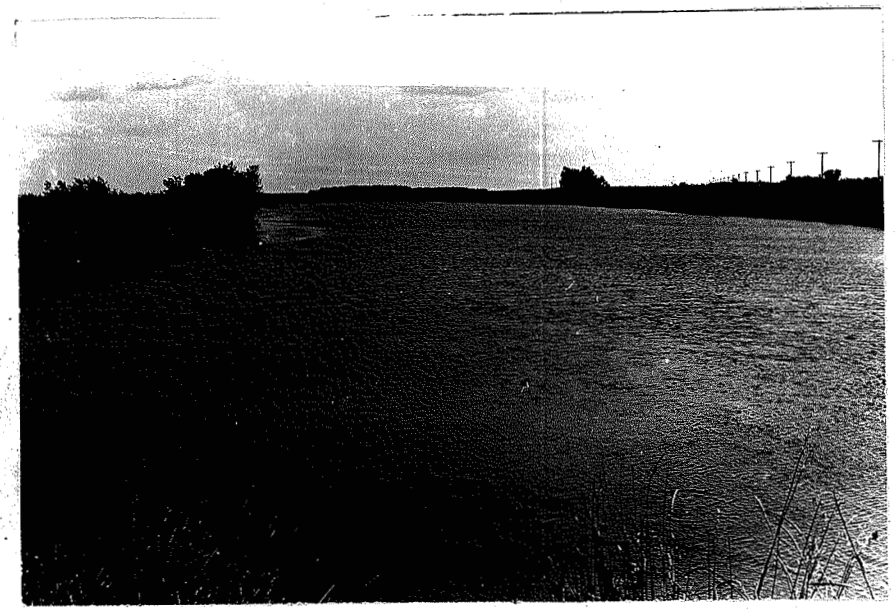


FIGURE 13
Blind Channel - Site four

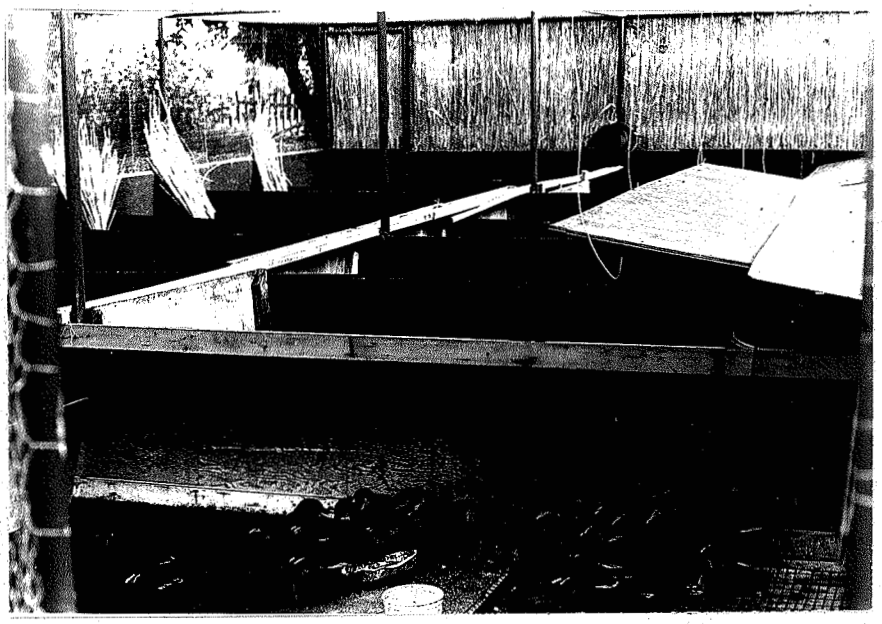


FIGURE 14
Rearing Pen

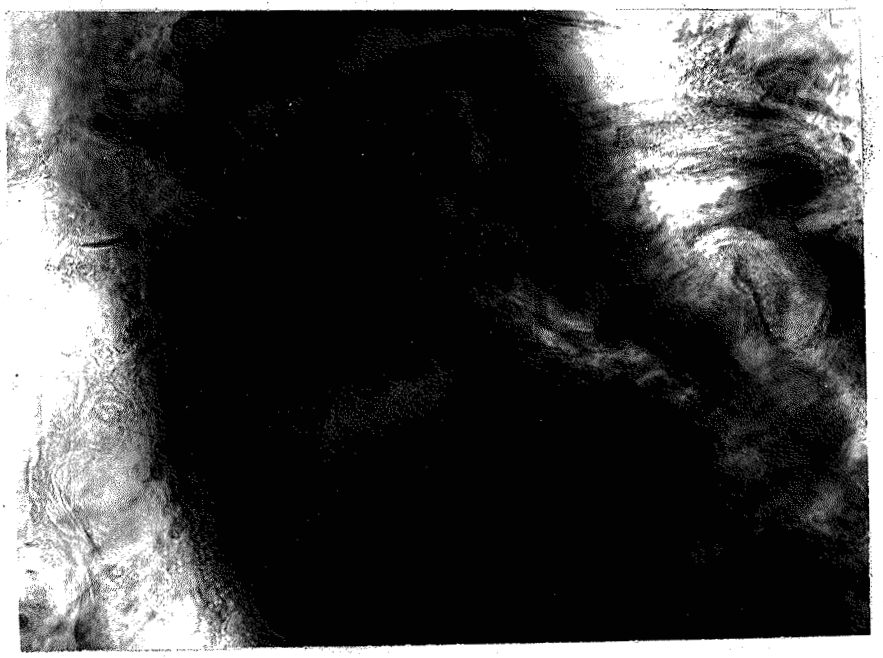


FIGURE 15
E. uncinata eggs in gut of Daphnia pulex (250X)

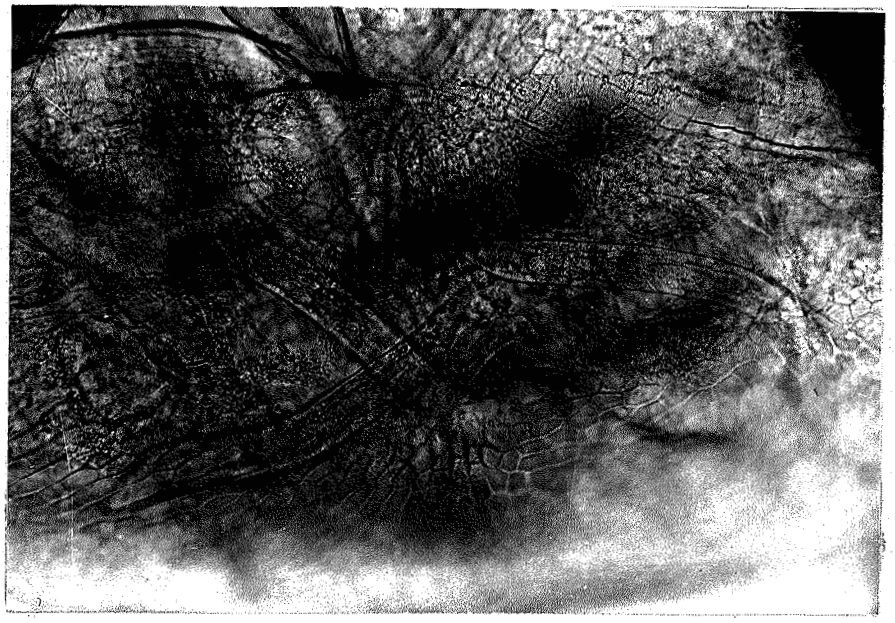


FIGURE 16
First stage E. uncinata juveniles in D. pulex hemocoel (400X)

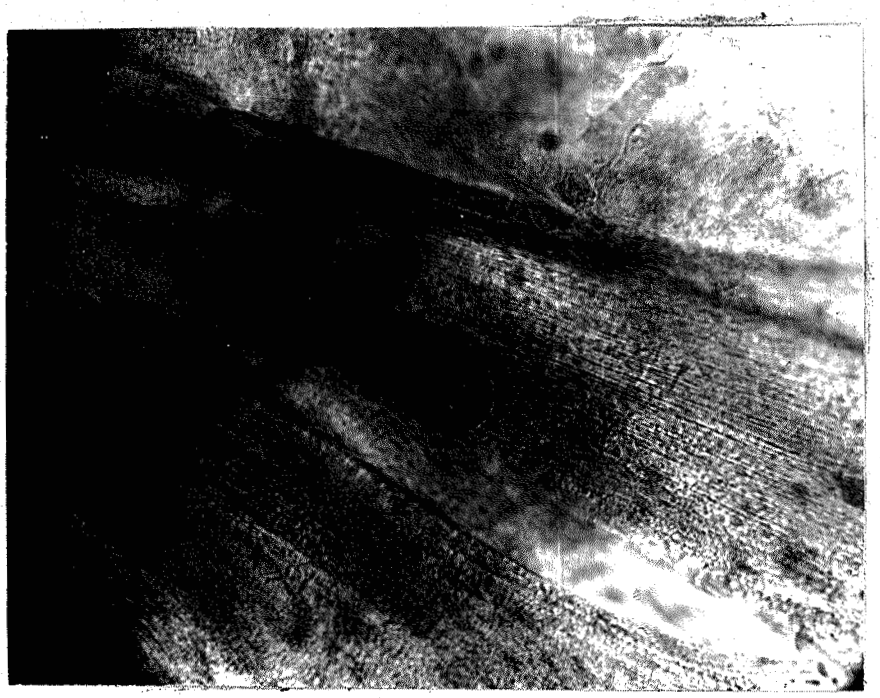


FIGURE 17
First stage E. uncinata in thoracic muscles of Daphnia (312.5X - Bright Field)

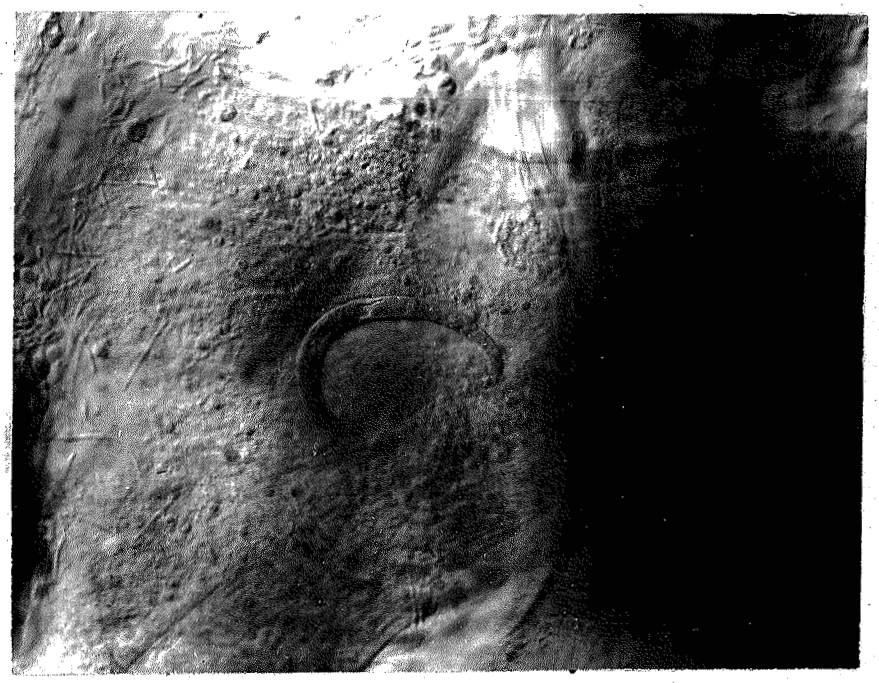


FIGURE 18
Same as Figure 17 (Interference contrast)

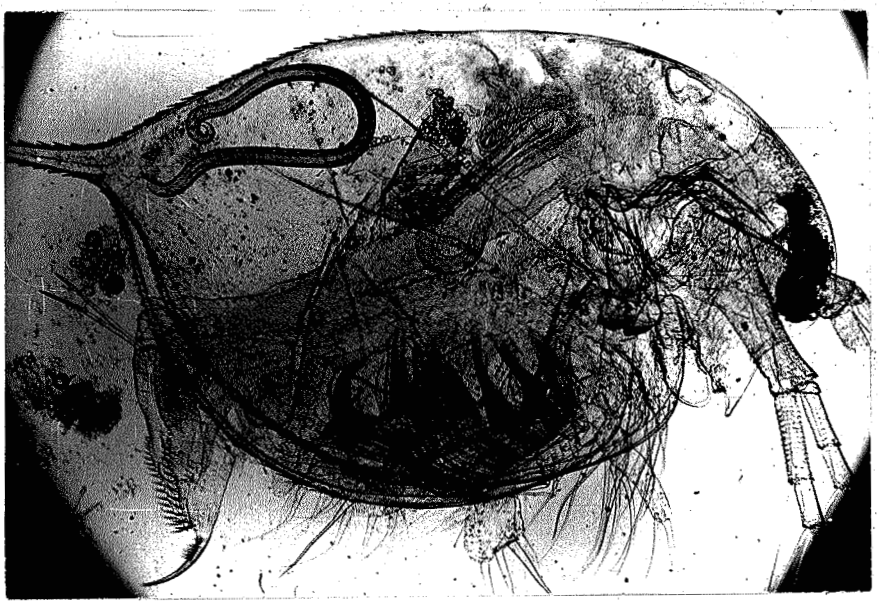


FIGURE 19
D. pulex with second and third stage E. uncinata juveniles (10X)

FIGURE 20
D. pulex with third stage E. uncinata juveniles (10X)

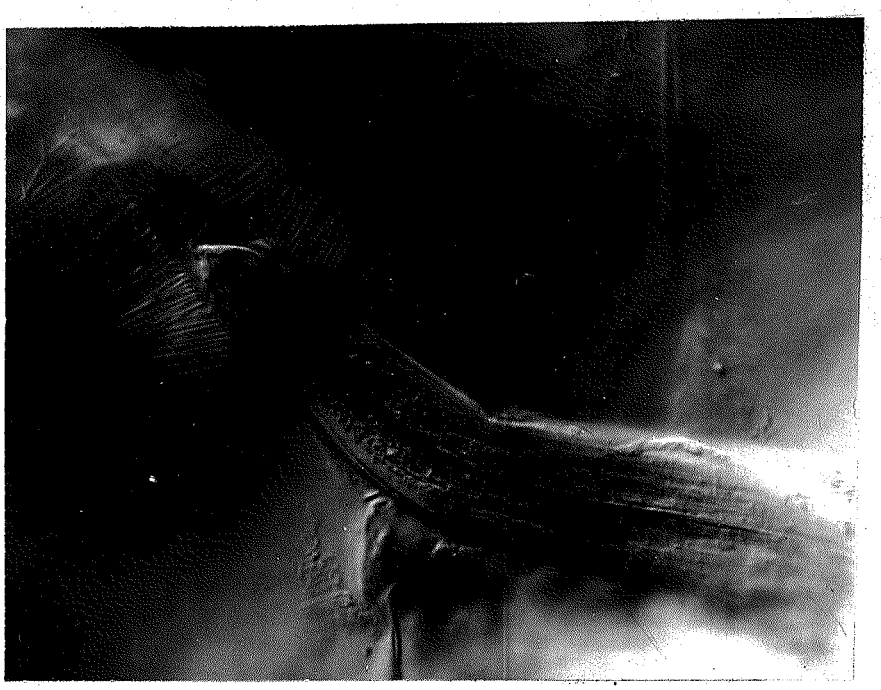


FIGURE 21
Third stage E. uncinata juvenile in gill filament of D. magna (400X - Interference contrast)

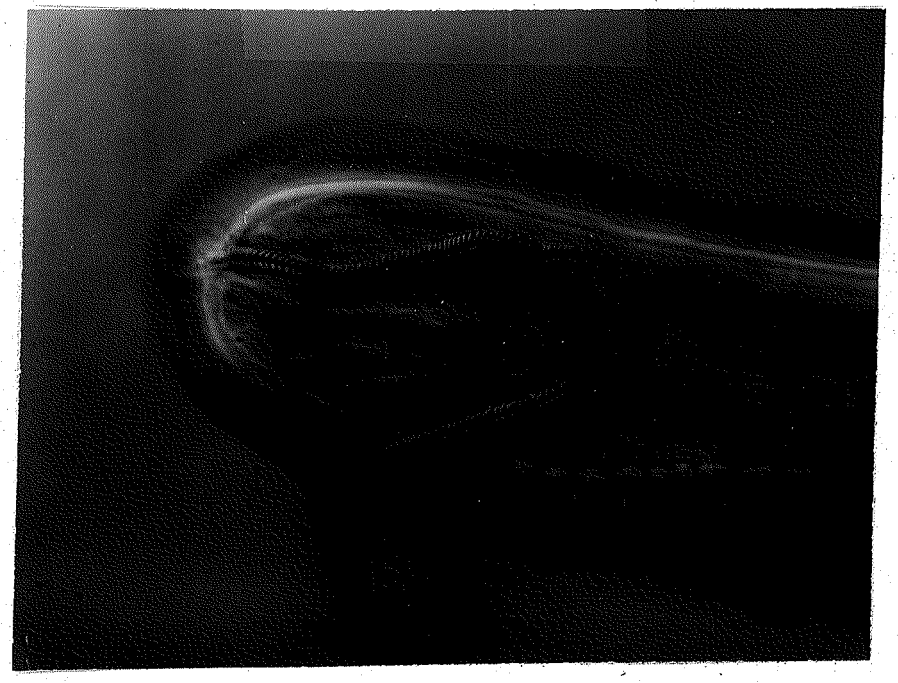


FIGURE 22
Cordons of fourth stage E. uncinata (400X - Interference contrast)

FIGURE 23
Moulting fourth stage E. uncinata (40X)

FIGURE 24
Adult female E. uncinata (10X)

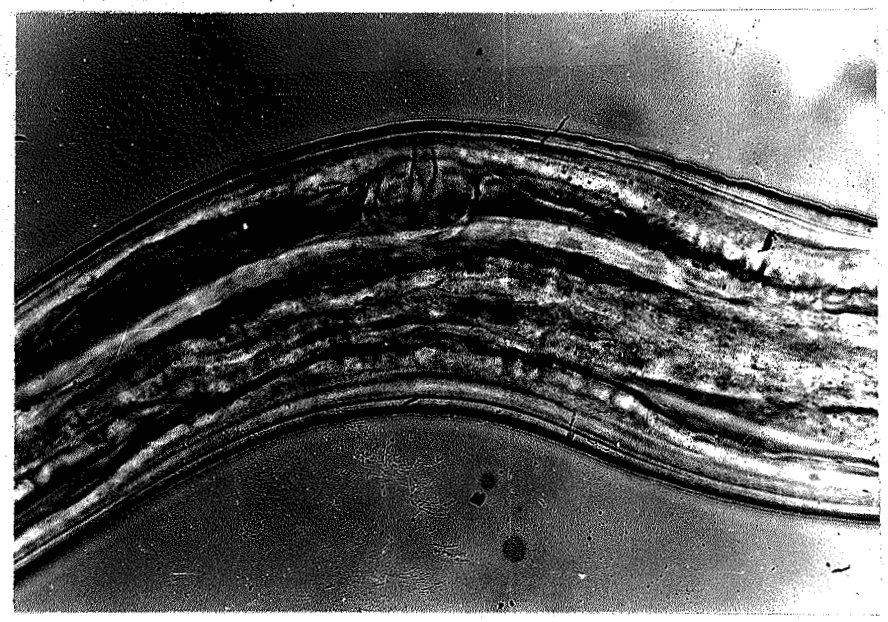


FIGURE 25
Developing vulva of fourth stage female E. uncinata (100X)

FIGURE 26
Developing vulva and ovijector of fourth stage female E. uncinata (100X - Interference contrast)

FIGURE 27
Ovijector and vulva of adult E. uncinata (100X)

FIGURE 28
Ovipositing E. uncinata (40X)

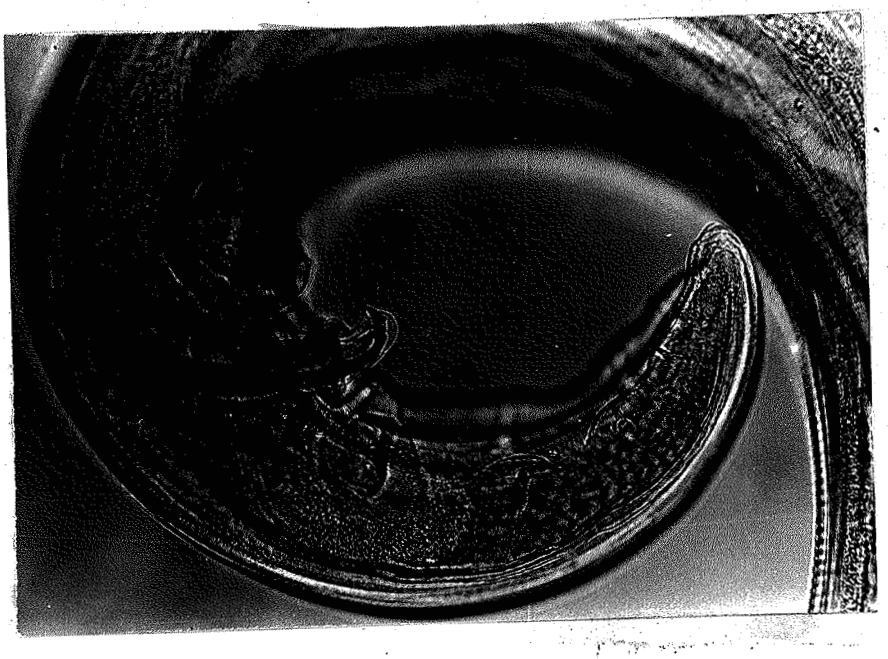


FIGURE 29
Distal end of adult male E. uncinata (100X)

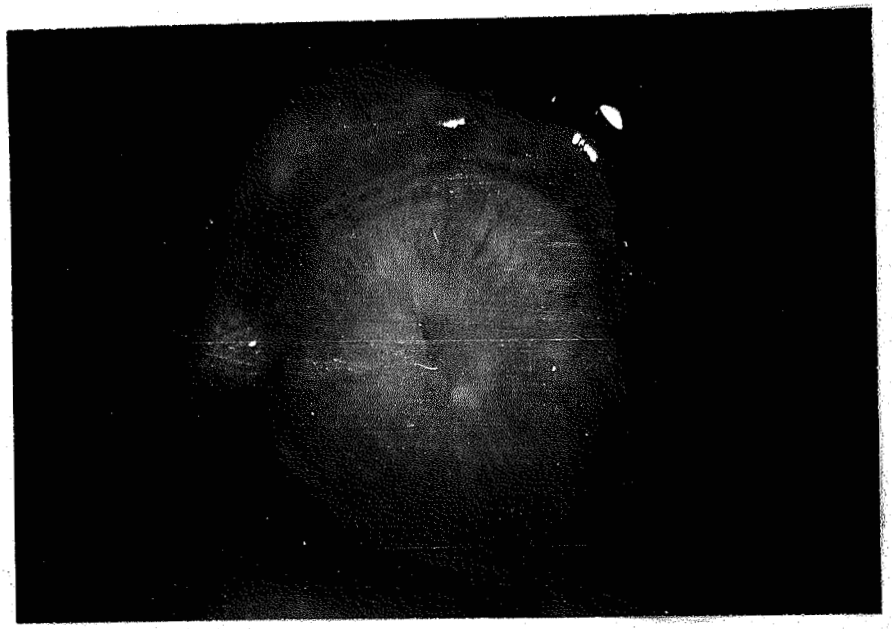


FIGURE 30
Swollen mucosa of isthmus from 10 day-old E. uncinata infection from a Delta Mallard (20X)

FIGURE 31
Granulomas from 20 day-old E. uncinata infection from a Delta Mallard (10X)

FIGURE 32
Granuloma from 37 day-old E. uncinata infection from a Delta Mallard (10X)

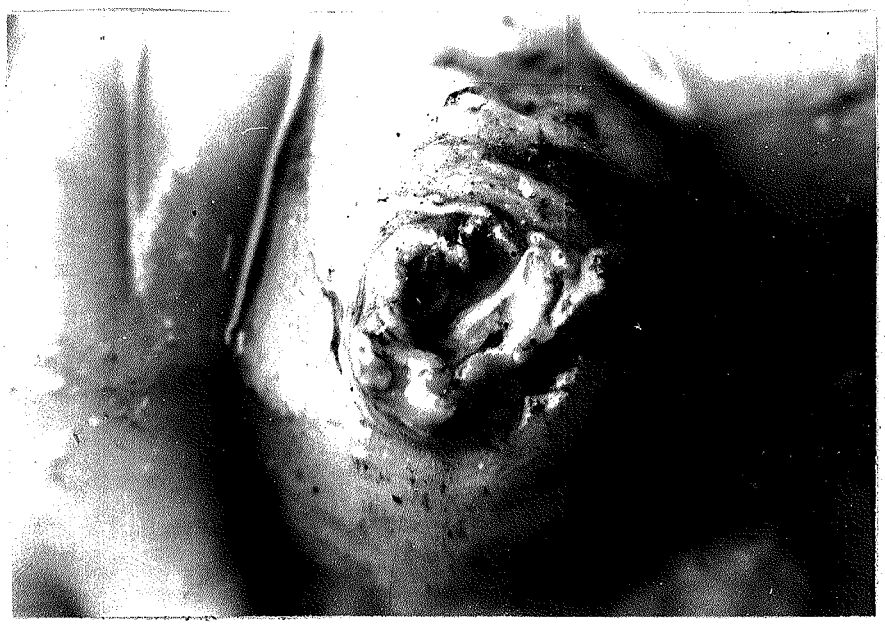


FIGURE 33
Granuloma with "plug" from 40 day E. uncinata infection from a domestic goose (10X)

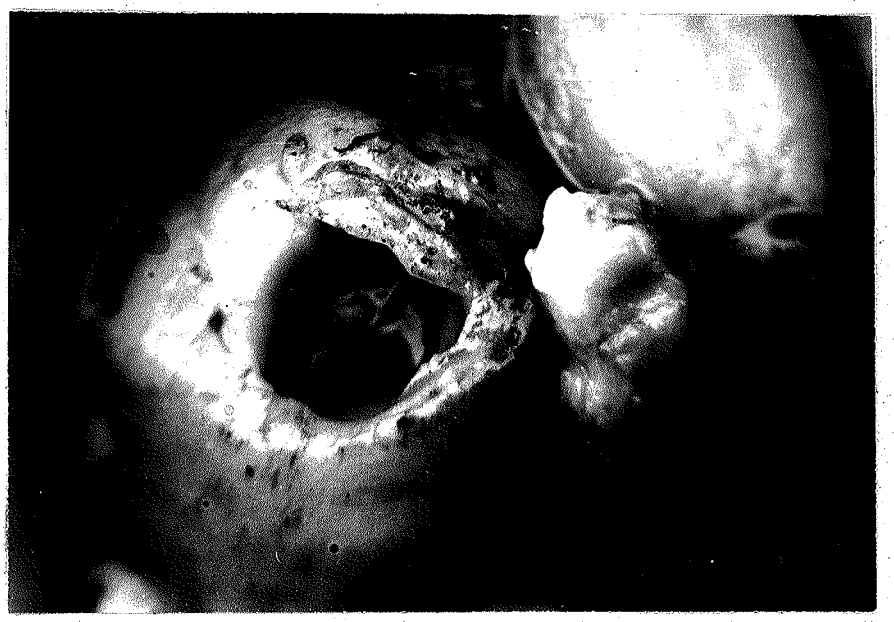


FIGURE 34
Granuloma with "plug" removed from 40 day E. uncinata infection from a domestic goose (10X)

FIGURE 35
Opened granuloma with E. uncinata from Delta Mallard with an estimated one year infection (10X)

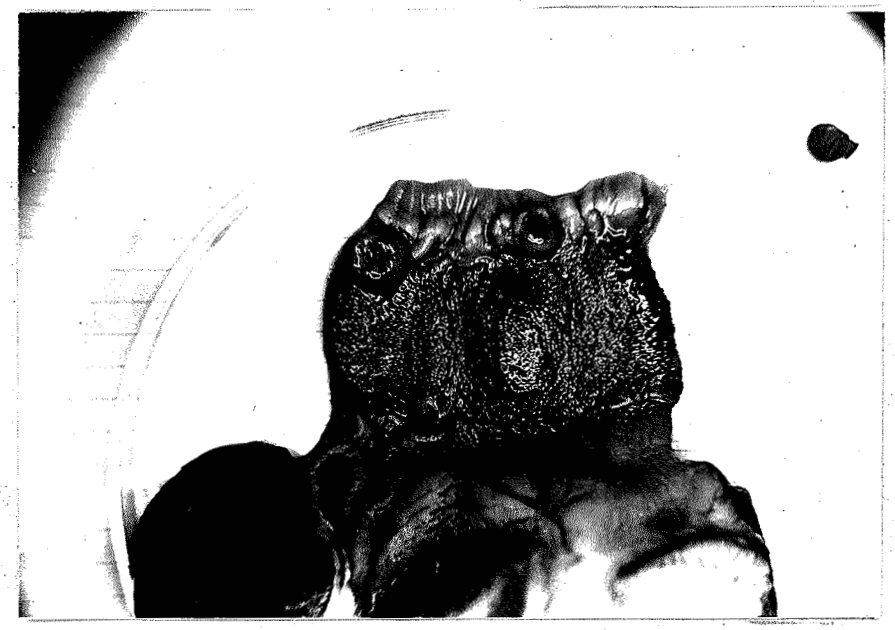


FIGURE 36
Proventriculus of domestic goose with 40 day E. uncinata infection

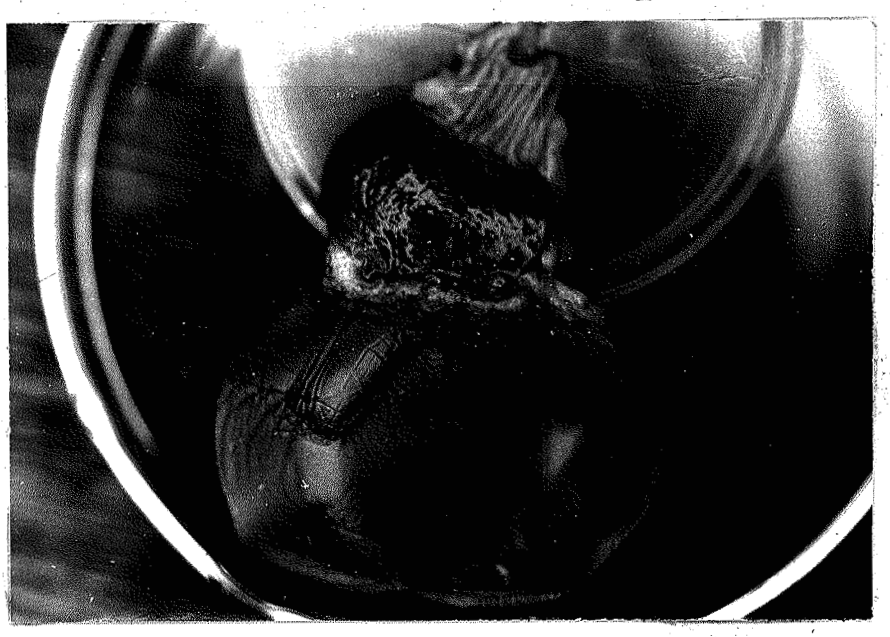


FIGURE 37
Proventriculus and gizzard of a coot 40 days after infection with E. uncinata

FIGURE 38
Granuloma with "plug" and eroded mucosa from blue-winged teal with 24 day-old E. uncinata infection (10X)

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SPECIMEN REFERENCE

No. _____ Specimen No. _____

Coll. Sheet. Reference _____ Date coll. _____ Date examined _____

Family _____ Genus _____ Species _____

Male _____ Female _____ Age _____ Wt. _____

Location _____

Condition _____

_____

Parasites _____

NO. ♂ _____ NO. ♀ _____ TOT. NO. _____ Cyst NO. _____

Slide or Vial Reference _____

Age infection _____ Original Infection NO. _____

Intermediate Host _____ Reference NO. _____

Remarks _____

_____

_____

_____

_____

_____

APPENDIX II

The classification of *Echinuria uncinata*.

(Chabaud, A. G. 1965)

Phylum Nemathelminthes
Class Nematodes
Subclass Secernentea
Order Spirudida
Suborder Spirurina
Superfamily Spiruroidea
Family Acuariidae (Railliet, Henry et Sisoff 1912)
Subfamily Acuariinae (Railliet, Henry et Sisoff 1912)
Genus *Echinuria* Soloviev, 1912
Species *uncinata* (Rudolphi, 1819)

(Hymen, L. H. 1951)

Phylum Aschelminthes
Class Nematoda
Order Spiruroidea
Family Acuariidae
Genus *Echinuria*
Species *uncinata*

Phylum Aschelminthes
Class Nematoda
Subclass Secernentea
Order Spirurida
Suborder Spirurina
Superfamily Acuarioidea (Sobolev, 1949)
Family Acuariidae
Subfamily Echinuriinae (Sobolev, 1943)
Genus *Echinuria*
Species *uncinata*