THE BIOLOGY OF OOCHORISTICA VACUOLATA HICKMAN (CESTODA)

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(With 20 figures in the Text)

ABSTRACT

Of 234 specimens of the skink lizard, *Egernia whitei* Lacépède) examined, 112 (47.9%) were found infected with *Oochoristica vacuolata* Hickman. The lizard showed no age resistance towards infection with the cestode. The degree of infection ranged from 1 to 27 worms per host, and 45% of the infected lizards harboured more than 3 tapeworms. Infected lizards showed no resistance to superinfection. The number of gravid worms in any one lizard varied from 1 to 24 but was generally less than 11. Forty-two per cent of infected lizards harboured more than 3 gravid worms. Whilst infection of the primary host may occur in almost any month of the year, the majority of infections take place in the months of January to April inclusive. The rate of development of the strobila ranged from one proglottis every 19 days to 1 a day. Tapeworms from infections acquired in mid-summer (January to February) are gravid by May, but those from infections acquired in late summer and autumn (i.e., after February) are not gravid until the following January or February. Infected lizards kept in the laboratory voided proglottides for a period of about 16 weeks in a year, usually from December to March inclusive. Those infected with only one tapeworm passed 2 to 3 segments per week. Increases in the degree of infection were not accompanied by corresponding increases in the number of proglottides voided. The adult cestode is estimated to live for four years and shed at least 123 proglottides. It undergoes a seasonal destrobilization when its host hibernates. In the field gravid proglottides are passed by infected lizards during the months October to May. The freshly voided gravid proglottis is quite active and may move 1 to 3 cm. away from the faeces. The oncosphere is surrounded by three membranes and a colloidal material. The latter is situated between the outer and middle membranes. The oncosphere is provided with penetration glands. After ingestion by the intermediate host it escapes from its investment by means of its hooks, probably aided by the secretions from the glands. The tenebrionid, *Cestrinus punctatissimus* Pascoe serves as a natural intermediate host. In addition, experiments reveal that the cockroach *Platyzosteria melanaria* Erichson, the dermestid *Anthrenocerus australis* Hope and the carabs *Gnathaphanus adelaidae* Castelnau, *Hypharpax moestus* Dejean, *Mecyclothorax ambiguus* Erichson, *Promecoderus gibbosus* Gray and *Homothes guttifer* Germar, are capable of serving as intermediate hosts. Following ingestion, the oncosphere takes 21 to 48 hours to enter the haemocoel of the intermediate host. The rate of development of the cysticercoid is affected by the ambient temperatures. In the summer months, January and February, only 21 days are required for the larva to become fully developed.

INTRODUCTION

Early in the course of my study of the cestode fauna of Tasmania, a high proportion (66.6%) of lizards belonging to the species *Egernia whitei* (Lacépède) was found to be infected with the cestode *Oochoristica vacuolata* Hickman. This prompted a study of the life cycle of the tapeworm. Moreover, as only experimental intermediate hosts were known for the three species of *Oochoristica* whose life cycles had, at that time, been investigated, it seemed desirable that an effort should be made to discover not only the experimental but also the natural intermediate hosts of *O. vacuolata*.

Recently Gallati (1959) has described the life cycle of a further species of *Oochoristica* but stated that he made no attempt to discover the natural intermediate host of the cestode.

There have been few reported investigations of the life cycle of reptilian cestodes, in fact, the only detailed studies appear to be those of Thomas (1934, 1941) on the ophidian tapeworm *Ophiotaenia perspicua* La Rue. However, its life history requires three instead of two hosts and is therefore not comparable with that of species of *Oochoristica*.

MATERIALS AND METHODS

The investigation of the life history of *Oochoristica vacuolata* involved—

(1) a study of the food, feeding habits, reproduction, infection and local distribution of the primary host, the skink lizard *Egernia whitei* (Lacépède);

(2) the maintenance of infected lizards to provide a supply of gravid proglottides;

(3) the raising of lizards from birth under controlled conditions to provide uninfected specimens for use in infection experiments;

(4) regular collection from the field of species of animals on which the lizard was found to feed, the subsequent examination of some of them for larval stages of the cestode, and the use of others in infection experiments in order to ascertain which of the species were potential intermediate hosts;

(5) an examination of the animals found feeding on the faeces of the lizard and the probability of such animals becoming infected.

During the period 1951-1958, specimens of *E. whitei* were collected from the Queen's Domain, Hobart, in every month of the year. Each was chloroformed and measured. The body cavity was opened and the sex of the lizard determined. The gut was then removed, placed in a little water in a Petri dish and examined under a dissecting microscope. The presence or absence of food in each of the three regions of the alimentary canal—stomach, small intestine and large intestine—was noted. The food was identified as completely as possible. A record was made of the number, position and maturity of any specimens of the cestode, *O. vacuolata*, present. The occurrence in the large intestine of any free proglottides was also noted.

Specimens of *E. whitei* collected from other localities were examined in a like manner.

Infected examples of *E. whitei* were obtained from among adult lizards collected in the field and kept in the laboratory for a week to a fortnight. Each lizard observed to pass gravid proglottides was placed in a numbered wooden box 52 x 22 x 18 cm. The top of the box was fitted with a movable glass lid leaving a gap of about 10 x 22 cm. at one end. This gap was closed by a wire mesh door for ventilation. The box was filled with sterilized earth to a depth of five to eight centimetres. A small jar sunk in the soil at one end of the box was kept filled with water. A 25 watt globe placed at the end opposite the wire door provided artificial heating (25°—35° C.), when required. A flat stone, about 15 x 18 x 5 cm. placed in the box near the door served for the lizard to hide under and also for it to rub against when moulting. Gravid proglottides were removed as soon as they were found and those not required for immediate use were stored in small glass specimen tubes plugged with cotton wool and containing a label on which was recorded the number of the lizard, the date and the approximate time of the day the proglottides were passed.

Some of the infected lizards were fed only on insects and spiders collected from areas not inhabited by *E. whitei*. From these lizards information on the rate of production of gravid proglottides by *O. vacuolata* and the longevity of the mature cestode was obtained.

Having ascertained the months in which the female *E. whitei* gives birth to her young, it was possible to obtain uninfected lizards for experimentation, by collecting from the field females in advanced stages of pregnancy and keeping them in a suitable vivarium until the young were born (Hickman, 1960). As soon as possible after their birth the young lizards were removed from the vivarium and each placed in a small wooden box (18 x 10 x 10 cm.) fitted with a glass front and a wire mesh top. The box was filled to a depth of about half an inch with earth which had been previously sterilized. A small flat stone under which the lizard might retreat was placed in the box. The boxes were kept in a room which received direct sunlight for most of the morning. On hot days after a period of exposure to sunlight, the boxes were shaded to avoid overheating the lizards. After the first day, the young lizards were fed with termites, ants, beetle larvae and spiders collected from areas not inhabited by *E. whitei*. Water for the lizards to drink was periodically sprayed into the box. During the first fortnight the faeces of the lizards were collected and examined for the presence of the remains of animals other than those with which the lizard had been fed. This afforded information on whether the lizard had fed prior to its removal from the vivarium in which it had been born and hence also a check on the possibility of it having become infected before being transferred to the boxes. Other uninfected specimens were obtained by collecting newly-born lizards from the field and keeping them under observation in the laboratory for a week or more. During this time they were fed with a known food, such as termites, their faeces being examined for the remains of other foods, the presence of which would indicate that the lizard had fed in the field and hence possibly become infected prior to capture.

After determining what animals served as food for *E. whitei*, specimens of many of these were collected regularly from the field in the vicinity of the retreats and runs of the lizard. Some of them were examined for natural infections, others were kept for infection experiments. The latter specimens were placed in Petri dishes or glass tubes plugged with cotton wool and kept at room temperature for a week or more before exposure to infection. In the early stages of the investigation the specimens were examined within a fortnight following exposure, so that cysticercoids resulting from the experimental infection could be distinguished by their immaturity from those which might have been present as a result of a prior natural infection. When, in this way, a positive indication of the successful experimental infection of a particular species had been obtained, several specimens of the same species were exposed to infection and examined at intervals of more than a fortnight. By so doing it was possible to obtain further information on the development of the cysticercoid.

In view of the possibility that the adults of some species of ants might only become infected through the feeding of their larvae, an attempt was made to establish colonies of several different species of ants in the laboratory. Thus colonies of *Rhyditoponera tasmaniensis* Em. and *Pheidole spp.* were successfully established under stones in flower pots filled with earth. Each flower pot stood in a dish and was surrounded by water to prevent the ants escaping. The ants were fed with previously killed termites. Periodically gravid proglottides instead of termites were offered to the ants. Subsequently larvae, pupae and adult ants were collected from the nests and examined for cysticercoids.

By observing the insects and other animals visiting the faeces deposited by *E. whitei* near its retreats in the field and also by making use of insect traps baited with the faeces of the lizard, it was possible to gain some indication of the species which fed on the faeces and which were therefore liable to become infected.

Oncospheres from the contents of gravid proglottides smeared on a slide were examined under a coverslip supported by petroleum jelly. Release of the oncosphere from its investments was effected

by exerting a slight pressure on the coverslip immediately above the oncosphere. Vital staining of the oncosphere was obtained using an aqueous solution (1 : 10,000) of neutral red.

Insects and other invertebrates being examined for developmental stages of the cestode were partly opened in a drop of water in a Petri dish on the stage of a dissecting microscope. Specimens found to be infected were dealt with in one or other of the following ways:

(*a*) Immediately offered to an uninfected lizard.

(*b*) Dissected further and some of the cysticercoids removed, examined in a drop of water on a slide, measured and drawn under the microscope. Other cysticercoids removed, fixed in Bouin's fluid, stained in alum carmine or Ehrlich's haematoxylin and mounted.

To facilitate their examination insects were usually killed by partly crushing their heads. When handling large numbers of ants it was found helpful to give them a preliminary chilling in a refrigerator.

The alimentary canals of a number of experimentally infected beetles were fixed in Bouin's fluid, embedded in wax and sectioned at 10 micra. The sections were stained in Ehrlich's haematoxylin.

DESTROBILIZATION AND THE GRAVID PROGLOTTIS

From Table 7 it may be seen that in July and August all the tapeworms present in infected lizards from the Domain were non-gravid, but in each of the other months of the year at least some of the cestodes were gravid. In some of the lizards collected in each month from October to May, inclusive, gravid proglottides occurred free in the rectum. Thus July, August and possibly September appear to be the only months in which gravid proglottides are not passed by infected lizards.

Infected lizards collected in the field and kept alive in the laboratory in boxes not artificially heated, passed gravid proglottides usually from December to March inclusive, i.e., for a period of sixteen weeks. When kept in boxes, which during the day were artificially heated to 30± 5° C., the lizards passed gravid proglottides from September to February, a period of twenty weeks.

The tapeworms in the infected lizards kept in the laboratory, terminated the production of gravid proglottides by undergoing destrobilization. As a result chains of semi-gravid and mature segments were passed together with the remaining gravid segments. The presence of chains of mature proglottides in the rectum of several lizards collected from the Domain during May indicated that destrobilization occurs naturally. Starvation of the host for a week was found to cause destrobilization of the tapeworm. With the approach of winter *Egernia whitei* becomes less active and eats less (Hickman, 1960). This seasonal starvation might well be the cause of the natural destrobilization of the cestodes in the infected lizards in the field.

A plentiful supply of food and restricted activity due to confined living conditions, caused infected lizards kept in heated boxes in the laboratory to become very fat. Eventually they were found to reduce their food intake and as a result their tapeworms destrobilized.

Gravid proglottides are passed with the faeces or merely with the urinary excretion of the lizard. They are entire, free and active. However, those passed at the time of destrobilization are sometimes inactive and embedded in faecal material. During movement the anterior end of the detached proglottis is always that which is nearer the scolex when the segment is part of the strobila. In locomotion dorsal and ventral surfaces are not distinguishable. The anterior end of the proglottis is first raised off the ground and by the contraction of the circular muscles in the raised part, it is extended. Eventually the extended part is lowered and the hind part is brought forwards by the coordinated action of the circular muscles of the posterior half and the longitudinal muscles of the entire proglottis.

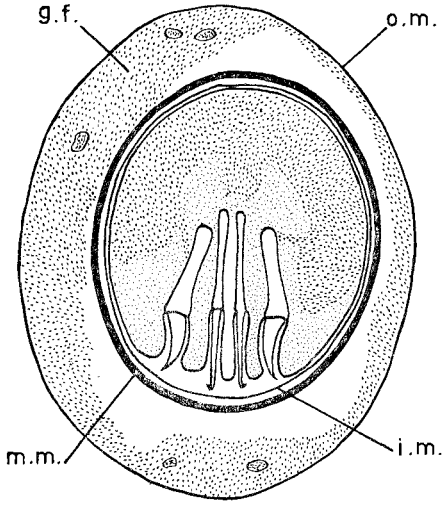
The direction of movement of the proglottis was found to be unrelated to moisture, gravity or light intensity. However, the duration of the movement was affected by moisture. Thus, provided conditions were moist the proglottis continued moving for approximately half an hour. Under dry conditions the period of movement was considerably less. As a result of its movements the proglottis usually travelled some distance from the faeces or excreta with which it had been passed. The distance travelled was found to vary with the kind of substratum on which the proglottis was voided. When passed on a rock, the maximum distance a proglottis was observed to travel was 3.0 cm. On this occasion it moved to the edge of the moist area formed by the liquid passed with the faeces of the lizard. The greatest distance moved by proglottides passed on soil was only 1.0 cm. On a glass surface they travelled distances up to 10.0 cm. On three occasions they were found to have moved up the side of a glass tank.

After cessation of movement the cuticle of the proglottis shrinks and the contents of the segment are exuded from the posterior end. The exudate is rather sticky and readily adheres to anything that touches it. The shrinking of the cuticle is apparently partly due to desiccation, for it was considerably inhibited when the proglottis was kept moist. Moreover, shrivelled proglottides were found to swell again when placed in a drop of water. After seven years in a glass specimen tube plugged with cotton wool a proglottis and in particular its exuded contents were still relatively soft. However, the exudate was no longer sticky and, as will be shown later, the oncospheres were no longer viable.

A gravid proglottis contains up to 300 eggs. As the segment shrinks the majority of the eggs are exuded with the contents.

THE ONCOSPHERE AND ITS INVESTMENTS

When exuded from the gravid proglottis the oncosphere is enclosed in three membranes (Fig. 1.). At the time of my previous description of the oncosphere (Hickman, 1954) I had not discovered the innermost investment.



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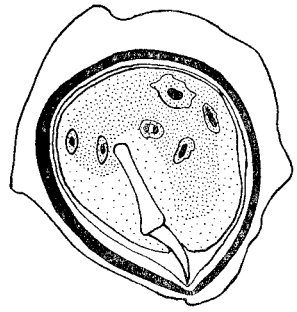

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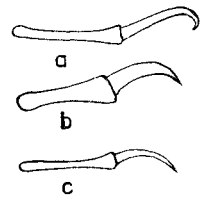

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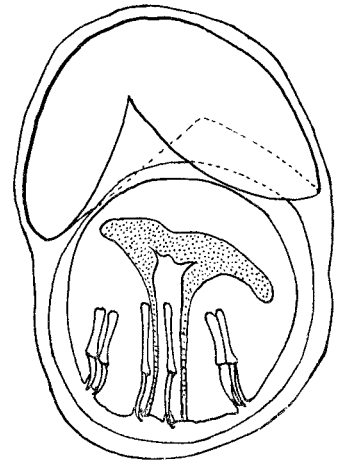

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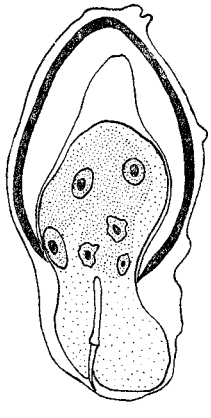

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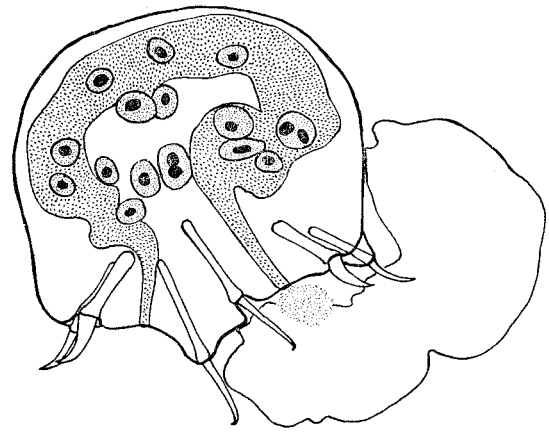

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FIG. 1.—Egg from a voided gravid proglottis, showing the membranes surrounding the oncosphere. *g.f.*, granular fluid; *i.m.*, inner membrane; m.m., middle membrane; *o.m.*, outer membrane.

FIG. 2.—Longitudinal section of egg (from transverse section of mid-gut of *Cestrinus punctatissimus*) showing the middle membrane grooved on the inside in the region near the hook.

FIG. 3.—Emergence of the oncosphere after mechanical rupture of the middle membrane. (Free-hand drawing.)

FIG. 4.—Longitudinal section of an oncosphere escaping from its investments. (From transverse section of the gut of *C. punctatissimus*).

FIG. 5.—An oncosphere nearly free from its inner membrane and exuding the contents of the penetration glands.

FIG. 6.—Hooks of the oncosphere. *a.* median hook, *b.* ventro-lateral hook, *c.* dorso-lateral hook.

Between the outer and middle membranes is a fluid, which is usually granular and contains a few scattered nuclei. When fixed the fluid coagulates and sometimes gives the appearance of an additional membrane.

The outer membrane (uterine capsule) has an irregular shape and is often slightly wrinkled. Initially it is rather thin, but in eggs kept for seven years in glass tubes plugged with cotton wool, this outer membrane had become slightly thickened.

The middle membrane (embryophore) is spherical to ovoid in shape. Externally it is marked by a reticulation of grooves. It is thicker, more rigid and more readily stained than either the external or internal membranes.

The inner membrane is very thin and is closely applied to the oncosphere. It was first detected when oncospheres which had been mechanically liberated from their embryophores failed to stain with neutral red. In order to stain the oncospheres it was necessary to rupture the inner membrane.

The oncosphere possesses three pairs of hooks (Figs. 5 & 6) and since the hook-bearing region is foremost during locomotion of the embryo, the region is considered anterior. Each hook exhibits three parts, handle, guard and blade. The handle is completely embedded in the body of the embryo; the guard is attached to the cuticular surface of oncosphere; the blade projects beyond the surface. When the oncosphere is enclosed in its membranes the blade of the hook, although appearing to be enclosed within the body of the oncosphere, is actually in a deep depression of the cuticle. Of the three pairs of hooks, one is antero-median and two are antero-lateral. The median hooks are longer and more slender than the lateral hooks. They are similar and the distal extremities of their blades are strongly curved towards what is here designated the ventral surface. The corresponding hooks of the antero-lateral pairs are similar and their blades show a gradual horizontal curvature towards the posterior. The dorsal hooks are slender while the ventral ones are stout. The average measurements of the oncosphere, its investments and hooks are given in Table 1.

The movements of the hooks of liberated and also non-liberated oncospheres were observed on a number of occasions. They comprised an initial forward movement of the median hooks accompanied by a slight forward and then backward sweep of the blades of the lateral pairs. The median pair were then drawn down and back in a clawing manner. At the same time the handles of the lateral pairs were drawn inwards and backwards so that the blades became directed forwards parallel to the blades of the median pairs.

Although a detailed histological study of the oncosphere was not undertaken, the staining of live specimens with neutral red revealed the presence of a horizontal "U"-shaped glandular structure, the two attenuated extremities of which passed forwards to apparently open between the median and lateral pair of hooks. Pores were observed with certainty only once and on this occasion a fluid was seen exuding from one of them (Fig. 5). In form this glandular structure is comparable with the glands observed by Reid (1948), Millemann (1955), Ogren (1955, 1957) and Gallati (1959) in the oncospheres of a number of different cestodes and referred to as penetration glands by Reid (1948) and epidermal glands by Ogren (1957). A variable number of large oval cells lying mainly ventral to the body of the glandular structure were also revealed by staining with neutral red. Muscular strands passing both anteriorly and posteriorly from the guard and handle of each hook were seen in both stained and unstained oncospheres. In one specimen strands from the proximal end of the handles of all hooks were seen to converge and form two groups, one passing forwards to the cuticle immediately above the median hooks, the other passing backwards to the cuticle of the posterior of the oncosphere.

During the present study only one abnormal oncosphere was observed. In this specimen there was a complete duplication of the hooks.

Viability tests were made on oncospheres from proglottides kept for various periods (up to 45 months) at room temperature in glass specimen tubes plugged with cotton wool. A total of forty-six tests were made using *Anthrenocerus australis* Hope, *Hypharpax moestus* Dejean, *Mecyclothorax ambiguus* Erichson, and *Cestrinus puntatissimus* Pascoe as hosts. The proglottides offered to the larvae of *A. australis* were left dry, whilst those offered to the other hosts were first moistened with a drop of water. Thirty-eight of the tests involved oncospheres from proglottides which had been kept for more than a month. All except two of these gave negative results. In two cases, oncospheres from a proglottis kept for 366 days proved viable on being fed to larvae of *A. australis*. In the eight remaining tests, oncospheres from proglottides stored for periods up to a month were used. All of these gave positive infections.

TABLE 1

Measurements (average, in micra) of the oncosphere, its investments and hooks. The measurements are based on 50 oncospheres taken from voided proglottides.

Oncosphere (liberated and slightly compressed) with:		
(*a*) median hooks extended	48.3	41.5
(*b*) median hooks retracted	43.7	48.3
Outer investment (uterine capsule):		
(*a*) slightly compressed	50.5	42.5
(*b*) strongly compressed	59.8	55.2
Middle investment (embryophore):		
(*a*) slightly compressed	41.5	34.5
(*b*) strongly compressed	45.0	39.0
Inner investment:		
(*a*) slightly compressed	39.0	32.0
(*b*) strongly compressed	42.6	37.0
Median hooks:		
blade	9.7	—
handle	13.8	—
Lateral hooks:		
blade	9.7	—
handle	11.5	—

TABLE 2

Analysis of the gut content of 15 specimens of *Egernia whitei* infected with very immature *Oochoristica vacuolata* having from 0 to 4 segments.

Number of segments in strobila of the cestode	Gut content														
	Formicidae	Carabidae	Chrysomelidae	Dermestidae	Scarabaeidae	Curculionidae	Diptera	Lepidoptera	Hemiptera	Orthoptera	Thysanoptera	Phalangida	Acarina	Aranéida	Isopoda
0	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—
0	+	—	—	—	—	—	—	—	+	—	—	—	—	—	—
0	+	—	—	—	—	—	—	—	—	—	—	—	—	+	—
0	+	—	—	—	—	—	—	+	—	+	—	—	—	—	—
0	+	—	—	—	+	—	—	—	—	—	—	—	—	—	+
0	+	+	—	—	—	—	—	—	+	+	—	—	—	+	—
0	+	—	+	—	—	+	+	+	+	—	—	—	—	—	—
0	+	—	—	—	—	—	+	+	—	—	—	+	+	+	—
0	+	—	+	—	—	—	+	+	+	—	—	—	—	—	+
3	+	+	+	+	+	+	+	—	+	—	+	—	—	+	—
4	+	—	+	—	—	+	—	+	—	—	—	—	—	+	—
4	+	—	—	—	—	+	—	—	+	—	—	—	—	—	—

EXPERIMENTAL AND NATURAL INTERMEDIATE HOSTS

Examination of the gut contents of specimens of *Egernia whitei* collected throughout the year gave information as to what insects, &c., served as food for the lizard (Hickman, 1960). Special attention was given to the gut contents of lizards which harboured immature specimens of *Oochoristica vacullata* having a small number of segments, 4 or less. It was thought that such lizards might have acquired their infection shortly before being collected and that remains of the intermediate host might still be in the alimentary tract. An analysis of the gut contents of 15 of these lizards is shown in Table 2.

The fact that voided proglottides are usually found away from the faeces with which they have been passed, suggested that the intermediate host might be non-coprophagous. However, since gravid proglottides voided at the time of destrobilization in the cestode often remain enclosed in the faecal pellets, the likelihood of coprophagous animals serving as intermediate hosts could not be disregarded.

Animals found feeding on or showing an interest in the faeces of the lizard, included an ant (*Camponotus consobrinus* Erichson), an isopod (*Eluma caelatum* (Miers)), an oribatid mite and the larva of a dipteron. On a number of occasions *Camponotus consobrinus* was observed carrying the faecal pellets of the lizard. The isopod, mite and dipteron were found feeding on the lizards' faeces used as bait in insect traps.

Twenty-nine species of invertebrates were tested for their susceptibility to infection. They comprised representatives of the Mollusca, Myriapoda, Isopoda and Insecta (Formicidae, Carabidae, Tenebrionidae, Dermestidae, Elateridae, Curculionidae, Scarabaeidae, Orthoptera, Diptera, Lepidoptera). The results of these tests are summarised in Table 3. Unfortunately the slow rate of production of proglottides by the adult tapeworm, the relatively small number of cestodes in an infected lizard and the difficulty of maintaining a large number of lizards, limited the supply of freshly voided proglottides for experimental purposes and hence restricted the number of tests that could be made at any one time.

Dipterous larvae and oribatid mites recovered from faecal-baited insect traps were placed in faeces contaminated with gravid proglottides. Other species tested were given a preliminary period of starvation, after which they were offered either a freshly voided proglottis, or one that had been previously voided. In the latter case the proglottis was usually moistened before being offered. The interest in the segment displayed by the species being tested was noted and those species showing no interest were then offered the proglottis mixed with their food.

Isopods, carabs, tenebrionids and cockroaches showed a definite interest in and preference for freshly voided proglottides. On the other hand the larvae of *Anthrenocerus australis* generally refused freshly voided proglottides, moistened proglottides and the sticky exudate of segments. How-

TABLE 3

Summary of the infection of animals examined for experimental and natural infection.

Species	Infection			
	Experimental		Natural	
	Number of specimens		Number of specimens	
	tested	infected	examined	infected
OLIGOCHAETA	—	—	3	—
GASTROPODA—Stylomatophora	3	—	38	—
MYRIAPODA—Diplopoda	—	—	18	—
Chilopoda	3	—	3	—
ISOPODA				
Porcellio scaber	30	—	308	—
Armadillidium vulgare	5	—	79	—
Eluma caelatum	6	—	122	—
ARACHNIDA—Acarina				
Oribatidae	9	—	36	—
Unidentified	—	—	11	—
INSECTA				
Formicidae				
Camponotus consobrinus	60	—	3003	—
Camponotus sp.	—	—	54	—
Rhyditoponera tasmaniensis	40	—	1266	—
Pheidole sp.	86	—	1386	—
Pheidole sp.	168	—	653	—
Orectognathus antennatus	—	—	88	—
Polyrachis sp.	—	—	52	—
Dolichoderinae—(3 spp)	30	—	6057	—
Carabidae				
Gnathaphanus adelaidae	67	6	1135	—
Hypharpax moestus	83	40	323	—
Mecyclothorax ambiguus	33	24	158	—
Promecoderus gibbosus	5	1	15	—
Homothes guttifer	4	1	20	—
Unidentified spp. adult	—	—	245	—
larvae	—	—	26	—
Tenebrionidae				
Cestrinus punctatissimus	65	21	1356	1
Unidentified spp.	—	—	20	—
Dermestidae				
Anthrenocerus australis	1	1	12	—
Unidentified spp. adult	—	—	49	—
Byrrhidae				
Microchaetes scoparius	—	—	2	—
Chrysomelidae				
Monochirus fimbriatus	—	—	2	—
Unidentified spp. adult	—	—	115	—
Scarabaeidae				
Aphodius sp.	3	—	16	—
Unidentified spp. adult	—	—	4	—
larvae	5	—	11	—
Curculionidae				
Unidentified spp. adult	3	—	72	—
Elateridae				
Unidentified spp. adult	8	—	85	—
larvae	—	—	4	—

TABLE 3—*continued.*

Species	Infection			
	Experimental		Natural	
	Number of specimens		Number of specimens	
	tested	infected	examined	infected
Pselaphidae				
Unidentified spp. adult	—	—	77	—
Staphylinidae				
Unidentified spp. larvae	—	—	23	—
Coleoptera				
(unidentified)	—	—	42	—
Hemiptera				
Unidentified spp.	—	—	136	—
Lepidoptera				
Unidentified spp. adult	—	—	134	—
larvae	3	—	151	—
Diptera				
Unidentified spp. adult	—	—	78	—
larvae	51	—	30	—
Orthoptera				
Unidentified spp.	3	—	12	—
Dictyoptera				
Platyzosteria melanaria	4	2	35	—
TOTAL	778	96	17,562	1

ever, they would feed on the dried and shrivelled proglottis. Only one curculionid fed on a proglottis. The ants, *Camponotus consobrinus* and *Pheidole* spp. were the only other insects among those tested to show any interest in the proglottis. Only on two occasions was *C. consobrinus* observed to feed on the segments. The species of *Pheidole* were never observed feeding on the proglottides, but were often seen to take them down into their nests.

From Table 3 it may be noted that specimens of the cockroach, *Platyzosteria melanaria* Erichson, the dermestid *Anthrenocerus australis,* the tenebrionid *Cestrinus punctatissimus,* and the carabs, *Gnathaphanus adelaidae* Castelnau, *Hypharpax moestus, Mecyclothorax ambiguus, Promecoderus gibbosus* Gray and *Homothes guttifer* Germar were all found to be infected after feeding on the proglottides or on the proglottides mixed with their food. That these infections were probably brought about experimentally is apparent from a comparison of the results obtained in the case of specimens which had been subjected to artificial infection, with those for specimens of the same species which had not been so treated.

Nearly 73 per cent of the specimens of *Mecyclothorax ambiguus* and about 48 per cent of the specimens of *Hypharpax moestus* were infected experimentally. *Cestrinus punctatissimus* proved less susceptible to infection, approximately 32 per cent of the specimens being infected. Of interest is the apparent resistance to infection of the great majority of *Gnathaphanus adelaidae.* Although at least thirty-two specimens of this species each devoured an entire proglottis, only six became infected. The cysticercoids in five of these appeared exceptionally granular and opaque. The number of specimens of *Promecoderus gibbosus, Homothes guttifer* and *Platyzosteria melanaria* tested was insufficient to give an adequate estimate of the susceptibility of these species to infection. As previously stated the larvae of the dermestid, *Anthrenocerus australis* would not readily feed on freshly voided proglottides and with one exception, all individuals of this species were fed with dried shrivelled proglottides. Owing to the possible loss of viability by the oncospheres in dried proglottides, the results of the experiments with the dermestid may not indicate the true susceptibility of this species to infection. Hence only the result of the experiment in which a freshly voided proglottis was used is given in Tables 3 and 4.

Considerable intra- and inter-specific variation in the degree of infection of specimens of the various species was found (Table 4). Different individuals of the one species when fed with whole progolttides did not always become infected to the same degree. This may have been due to the variation in the number of oncospheres contained in a proglottis. However, the consistently low infection in *Cestrinus punctatissimus* would appear to be due to some factor peculiar to this species. Although some heavy infections did occur in both *Mecyclothorax ambiguus* and *Hypharpax moestus,* a comparison of the degree of infection in these species with the number of oncospheres contained in a proglottis indicates that rarely, if ever, do all the oncospheres succeed in penetrating into the haemocoel of the host.

In the search for the natural intermediate host 17,562 invertebrate animals were examined (Table 3). A naturally infected specimen was first discovered four years after the search had begun. It was identified as *Cestrinus punctatissimus* Pascoe, a tenebrionid, which as indicated above had proved susceptible to experimental infection. Four cysticercoids removed from the body cavity of the beetle were immediately pipetted down the throat of an uninfected lizard raised under controlled conditions. On dissection twenty-nine days later the lizard was found to contain one immature *Oochoristica vacuolata* having 7 segments.

At the time of the discovery of the naturally infected specimen of *C. punctatissimus,* 634 specimens of this beetle had been examined. Subsequent examination of a further 722 specimens failed to reveal any other infected individuals. The frequency of infection of the beetle is thus very low.

As may be seen from Table 2, *C. punctatissimus* was not found in the gut of those lizards, which had apparently become infected just prior to being collected from the field. Moreover, it occurred in only five of the two hundred and thirty-four lizards examined. These facts together with the low frequency of infection of the beetle can hardly account for the high frequency of infection (47.9%) of the primary host (Table 8).

From the infection experiments it is apparent that quite a wide range of insects could act as intermediate hosts. However, *C. punctatissimus* was the only species found naturally infected. If there are a number of different species acting as intermediate hosts, then, to give a 47.9% infection of the primary host none of them would necessarily need to have a high frequency of infection. This may account for the fact that no other natural infection was found among the animals examined.

Although a number of carabs appear probable alternative intermediate hosts, they showed a low frequency of occurrence in the gut of those lizards which had apparently acquired their infection immediately prior to being collected (Table 2). Moreover, not one of the 1,922 carabs collected in the field was found to be infected (Table 3).

It was found that freshly voided proglottides never remained long in the field, and hence were not likely to become sufficiently dried and shrivelled for dermestid larvae to feed on them. Therefore, it is improbable that these insects act as natural intermediate hosts.

The inadequacy of the data on the cockroach, *Platyzosteria melanaria,* makes it difficult to say to what extent this species may act as in intermediate host.

The frequency of occurrence of the Formicidae, Diptera, Hemiptera, Lepidoptera and Chrysomelidae in the food of apparently newly infected lizards (Table 2) suggests that eventually some species in one or more of these groups may be found to serve as intermediate hosts.

DEVELOPMENT IN THE INTERMEDIATE HOSTS

Ingestion of proglottides by *Cestrinus punctatissimus, Anthrenocerus australis* and *Platyzosteria melanaria* is slow and accompanied by considerable mastication. The carabs, however, eat the proglottides rapidly and do not appear to subject the segments to much chewing. If the eventual liberation of the oncospheres is dependent on the rupture of their investments (particularly the embryophore) by the action of the mandibles of the host, it would be expected that in the case of the insects that chewed the proglottis a higher percentage of oncospheres would be liberated and hence produce a greater degree of infection than in the case of insects which did not chew the proglottis. This, however, was found not to be so, since the carabs were the more heavily infected (Table 4).

The absence of a crop in *C. punctatissimus* results in the ingested proglottis quickly entering the mid-gut. Oncospheres still enclosed in their membranes were found in the mid-gut of a specimen dissected 3½ hours after it had fed on a proglottis (Table 5). The mid-gut is long, extending through the meso-thorax, metathorax and anterior half of the abdomen. As a result the proglottis takes some time to pass through into the hind gut. Some non-liberated oncospheres were still in the mid-gut of specimens of *C. punctatissimus* infected 52 hours previously (Table 5). There is thus a considerable period during which oncospheres may escape from their membranes.

In the carabs, the ingested proglottis passes into an extensive crop. The period spent in the crop by the proglottis was not ascertained. However, non-liberated oncospheres were found in the mid-gut of a specimen of *Mecyclothorax ambiguus* dissected 21 hours after being fed with a proglottis. Liberated oncospheres were also present in the wall of the gut and some had succeeded in penetrating into the haemocoel. A similar location of oncospheres was found in specimens of *Hypharpax moestus* dissected 48 to 50½ hours after ingestion of proglottides.

The wall of the alimentary canal between the fore and mid-gut regions in the carabs and also in *C. punctatissimus* is furnished with spines. They are larger and more numerous in the carabs than in *C. punctatissimus.* Whether they play any part in the liberation of the oncospheres is not known. It is conceivable, however, that they could puncture the investments and thus allow fluids from the gut of the insect to enter and possibly activate the oncosphere.

TABLE 4

Degree of infection of intermediate hosts infected experimentally with *Oochoristica vacuolata*. Only the infections of those specimens which had been offered whole and freshly voided proglottides are recorded.

Number of larvae in each specimen of host	Host species and number of specimens infected							
	Cestrinus punctatissimus	*Hypharpax moestus*	*Mecyclothorax ambiguus*	*Gnathaphanus adelaidae*	*Homothes guttifer*	*Promecoderus gibbosus*	*Anthrenocerus australis*	*Platyzosteria melanaria*
1	7	7	4	4	—	—	—	—
2	4	4	1	—	1	—	—	—
3	1	3	—	—	—	—	—	—
4	1	—	—	—	—	—	1	—
5	1	2	1	1	—	—	—	2
6	1	1	1	—	—	—	—	—
8	—	—	1	—	—	—	—	—
9	—	2	—	—	—	—	—	—
10	1	2	2	—	—	—	—	—
11	1	—	—	—	—	—	—	—
12	1	2	1	—	—	—	—	—
14	1	—	1	—	—	—	—	—
16	1	2	2	1	—	—	—	—
17	—	1	—	—	—	—	—	—
18	1	1	—	—	—	—	—	—
19	—	—	1	—	—	—	—	—
20	—	—	1	—	—	—	—	—
21	—	1	—	—	—	—	—	—
22	—	1	—	—	—	—	—	—
23	—	2	—	—	—	—	—	—
25	—	—	1	—	—	—	—	—
26	—	1	—	—	—	—	—	—
34	—	2	—	—	—	—	—	—
35	—	1	—	—	—	—	—	—
39	—	—	—	—	—	1	—	—
44	—	—	1	—	—	—	—	—
47	—	1	—	—	—	—	—	—
53	—	—	1	—	—	—	—	—
60	—	—	1	—	—	—	—	—
70	—	—	1	—	—	—	—	—
83	—	—	1	—	—	—	—	—
86	—	—	1	—	—	—	—	—
97	—	—	1	—	—	—	—	—
Total infected	21	36	24	6	1	1	1	2
Total tested	65	79	33	67	4	5	1	4

In sections of non-liberated oncospheres present in the mid-gut of infected beetles, the embryophore was found grooved internally in the vicinity of the hooks of the oncosphere (Fig. 2). In transverse sections the groove was evident on opposite sides whilst in vertical longitudinal sections it was present only at one end. It appeared to extend in a horizontal plane around the inside of that half of the embryophore nearest the hooks and to coincide with the plane of movement of the lateral hooks. Sections of oncospheres in the act of escaping from their embryophores revealed that the embryophore ruptures along the groove (Fig. 4). Thus the grooving and eventual splitting of the embryophore is probably effected by the action of the lateral hooks of the oncosphere. By pushing the median hooks through the split, the oncosphere is able to pull itself out of the inner membrane and embryophore. The inner membrane,torn open as the lateral hooks scrape against the inside of the embryophore, is left behind inside the latter investment. The escape of the oncosphere from the outer membrane was not observed. However, it seems likely that the lateral hooks also tear open this membrane. There was no evidence that any one of the membranes was dissolved by the action of either the intestinal juice of the host or secretions of the oncosphere. Oncospheres, when passed out with the faeces of the host, were found to be still enclosed in their membranes.

TABLE 5

Time taken by oncospheres of *Oochoristica vacuolata* to reach the mid-gut, wall of mid-gut and haemocoel of different intermediate hosts.

Host; time and date fed with proglottis	Time and date host examined	Oncospheres	
		Period in host (hours)	Location in host
Cestrinus punctatissimus:			
1.00 p.m. 19/12/1958	4.30 p.m. 19/12/1958	3.5	Mid-gut.
9.30 a.m. 8/2/1960	9.30 a.m. 9/2/1960	24.0	Mid-gut.
3.00 p.m. 26/2/1962	3.00 p.m. 28/2/1962	48.0	Haemocoel.
4.00 p.m. 22/3/1962	8.30 p.m. 24/3/1962	52.5	Mid-gut, wall of mid-gut and haemocoel.
Hypharpax moestus:			
9.30 a.m. 7/2/1960	9.30 a.m. 9/2/1960	48.0	Mid-gut and wall of mid-gut.
11.30 a.m. 10/2/1960	2.00 p.m. 12/2/1960	50.5	Wall of mid-gut and haemocoel.
Mecyclothorax ambiguus:			
6.45 p.m. 2/3/1962	9.45 p.m 3/3/1962	27.0	Mid-gut.
4.00 p.m. 22/3/1962	1.00 p.m. 23/3/1962	21.0	Mid-gut, wall of mid-gut and haemocoel.

Oncospheres penetrating the wall of the mid-gut were seen in a number of sections, but it was impossible to determine whether they were passing through or between the cells of the enteric epithelium. They move with their hooks foremost and apparently use them to make their way through to the haemocoel of the host.

Oncospheres which had penetrated the wall of the gut were found free in the haemocoel of the metathorax and abdomen. They were lodged amongst parts of the fat body, muscles, Malpighian tubules and other organs.

In the subsequent development of the oncosphere into a cysticercoid, four stages can be recognized. *Stage* 1.—The transformation of the oncosphere into a solid ball of cells. *Stage* 2.—The formation of a cavity—the primitive lacuna—in the developing larva. *Stage* 3.—Differentiation of the scolex accompanied by an elongation of the larva. *Stage* 4.—Invagination of the differentiating scolex into the primitive lacuna, followed by the completion of the scolex and the final development of the larva into an infective cysticercoid.

Stage 1.—Soon after reaching the haemocoel the oncosphere ceases moving its hooks and becomes spherical. The internal structure of the oncosphere disappears and in its place there is formed a number of spherical cells. Multiplication of these cells follows and the developing larva soon becomes a solid ball of cells. The hooks retain approximately the same arrangement as in the oncosphere. By the end of the Stage 1 in development, the larva had increased in diameter to 80-90 micra, i.e., to approximately twice the size of the original oncosphere (Fig. 7).

Stage 2.—Future development of the larva indicates that the hook bearing region is now more appropriately regarded as the posterior.

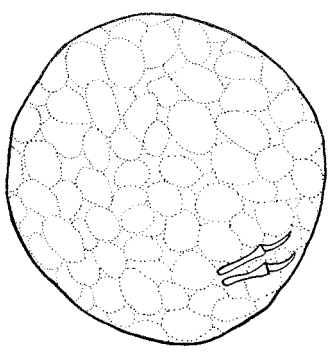
A small cavity—the primitive lacuna—soon appears among the cells of the anterior of the larva (Fig. 8a). As the larva increases in size the lacuna enlarges and becomes transversely oval. The cells anterior to the cavity multiply more rapidly than those at the posterior and cause the larva to become slightly elongated. A few calcareous granules appear among the proliferating cells. The dorso-lateral hooks loose their position and are displaced up to 69 micra from the ventro-lateral hooks towards the anterior of the larva. At the close of Stage 2 the anterior of the larva has become slightly conical and has a rather dense appearance indicating that the cells in this region are beginning to differentiate into the future scolex (Fig. 8b). The larva, now approximately 300 x 260 micra contains a lacuna 156 x 195 micra.

Stage 3.—Early in this stage the primordia of the suckers appears as dense oval clusters of cells in the anterior of the larva. The margins of the suckers soon become apparent but their musculature is not fully formed until later. Whilst the musculature of the scolex is forming, an excretory system is also developed. Two pairs of lateral canals, which in the anterior of the scolex are united by a single transverse vessel, pass to the posterior of the larva and enter separately into a small vesicle. The latter eventually opens to the exterior through a single median pore. Calcareous granules become more numerous, as many as ten being observed in one larva at this stage. During this phase of development the larva grows more in length than in width and may measure up to 492 x 315 micra (Fig. 9).

Stage 4.—The invagination of the scolex, which now occurs, marks the onset of Stage 4, the final phase in the development of the cysticercoid. As the musculature of some larvae was not fullly developed at the time of invagination, further

differentiation must take place subsequently, i.e., after the invagination of the scolex. Just how long this differentiation requires was not determined.

Fully developed and infective cysticercoids measure approximately 390 micra long and 325 micra wide and have suckers 91 to 97 micra in diameter. On being removed from the haemocoel of the host and placed in water or saline they immediately become active and evaginate their scolex. Such evaginated larvae, when fullly extended, measure up to 1.2 mm. in length and 180.0 micra in width. The scolex measures approximately 195 micra in length and 255 micra in width. Numerous calcareous granules occur, particularly in the neck region. The embryonic hooks are present but scattered in the posterior of what is destined to be the first formed segment (Fig. 10).



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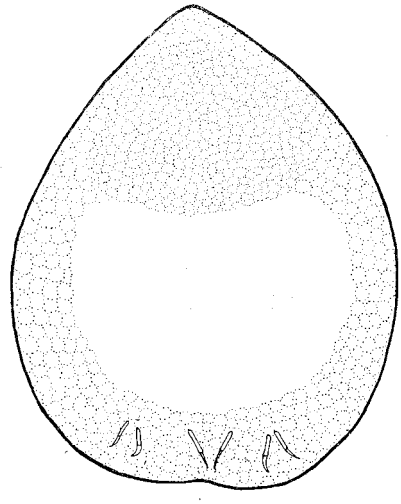

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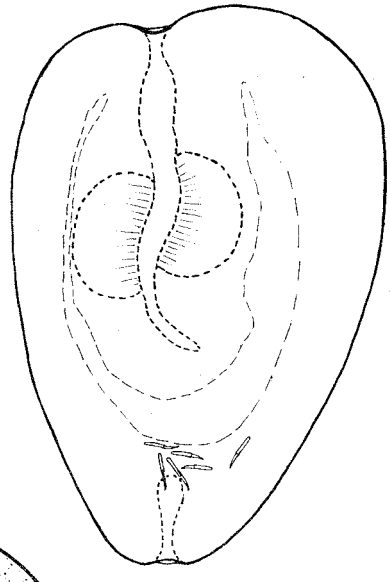

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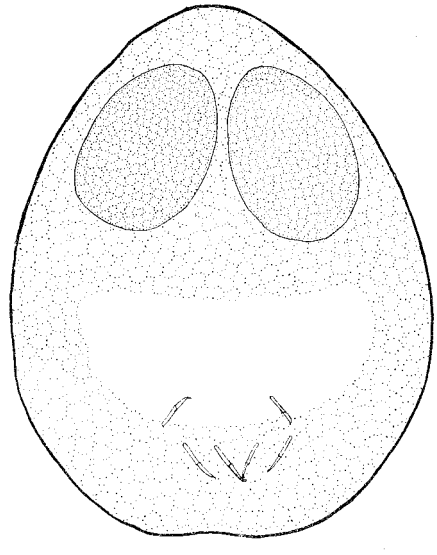

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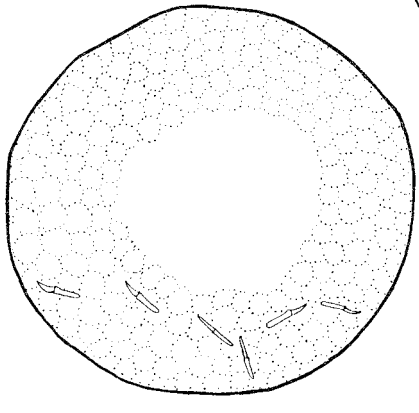

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DEVELOPMENT OF THE CYSTICERCOID

FIG. 7.—Stage 1.

FIG. 8A.—Early Stage 2.

FIG. 8B.—Late Stage 2.

FIG. 9.—Stage 3.

FIG. 10.—Mature cysticercoid.

TABLE 6

Development of cysticercoids of *Oochoristica vacuolata* in different intermediate hosts. (Grouping according to the stage reached.)

Host and date when fed with a proglottis	Date examined	Larvae		
		Period in host (days)	Number found	Stage reached (see text)
Cestrinus punctatissimus:				
Nov. 5th, 1958	Nov. 25th, 1958	20.0	4	2
Feb. 15th, 1960	Mar. 2nd, 1960	15.0	16	2
Mar. 7th, 1962	Mar, 26th, 1962	19.0	2	2
Mar. 24th, 1960	Apr. 26th, 1960	33.0	1	2
Oct. 18th, 1958	Nov. 25th, 1958	38.0	2	3
Nov. 26th, 1958	Dec. 19th, 1958	23.0	18	3
Jan. 5th, 1956	Feb. 2nd, 1956	28.0	12	4
Feb. 15th, 1960	Mar. 11th, 1960	24.0	11	4
Mar. 2nd, 1962	Apr. 2nd, 1962	30.6	1	4
Dec. 30th, 1955	Feb. 20th, 1956	52.0	14	4 (infective)
Hypharpax moestus:				
Jan. 11th, 1955	Jan. 18th, 1955	7.0	2	1
Jan. 11th, 1955	Jan. 21st, 1955	10.0	2	2
Mar. 17th, 1962	Mar. 30th, 1962	13.0	3	2
Mar. 18th, 1960	Apr. 7th, 1960	20.0	10	2
Mar. 19th, 1960	Apr. 26th, 1960	38.0	2	3
Dec. 9th, 1955	Jan. 30th, 1956	52.0	47	4
Jan. 10th, 1956	Feb. 14th, 1956	35.0	23	4
Feb. 8th, 1956	Mar. 1st, 1956	21.0	12	4
Mar. 2nd, 1962	Apr. 2nd, 1962	30.6	23	4 (infective)
Mecyclothorax ambiguus:				
Mar. 21st, 1962	Apr. 2nd, 1962	12.0	10	1
Dec. 3rd, 1954	Dec. 21st, 1954	18.0	2	2
Mar. 18th, 1962	Apr. 17th, 1962	29.8	8	2 and 3
Feb. 2nd, 1955	Feb. 27th, 1955	25.0	60	3
Jan. 24th, 1955	Feb. 25th, 1955	32.0	97	4
Jan. 11th, 1956	Feb. 15th, 1956	35.0	14	4 (infective)
Mar. 1st, 1962	Mar. 30th, 1962	29.0	19	4 (infective)
Gnathaphanus adelaidae:				
Jan. 10th, 1956	Jan. 20th, 1956	10.0	2	2
Feb. 16th, 1956	Feb. 28th, 1956	12.0	2	2
Mar. 6th, 1962	Mar. 30th, 1962	24.0	1	2
Feb. 7th, 1956	Mar. 15th, 1956	36.0	5	4
Promecoderus gibbosus:				
Feb. 21st, 1955	Apr. 2nd, 1955	40.0	2	4
Homothes guttifer:				
Jan. 31st, 1955	Feb. 28th, 1955	28.0	39	3 and 4
Anthrenocerus australis:				
Mar. 7th, 1955	Apr. 9th, 1955	33.0	4	2
Feb. 2nd, 1956	Mar. 31st, 1956	58.0	2	4
Platyzosteria melanaria:				
Feb. 25th, 1962	Mar. 18th, 1962	21.0	5	2
Mar. 4th, 1962	Apr. 2nd, 1962	29.0	5	4

TABLE 7

A summary of the infection of specimens of *Egernia whitei* examined during the years 1951-1958.

Months	Number of specimens of *Egernia whitei*					
	examined	infected	containing			
			evaginated cysticercoids	immature worms	mature worms	gravid worms
July	6	6	1	5	3	—
Aug.	6	3	1	1	1	—
Sept.	13	6	—	5	2	2
Oct.	30	18	1	9	9	10
Nov.	15	11	2	2	2	10
Dec.	8	6	—	3	3	4
Jan.	12	6	2	3	3	5
Feb.	57	23	1	10	10	21
March	40	10	2	4	3	4
April	23	14	4	11	6	8
May	18	7	—	5	3	5
June	6	2	—	1	1	1
TOTAL	234	112	14	59	46	70

TABLE 8

Length (age) of *Egernia whitei* in relation to infection with *O. vacuolata* for the years 1951-1958.

Year (Feb. to Jan.)	Lizards with						Total number of lizards examined	Total number of lizards infected	Percentage infection of total examined
	snout-vent length ≦ 55 mm.			snout-vent length > 55 mm.					
	Number examined	Number infected	Percentage infected	Number examined	Number infected	Percentage infected			
1951-2	—	—	—	45	30	66.6	45	30	66.6
1954-5	5	4	80.0	40	31	77.5	45	35	77.8
1955-6	34	5	14.7	29	20	69.0	63	25	39.7
1956-7	27	6	22.2	14	8	57.1	41	14	34.1
1957-8	34	5	14.7	6	3	50.0	40	8	20.0
TOTAL	100	20	20.0	134	92	68.7	234	112	47.9

In multiple infections the larvae were not always all of the same size nor at the same stage in development. This could be due to one or more factors. It is possible that not all the larvae entered the haemocoel at the same time. Sections of the gut of an infected *Mecyclothorax ambiguus* revealed that whilst some oncospheres were still in the crop, others had succeeded in penetrating into the haemocoel. The different positions occupied by the cestode larvae in the haemocoel of the host may favour a differential growth of the larvae. Lastly, the variations in the rates of growth may be due in part to inherited differences in the oncospheres. In heavy infections (60 to 97 cysticercoids) the ranges in size and stages reached by the larvae were the same as in light infections.

On two occasions some of the cysticercoids present in *Hypharpax moestus* were found to be enclosed in a thin membrane. As mentioned previously, *Gnathaphanus adelaidae* exhibited a marked resistance to infection. Of sixteen larvae present in one of the six infected specimens of this species, six were enclosed in thick fibrous cysts and were found adhering to parts of the reproductive organs. Some of the encysted larvae were very small and appeared to be oncospheres which had failed to develop. Others were abnormal in that although only at Stage 2, they had become markedly elongated. The larvae not enclosed in cysts were all at Stage 2 in their development but varied considerably in size.

The rate of development of cysticercoids in various intermediate hosts is evident from Table 6. The available data on the development in *Gnathaphanus adelaidae, Promecoderus gibbosus, Homothes guttifer, Anthrenocerus australis* and *Platyzosteria melanaria* is inadequate but is included for comparison. The time taken for the complete development of cysticercoids in *Cestrinus punctatissimus, Hypharpax moestus* and *Mecyclothorax ambiguus* is nearly the same. Thus specimens of these three species infected early in March were found to contain fully developed cysticercoids after 29 to 30.6 days. The cysticercoids from *H. moestus* and *M. ambiguus* proved infective. Unfortunately, in giving the specimen of *C. punctatissimus* containing cysticercoids to an uninfected lizard some difficulty was experienced and the cysticercoids may have died before being swallowed, thus accounting for the failure of the lizard to become infected. However, morphologically, the cysticercoids from *C. punctatissimus* were comparable with those from the other two hosts. Temperature has a noticeable effect on the rate of development, which is markedly slower in the colder months than in the warmer months. Owing to the scarcity of fresh proglottides it was possible to infect only a few beetles in October, November and December, but from the results obtained it is clear that the larvae in beetles infected in these months would not be fully developed in less than 55, 45, and 30 days respectively. The shortest period for the development of cysticercoids in beetles infected early in January was 28 days. Since the development of larvae to Stage 2 occurred in a minimum time (10 days) in those beetles infected early in January, it is probable that in this month development of cysticercoids is completed in less than 28 days. In February cysticercoids were found to develop in 21 days. Thus a specimen of *Hypharpax moestus* infected on February 8th and examined in March 1st was found to contain 12 fully developed cysticercoids. As mentioned previously development in March takes 29 to 30.6 days. In April it is slower and may be as long as in October and November or even longer.

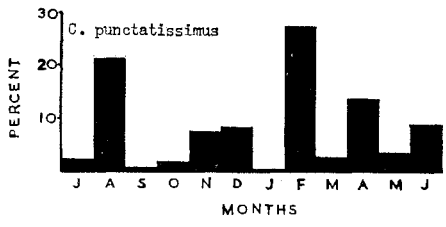
In the case of those hosts whose adults live only from Spring to Autumn, infected individuals containing fully developed cysticercoids might be expected to occur in December, January, March, April and possibly May, provided there was no infection during their larval stage. If infection of the beetles occurred in their larval stage, then individuals harbouring infective cysticercoids could occur at any time from Spring to Autumn. In species whose adults live for a longer period, individuals containing infective cysticercoids might occur in any month of the year. The only naturally infected specimen of *Cestrinus punctatissmus* so far discovered was collected in February (11/2/58) and was found to contain at least one fully developed and infective cysticercoid. Adults of *C. punctatissimus* occur throughout the year (Fig. 11) so it is possible for infected specimens to be present in any month. The cockroach, *Platyzosteria melanaria* was not collected in the field every month of the year but since it takes at least a year for the nymphs to complete development, it too must also occur throughout the year. Adults of *Gnathaphanus adelaidae* were found in every month except July and were particularly numerous in the period November to April inclusive (Fig. 12). Although adults of *Mecyclothorax ambiguus* were collected in every month except July, September and October, they were more abundant from December to March (Fig. 13). Adults of *Hypharpax moestus* were noticeably restricted to the period October to April, and most numerous in January, February and March (Fig. 14). The data on the occurrence of the other host species are inadequate.

INFECTION OF THE PRIMARY HOST

From 1951 to 1958, two hundred and thirty-four lizards were collected from the Domain and examined for the tapeworm *Oochoristica vacuolata*. No lizards were collected in 1953. A total of 112 were infected, representing 47.9% of the total number examined (Table 8).

Very immature specimens of *Oochoristica vacuolata* each with only one proglottis (evaginated cysticercoids) were found in some of the infected lizards collected from the field in July, August, October, November, January, February, March and April (Table 7). It therefore seems that infection of the primary host may occur in almost any month of the year. The occurrence of both *Cestrinus punctatissimus* and *Platyzosteria melanaria* would allow infection at practically any time of the year. The majority of recently infected lizards found were collected during the period January to April (Fig. 15). Also a particularly high percentage of infected lizards was found to harbour immature worms in April and May (Fig. 16). If the carabs, especially *Hypharpax moestus* and *Mecyclothorax ambiguus* act as intermediate hosts and only become infected when adult, their occurrence in the months of November to April might be expected to bring about, particularly in the period January to April, an increase in the number of infected lizards. However, the fact that the feeding activity of *Egernia whitei* is at a maximum from November to March may also contribute to this increase in the number infected.

There is no evidence of any age resistance, the percentage infection of large (old) lizards being higher than that of smaller (younger) lizards (Table 8). Thus, 68.7% of lizards with a snout-vent length of more than 55 mm. were infected compared with 20% of lizards with a snout-vent length of 55 mm. or less.



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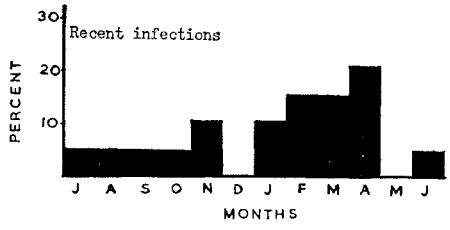

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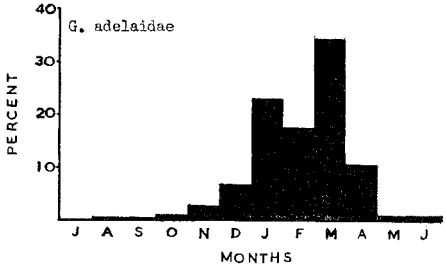

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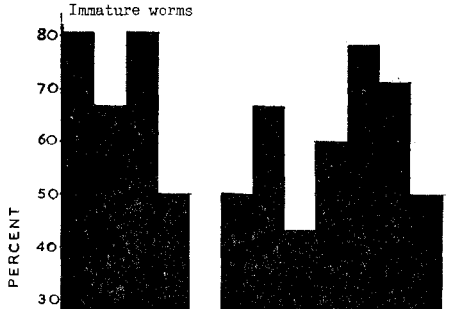

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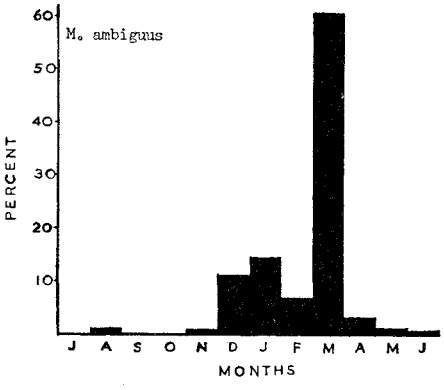

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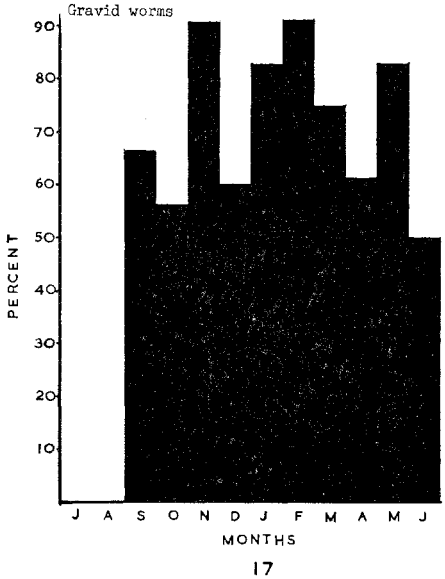

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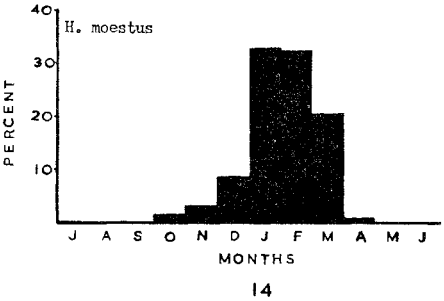

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FIG. 11.—The monthly percentages of the total number of *Cestrinus punctatissimus* collected from 1951 to 1958.

FIG. 12.—The monthly percentages of the total number of *Gnathaphanus adelaidae* collected from 1951 to 1958.

FIG. 13.—The monthly percentages of the total number of *Mecyclothorax ambiguus* collected from 1951 to 1958.

FIG. 14.—The monthly percentages of the total number of *Hypharpax moestus* collected from 1951 to 1958.

FIG. 15.—The monthly percentages of the total number of *Egernia whitei* collected during the period 1951 to 1958 and infected with *Oochoristica vacuolata* of 1 to 4 segments.

FIG. 16.—The monthly percentages of *E. whitei* collected during the period 1951 to 1958 and infected with immature *O. vacuolata*.

FIG. 17.—The monthly percentages of *E. whitei* (estimated to be more than one year old) collected during the period 1951 to 1958 and infected with gravid *O. vacuolata*.

TABLE 9

Analysis of the infection of eleven specimens of *Egernia whitei* showing multiple infections.

Number of cestodes present	Number of proglottides in strobilae cestodes
2	5, 28
2	14, 40
3	4, 14, 36
3	7, 14, 29
3	18, 34, 37
4	8, 8, 14, 40
5	3, 13, 25, 31, 33
6	1, 1, 30, 31, 34, 34
6	20, 20, 20, 38, 38, 38
6	8, 32, 33, 37, 38, 40
9	4, 4, 4, 4, 4, 4, 4, 40, 42

The degree of infection (Fig. 18) ranged from 1 to 27 worms per host for lizards from the Domain. Approximately 45% harboured more than three tapeworms. However, one lizard from East Risdon, Tasmania, was found infected with 31 tapeworms. In this case the worms were very immature (0-10 segments) and appeared to have been acquired from a single infection or at least at approximately the one time. Two other similar cases of heavy infection were found. One of these, again from Risdon, contained 20 tapeworms each with three proglottides. The other was collected on the Domain and harboured 27 tapeworms, 20 of which were immature (each consisting of only the scolex and the first formed segment). The seven other worms were fully gravid. The infection of this latter specimen indicates that multiple infections may occur. In fact, 11 other obvious cases of multiple infections were found (Table 9). Moreover, one lizard, which had been kept in the laboratory for two months and which, having voided proglottides, was known to be infected, was experimentally infected with more worms. On examination 17 days later, the lizard was found to harbour 22 tapeworms. Four of the tapeworms were gravid and had 21, 22, 23 and 24 proglottides respectively. They measured 10.5, 14.0, 17.0 and 14.0 mm in length. Each was devoid of its first formed proglottis. The other 18 worms were immature or mature having 9, 10, 11*, 12, 12, 12, 12, 13, 13, 13, 13*, 14, 14, 14, 15*, 15*, 16* and 16* proglottides respectively. In six of these worms (those with an asterisk), the strobila terminated with the first formed proglottis which still had the oncospheric hooks embedded in its cuticle. The 18 worms ranged in length from 4.5 to 8.0 mm. and were obviously from the experimental infection, whilst the four gravid worms were from some prior infection.

From the foregoing, it is apparent that infected lizards do not possess any resistance to additional infection. Since multiple infections occur, the degree of infection does not necessarily indicate the number of worms acquired from one infection. An analysis of 55 probable cases of single infections reveals that only 36.4% involved more than three worms (Fig. 19).

Nearly 42% of the lizards harboured more than three fully mature or gravid tapeworms. The maximum number of gravid worms found in any one lizard was 24 (Fig. 20). It is possible that in heavy infections (or as the degree of infection increases as a result of multiple infections) some of the tapeworms are expelled before they become gravid. Thus, six months after infection, one experimentally infected lizard was observed to void an immature worm of 10 proglottides. After 12 months the remaining worms were gravid and shed proglottides. Unfortunately, when the lizard was eventually examined it was found to have voided all the worms. Hence the degree of infection could not be determined.

RATE OF DEVELOPMENT OF THE STROBILA OF OOCHORISTICA VACUOLATA

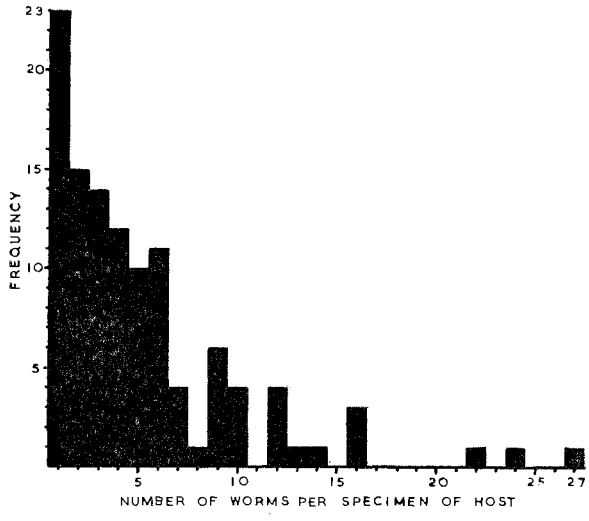
The number of proglottides in the strobila of the tapeworms of experimentally infected lizards increased at rates ranging from one every 21.9 days to one a day (average one every three days). The tapeworms in heavy infections often differed from one another in the rate at which they developed proglottides. In one lizard infected with 13 tapeworms, the number of proglottides in the strobila of the individual worms after 41 days ranged from four to 20.

From the number of proglottides in the strobila of tapeworms from naturally infected lizards, estimated to be less than 15 months old, it would appear that the natural increase in the number of proglottides ranges from one every 19 days to one a day (Table 10). For instance, one lizard captured and examined on the 4/3/56 was found to harbour two worms of 26 and 32 proglottides respectively. The lizard measured only 43 mm. in snout-vent length and therefore had been born, at the earliest, not more than 39 days previously. Assuming the lizard acquired its infection within a week after birth, the tapeworm must have developed proglottides at the rate of approximately one a day. Thus in newly born lizards which acquire their infection early in February, the tapeworms could become gravid and shed proglottides before the end of the summer.

TABLE 10

The number of proglottides in the strobila of tapeworms taken from five naturally infected lizards estimated to be less than 15 months old.

Date lizard collected and examined	Snout-vent length (mm)	Estimated age of lizard (maximum in days)	Number of cestodes present	Range in number of proglottides in strobila of tapeworm
4/3/56	43	39	2	26-32
25/10/56	46	274	6	14-25
25/2/57	58	396	2	40-42
25/3/57	52	424	1	46
11/4/57	52	441	5	32-41



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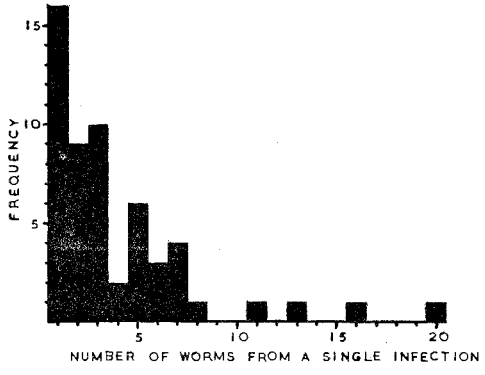

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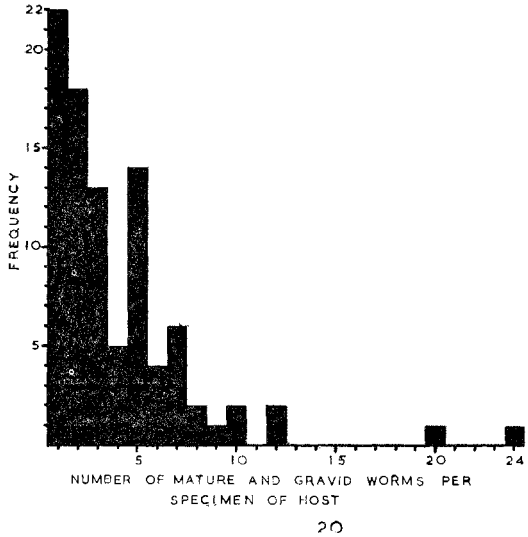

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FIG. 18.—Frequency histogram of the degrees of infection of *Egernia whitei* with *Oochoristica vacuolata*.
FIG. 19.—Frequency histogram of the degrees of infection of 55 probable cases of single infection of *E. whitei* with *O. vacuolata*.
FIG. 20.—Frequency histogram of the degrees of infection of *E. whitei* with mature and gravid *O. vacuolata*.

The largest tapeworms from lizards estimated to be approximately one year old had 32 to 46 proglottides. A naturally infected lizard estimated to have been no more than 11 months old when collected on 28/12/54 did not void proglottides until 14/1/55. On 26/4/55 it was examined and found to harbour six gravid worms. Moreover, a lizard raised in captivity and infected experimentally on the 5/3/56 was first observed to void proglottides on the 13/1/57. It therefore seems that tapeworms acquired after February do not become gravid until the following January or February.

In November, January, February and May a high percentage of infected lizards was found to harbour gravid worms (Fig. 17). The majority of infections appear to occur in the period January to April inclusive. As indicated previously, tapeworms which had become completely gravid by the end of the summer would have recovered from their winter destrobilization by November. Thus a high percentage of infected lizards could be expected to harbour gravid worms in May, November, January and February.

A summary of the number of proglottides voided by five naturally infected lizards (A-E), kept in the laboratory, is given in Table 11. Each of the three lizards (*A, B* & *C*) infected with only one tapeworm voided two to three segments per week, lizard *D* infected with four, passed five proglottides per week and *E*, infected with five, voided six to seven per week. Thus the increase in degree of infection was not accompanied by a corresponding increase in the number of proglottides voided.

Lizard *B* was collected from the field on 28/12/54. Twenty-one days later, on 18/1/55, it was observed to void a proglottis. Its tapeworm may thus have been acquired the preceding summer and only just become gravid. The lizard voided the worm completely on 23/1/58, i.e., after approximately three years. The tapeworm had shed at least 123 gravid segments during this time. A monthly analysis of the number of proglottides voided by the lizard is given in Table 12. The majority of segments were voided during January and February. The number of proglottides passed in December reached a maximum in the third year. Thus the tapeworm recovered from the effects of the winter destrobilization quicker in the third year than in the second year. It is probable that the worm would have been larger and possessed a greater number of proglottides at the onset of the second winter than at the commencement of the first winter. After destrobilization a correspondingly greater number of mature segments would have been retained to become gravid and eventually to be voided during December. Assuming lizard *B* had acquired the infection in the summer of 1954, the tapeworm would have been approximately four years old when voided. Specimen *C* was maintained in an artificially heated vivarium and although it commenced voiding proglottides several months ahead of the other lizards and continued to do so for a longer period, the total number of segments voided in the year was about the same. Lizard *E* collected on the 28/12/54 voided a proglottis the following May. It was still infected when examined on 27/8/56. Assuming this lizard to have become infected in the summer of 1954 then the five worms were at least 2½ years old when the lizard was dissected.

TABLE 11

Summary of the number of proglottides voided by five naturally infected specimens of *Egernia whitei* kept in captivity.

Lizard	Number of cestodes	Months and number of weeks during which proglottides were voided	Number of proglottides voided	
			Total	Per week
A	1	Dec.-Feb.; 13	38	2-3
B	1	1st year: Jan.-Mar.; 10	27	2-3
		2nd year: Dec.-Mar.; 16	43	2-3
		3rd year: Dec.-Mar., 16	45	2-3
		4th year: Nov.-Jan.; 9	8	1
C	1	Sept.-Feb.; 20	44	2
D	4	Sept.-Jan.; 17	84	5
E	5	1st year: Jan.-Mar.; 13	93	7
		2nd year: Dec.-Mar.; 15	92	6

TABLE 12

Analysis of the number of proglottides voided by lizard *B* each month 1954-1958.

Year	Number of proglottides voided					
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr. to Oct.
1954-5	?	?	6	13	8	0
1955-6	0	8	15	18	2	0
1956-7	0	15	10	13	7	0
1957-8	4	3	1	—	—	—
TOTAL	4	26	32	44	17	0

The lizard, mentioned previously, which had been raised in captivity and infected experimentally on 5/3/56 remained infected for four years, that is until 6/3/60. However, during this time it voided only 21 proglottides. Two proglottides were passed in the first year and none in the second year. From the 21/8/58 the lizard's vivarium was artificially heated. The lizard recommenced passing proproglottides on the 30/10/58 and continued to do so until 21/1/59. During this period 18 proglottides were passed. A further segment was voided on the 6/3/60. When the lizard was examined in the 11/2/61 no tapeworms were found in its gut. There appears no obvious explanation for the small number of proglottides passed by this experimentally infected lizard. It fed on the same variety of food as did the other five lizards. However, it was less than a month old when infected, whereas each of the other lizards was estimated to be at least two years old. Thus the total amount of food consumed by the young lizard may have been appreciably less than that taken by any one of the older lizards. This smaller amount of food consumed by the young lizard might well account for the small number of proglottides passed during the initial two years. The marked increase in the number of segments voided in the third year, when the vivarium was artificially heated, could be attributed to the greater amount of food consumed under the warmer conditions by the now older lizard.

The number of proglottides which *O. vacuolata* retains after destrobilization varies. Specimens, which had undergone destrobilization in lizards kept in the laboratory, were found to have 14 to 28 proglottides. In each instance the tapeworm had shed all its gravid segments and often some of the mature segments but never the entire strobila.

DISCUSSION

Intermediate hosts of other species of Oochoristica

Of the 69 probably valid species of the genus *Oochoristica,* 47 are parasitic in reptiles and 22 in mammals. The life cycles of only four species, namely *O. ratti* Yamaguti and Miyata (= *O. symmetrica* (Baylis) Meggitt), *O. scelopori* Voge and Fox, *O. deserti* Millemann, *O. procyonis* Chandler (syn: *Atriotaenia procyonis* Spassky) have been recorded (Rendtorff, 1948, Millemann and Read, 1953, Millemann, 1955, Gallati, 1959). However, in the case of these four cestodes only experimental intermediate hosts are known. Further only one of the four, namely *O. scelopori,* is parasitic, during its adult stage, in a reptile. The others are parasites of mammals.

Rendtorff (1948) successfully infected with *O. symmetrica* the following insects:—*Trogoderma versicolor, Attagenus piceus, Anthrenus verbasci* (DERMESTIDAE); *Tribolium confusum, T. ferrugineum* (TENEBRIONIDAE); *Tenebroides mauritanicus* (TROGOSITIDAE); *Plodia interpunctella* (LEPIDOPTERA). He was unable to infect oribatid mites belonging to the genus *Calumna,* the cockroach, *Blatta orientalis* and the tenebrionids *Tenebrio molitor* and *T. obscurus.*

Millemann and Read (1953) found that cysticercoids of *O. scelopori* would develop in *Tribolium confusum.*

Millemann (1955) obtained development of cysticercoids of *O. deserti* in the dermestid, *Dermestes maculatus;* the tenebrionids *Tribolium confusum, Gnathocerus cornutus, Tenebrio molitor* and in the lepidopteron *Ephestia cautella.* Only one of the 60 specimens of *Tenebrio molitor* tested became infected. Millemann was unable to infect *Attagenus piceus* and unidentified mites belonging to the family Acaridae (syn: Tyroglyphidae).

Gallati (1959) experimentally infected *Tribolium castaneum* with *O. procyonis.*

The results of my investigations support the conclusion that coleoptera belonging to the families Dermestidae and Tenebrionidae are potential intermediate hosts for species of *Oochoristica.* Moreover, my discovery of a natural infection of *Cestrinus punctatissimus* with *O. vacuolata,* shows that in this species at least, a tenebrionid does in fact serve as an intermediate host. In addition, for the first time, carabs and cockroaches are shown to be potential hosts. Table 13 lists the 20 insects now known as potential intermediate hosts of the five species of *Oochoristica.* In only one case, namely *Cestrinus punctatissimus,* has the insect been shown to serve as a natural host.

Up till now carabs have been recorded as intermediate hosts only for avian cestodes belonging to the genera *Hymenolepis, Raillietina* and *Choanotaenia* (Wetzell, 1938). So far only one species of *Hymenolepis,* namely *H. carioca* has been reported from carabs (Cram and Jones, 1929). However, Enigk and Sticinsky (1959) have shown that the experiment by Cram and Jones was not conclusive and that in fact carabs do not serve as intermediate hosts for this species. It should be noted that both dermestids and tenebrionids also serve as intermediate hosts for a number of species belonging to these three genera. According to Beier (1961) the only cestodes recorded from cockroaches are *Hymenolepis* sp. and *Taenia saginata.* Faust (1949) mentions three species of cockroaches which serve as intermediate hosts for *Hymenolepis diminuta.* I have been unable to find any confirmation of the record of cockroaches serving as intermediate hosts for *Taenia saginata.*

All attempts to infect mites with species of *Oochoristica* have so far failed. In contrast, mites are the only recorded intermediate hosts of species in other anoplocephalid genera. Millemann and Read (1953) considered that the biological and anatomical differences between cestodes of the subfamily Linstowiinae and other Anoplocephalid tapeworms, justified the elevation of the sub-family to the family Linstowiidae. However, Stunkard (1961) in a recent review of the taxonomy of the Anoplocephalidae concludes that "There is at present no virtue in attempts to elevate these subfamilies to family status". When the life cycles of species in other genera of the Linstowiinae are known, it may be possible to establish the true status of this group of cestodes.

The development of the cysticercoid

The pattern of the development of the cysticercoid of *O. vacuolata* agrees with the generalized scheme of development of cyclophyllidean tapeworms as proposed by Voge and Heyneman (1957). It is similar to that of the cysticercoids of *O. symmetrica, O. deserti* and *O. procyonis.* The development of the cysticercoid of *O. scelopori* has not been described.

Rendtorff found that the oncosphere of *O. symmetrica* reached the haemocoel of its host 48 hours after ingestion. According to Millemann, oncospheres of *O. deserti* take 24 hours to enter the haemocoel. Gallati found that those of *O. procyonis* reached the haemocoel after 38 hours. The oncospheres of *O. vacuolata* take 21 to 48 hours to enter the haemocoel of the host.

Rendtorff and Millemann both found that the environmental temperature of the intermediate host affected the rate of development of cysticercoids. Rendtorff discovered that, although cysticercoids of *O. symmetrica* may reach maturity in nine days during warm weather, they generally require a minimum of 18 days. Millemann obtained mature cysticercoids of *O. deserti* from adult *Tribolium confusum* after 27 days in summer. In colder months the cysticercoids were still immature after 22 days in the intermediate host. From infection experiments conducted under controlled temperature, he was able to show that at 30° C. the larvae reached maturity in 17 days, whilst at 26° C. they required 20 days. At 20° C. the larvae were still immature after 48 days. Gallati found that the cysticercoids of *O. procyonis* reached maturity and were infective after 10 days in *Tribolium castaneum* kept at room temperature (22° to 29° C.). In the present investigation, the rate of development of the cysticercoids of *O. vacuolata* was likewise found to be affected by changes in the environmental temperature of the intermediate hosts. During the warmer months (January and February) the minimum time required for cysticercoids of *O. vacuolata* to reach maturity was 21 days. In March cysticercoids required a minimum of 29 days to become infective.

The mature cysticercoids of *O. procyonis* and *O. vacuolata* are considerably larger than those of *O. symmetrica* and *O. deserti.* Those of *O. vacuolata* are slightly larger than the cysticercoids of *O. procyonis.*

The gravid proglottis and destrobilization

Freshly voided proglottides of *Oochoristica vacuolata* are quite active. There appears to be no record of the gravid segments of other species of *Oochoristica* behaving in this manner. However, the voided proglottides of *Davainea proglottina, Raillietina cesticillus, Dipylidium caninum* and *Taenia saginata* are known to exhibit considerable activity and often move some distance from the faeces with which they have been voided.

TABLE 13.

Intermediate hosts for five species of *Oochoristica*.

Intermediate host	*Oochoristica symmetrica* (syn. *O. ratti*)	*Oochoristica deserti*	*Oochoristica procyonis* (syn. *Atriotaenia procyonis*)	*Oochoristica scelopori*	*Oochoristica vacuolata*
COLEOPTERA—Dermestidae:					
Trogoderma versicolor	+	—	—	—	—
Attagenus piceus	+	0	—	—	—
Anthrenus verbasci	+	—	—	—	—
Dermestes maculatus	—	+	—	—	—
Anthrenocerus australis	—	—	—	—	+
Tenebrionidae					
Tribolium confusum	+	+	—	+	—
T. ferrugineum	+	—	—	—	—
T. castaneum	—	—	+	—	—
Gnathocerus cornutus	—	+	—	—	—
Tenebrio molitor	0	+	—	—	—
Cestrinus punctatissimus	—	—	—	—	+
Trogositidae					
Tenebroides mauritanicus	+	—	—	—	—
Carabidae					
Hypharpax moestus	—	—	—	—	+
Mecyclothorax ambiguus	—	—	—	—	+
Gnathaphanus adelaidae	—	—	—	—	+
Promecoderus gibbosus	—	—	—	—	+
Homothes guttifer	—	—	—	—	+
DICTYOPTERA—Blattidae:					
Platyzosteria melanaria	—	—	—	—	+
LEPIDOPTERA—Pyralididae:					
Plodia interpunctella	+	—	—	—	—
Ephestia cautella	—	+	—	—	—

There have been few investigations of seasonal cycles in cestodes. Up till now nothing has been recorded of the effects on reptilian cestodes of the winter hibernation of their hosts. A number of workers have found that starvation of a host may bring about the destrobilization or even the elimination of its tapeworms (Reid, 1940, 1942, Dubinina, 1949, 1950; Oliger, 1950). Reid reported that starvation of fowls infected with *Raillietina cesticillus* resulted in the destrobilization or even the elimination of the entire tapeworm. Dubinina found that, by destrobilating, *Proteocephalus osculatus* was able to survive in the empty gut of its host, *Silurus glanis*, during the winter. Oliger, from a study of the causes of destrobilization of cestodes in heath hens, concluded that it resulted from the starvation of the tapeworms and not necessarily of the host. He believed that a seasonal decrease in the quantity of starch in the food of the heath hen resulted in the sugar content of the gut of the bird becoming inadequate for the nourishment of the entire worm. Destrobilization of *O. vacuolata* occurs naturally when its host, *Egernia whitei* hibernates. It can also be brought about experimentally by the starvation of the lizard for a week. There is no evidence that the natural variation in the diet of the lizard produces destrobilization.

The longevity of few tapeworms is known and there are no data on that of species of *Oochoristica*. Lizards infected with *O. vacuolata* and kept under controlled conditions in the laboratory retained their infection for a maximum of four years. Under natural conditions, multiple infections may occur and result in a competition between the worms of the new infection and those from prior infections. The resultant degree of infection is thus a dynamic equilibrium between gain and loss of worms. Hopkins (1959) has described a similar situation in the infection of *Gasterosteus aculeatus* with *Proteocephalus filicollis*. Since, in the laboratory, no multiple infections occurred, the four years may well represent the maximum longevity for *O. vacuolata*.

The investment, structure and hatching of the oncosphere

The descriptions of the investments of the oncospheres of different species of *Oochoristica* reveal that most workers have recognized only two membranes. The outer one, sometimes called a capsule, has been considered as either parenchymatous or uterine in origin. The inner membrane (actually the middle investment), sometimes referred to as

the shell or embryophore, is usually described as being thicker than the outer membrane and separated from it by a gelatinous or granular material. Although Cohn (1902, p. 64-65) recognized three layers around the oncosphere of *O. surinamensis,* they would appear to correspond with the outer membrane, gelatinous layer and middle membrane. Zschokke (1905, p. 58) seems to have been the first to recognize three membranes.

Ogren (1957, p. 508) in describing the development of the membranes around the oncosphere of *O. symmetrica* states that " As the epidermal glands continued to develop and secrete, a membrane with metachromatic properties formed beneath the capsule and was closely applied to the oncosphere (Fig. 21)". From the figure it is clear that this membrane is the innermost of three investments. If this is so then the capsule referred to in the text is really the middle membrane and not, as implied, the outer or vitelline capsule. This interpretation is supported by the fact that in a subsequent paper, Ogren (1959 (*b*)) stated that there may be four envelopes (including the colloidal or albuminous region) enclosing the cyclophyllidean oncosphere. The fourth membrane he found to be thin and located between the inner capsule (= middle membrane) and the oncosphere. However, Silverman (1954 (*b*)) found five membranes enclosing the taeniid oncosphere and recently Voge and Berntzen (1961) observed the same number of membranes around oncospheres of *Hymenolepis diminuta.*

Ogren considered the inner capsule (= middle membrane (to be derived from colloidal secretions of the epidermal glands of the oncosphere. He compared it with the embryophore of the oncospheres of the Taeniidae and Mesocestoididae which he considered was formed from detached epidermal cells. Because of this difference in mode of formation he termed the inner capsule (= middle membrane) of the oncospheres of the Linstowiinae, a pseudoembryophore. He found that the outer capsule or shell (= outer membrane) was formed from vitelline cell products and stated that nuclei from the uterine capsule were closely attached to it in sectioned material. This statement indicates he observed, at some stage in the formation of the membranes around the oncosphere, a distinct uterine capsule. Unfortunately he made no other mention of these capsules.

In *Oochoristica vacuolata* and possibly in other species of the genus, the oncosphere (in fully gravid segments) is surrounded by three membranes and a colloidal (or albuminous) material. The latter is situated between the outer and middle membranes. The outer membrane has been termed outer shell or capsule, uterine capsule, parenchymatous capsule, vitelline capsule or shell; the middle membrane, which is usually thickened, has been termed the shell, inner shell, inner capsule, embryophore, pseudoembryophore; the inner membrane, which has generally escaped detection, is very thin and closely applied to the oncosphere.

The general structure and in particular the penetration glands (epidermal glands) of oncospheres have received considerable attention in recent years (Reid, 1948; Ogren, 1950, 1955, 1956, 1957, 1958, 1959 (*a*), and 1962; Silverman, 1954 (*b*); Silverman and Maneely, 1955; Millemann, 1955; Enigk and Sticinsky, 1957; Gallati, 1959; Sawada, 1960, 1961). Their occurrence in oncospheres of species of *Oochoristica* was first detected by Rendtorff (1958) who observed two elliptical granular areas in an oncosphere of *O. ratti* (= *O. symmetrica*). They have since been found in the oncosphere of *O. deserti* by Millemann (1955), of *O. symmetrica* by Ogren (1957) and of *O. procyconis* by *Gallati* (1959). Millemann considered them comparable with those of *Raillietina. cesticillus* as described by Reid (1958). However, he was not able to determine the anterior extent of the glands nor observe any secretory pores. Likewise, Ogren found no ducts or pores and concluded that the secretion of the glands passes through the body surface. Gallati considered they were two unicellular glands and stated that " prior to their anterior termination the cells divide into 2 lobes which appear to empty individually near the median pair of hooks ". He thus implies that there are four pores. Recently Sawada (1961) has shown that each of the glands of the oncosphere of *Raillietina cesticillus* opens by two pores (one dorsal to the other), not one, as previously recorded (Reid, 1958). Further study of the glands in *Oochoristica vacuolata* may reveal four pores instead of the two observed during the present investigation. The general structure of the oncosphere of *O. vacuolata* appears similar to that of the oncospheres of *O. procyonis* and *O. symmetrica.* Moreover, it agrees well with Ogren's (1962) theoretical diagram and his description of an infective oncosphere.

Reid (1948) suggested that the secretion of the glands might assist the oncosphere in its penetration of the gut of the intermediate host. Silverman and Maneely (1955) concluded that the secretion of the glands of the oncospheres of *Taenia saginata* and *T. pisiformis* eroded the cells of the digestive mucosa. As mentioned previously Ogren (1957) proposed as one of the functions of the secretion of these glands the formation of a membranous substance around the oncosphere. He suggested the name " epidermal glands " as a nonfunctional name to replace " penetration glands ". Sawada (1961) observing the artificial hatching of oncospheres of *Raillietina cesticillus,* found that when the oncospheres were about to penetrate the shell membrane, the glands discharged a small quantity of fluid. He also found that the glands of oncospheres which had not penetrated the digestive canal of the intermediate host showed a positive staining reaction with P.A.S. technique, whilst those of oncospheres which had penetrated showed a negative reaction. From his observations he concluded that the secretion of the glands helped the oncosphere in its escape from its membranes and also in its penetration of the gut. Although he did not indicate how the secretion helped in the liberation of the oncosphere, he suggested that the polysaccharide complexes of the glands were spent in the erosion of the cells of the gut during the oncospheres penetration into the haemocoel.

Silverman (1954 (*a*)) found that the hatching of taeniid eggs involves (*a*) the digestion of the cement which binds together the rod-shaped blocks of the embryophore and the resultant disintegration of the embryophore, (*b*) and increase in the permeability of the oncospheral membrane, (*c*) the activation of the oncosphere, (*d*) the rupture of the

oncospheral membrane by the hooks of the embryo, and (*e*) the escape of the oncosphere.

According to Gallati (1959, p. 372) "Parodi and Alcarez (1946) reported that hatching of the oncospheres of *Multiceps serialis* and *Hymenolepis diminuta* is due to the mechanical perforation of the membranes and shell by the hooks, and not the action of the mouth parts or digestive juices of the host". However, Reid *et al.* (1951) found that the shell of the egg of *H. diminuta* was cracked off by the mandibles of the host. More recently, Voge and Berntzen (1961, p, 816) have stated that "During the process of hatching (of the eggs of *H. diminuta*), mechanical friction is necessary for breaking of the egg shell and rupture of the underlying membrane. The vitelline membrane apparently is digested or dissolved by substances present in the host, while the oncosphere coat and membrane rupture only with prolonged oncosphere activity, whether or not the vitelline membrane has disappeared". They also mention the possibility of the oncosphere, during its activity, liberating substances which act upon the coat and membrane from inside.

There has been no reported investigation of the hatching of eggs of species of *Oochoristica*. Gallati (1959) did not observe the hatching of the eggs of *O. procyonis* but states (p. 372) that "Unhatched eggs were often recovered from the lumen of the gut of insects 72 hours after the beetles were fed" and concluded that "Failure of such eggs to hatch after prolonged exposure to mechanical action of the embryonic hooks and the chemical action of the host's digestive enzymes lends credence to the probability that hatching consists of emergence of the oncosphere after the egg shell has been torn by the mouth parts of the beetle".

In the case of the hatching of the eggs of *O. vacuolata* there was no indication that the investments of the oncosphere were either dissolved or disintegrated by the digestive juices of the host and there was no evidence that they were ruptured by the host's mandibles. However, the embryophore of eggs in the gut of the host was found to be grooved internally in the plane of movement of the lateral hooks of the oncosphere. It is suggested that the oncosphere, activated by certain juices of the host which penetrate the egg membranes, gouges its way out of its investments by means of its hooks. In view of the observation of Sawada (1961) it is possible that the grooving of the embryophore by the hooks is aided by secretions from the penetration glands of the oncosphere.

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