Observations on the life-cycle of *Echinococcus oligarthrus* (Diesing, 1863) in the Republic of Panama

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The discovery of the first autocthonous case of hydatid disease in the Republic of Panama (Sousa and Lombardo Ayala, 1965) developed an interest in the taxonomic status of the species of *Echinococcus* involved, and led to a search for information on the morphology, biology and ecology of the species present in the area.

Thatcher and Sousa (1966) reported the occurrence of *E. oligarthrus* (Diesing, 1863) in several Panamanian wild felids. Two infected pumas (*Felis concolor* L.) and a jaguarundi (*F. yagouaroundi* Geoffroyi) were collected from a forested area north of Gatun Lake, near the inter-oceanic canal. More recently, Thatcher and Sousa (1967) reported the first recorded natural infection of *E. oligarthrus* in the jaguar (*F. onca* L.): a female jaguar shot in the area of Achiote, Colon Province, was found to be parasitized by adult *Echinococcus* in the small intestine. The identity of the worms was established from the study of mature proglottids and rostellar hooks.

Although *E. oligarthrus* is usually referred to in works dealing with the genus *Echinococcus* Rudolphi, 1801, little is known of its biological characteristics. On considerations entirely of type of definitive hosts and morphological characters, recent authors (Rausch and Nelson, 1963; Abuladze, 1964; Verster, 1965) recognized *E. oligarthrus* as a valid species. Rausch (1967) considered that not more than four species of the genus were to be considered as valid—*E. granulosus* (Batsch, 1786), *E. multilocularis* Leuckart, 1863, *E. oligarthrus* (Diesing, 1863) and *E. patagonicus* Szidat, 1960.

Only two species, *E. granulosus* and *E. multilocularis*, have been well studied and their life-cycle fully defined. Even though Cameron (1926) suggested that the hydatid named by Brumpt and Joyeux (1924) as *E. cruzi* from a Brazilian agouti (*Dasyprocta agouti* L.) was the larval stage of *E. oligarthrus*, no report defining the biological characteristics of the parasites is available to establish a valid criterion for the synonymy. Several authors (Sweatman and Williams, 1963; Rausch and Nelson, 1963; Thatcher and Sousa, 1966) have emphasized the need for experimental work and biological definition of the species in order to determine the true relationship between *E. cruzi* and *E. oligarthrus*.

Because of the increasing interest in tropical echinococcosis, the present study provides information on the development of *E. oligarthrus* in experimental animals, and leads towards an understanding of the life-cycle of the species in Panama. To our knowledge, no other species of *Echinococcus* has been reported to occur endemically in the area.

MATERIALS AND METHODS

Source of Infective Material

An infected puma (*F. concolor*), killed in a forested area north of Gatun Lake, near Achiote, served as the source of infective *E. oligarthrus* material for the experimental work.

The animal was heavily parasitized by adult worms (estimated number 100,000), many of which had well-developed gravid proglottids. The morphological characteristics of this material are described by Thatcher and Sousa (1966). Adult worms were collected by washing infected gut sections in tap-water and concentrating the parasites by sedimentation. Washed parasites and gravid segments were resuspended in physiological saline prior to use in the preparation of the infective material.

Method of Infection

The oral route of administration was followed in all efforts to induce primary hydatidosis. From 50 to 500 gravid proglottids and adults were fed to experimental hosts, either by stomach intubation or with a water-dropper dispenser.

In every attempt to infect experimental definitive hosts, the infective material (fertile hydatid cysts) was mixed with the usual meat ration given to the animals (canned food or ground raw meat). Following the ingestion of infective material, the animals were kept in quarantine until termination of the experiment and autopsy.

Experiment I was designed to demonstrate the susceptibility of laboratory rodents as intermediate hosts of *E. oligarthrus* material of puma origin. Experiment II was designed to demonstrate the susceptibility of various carnivores, including cats and dogs, to infection with experimentally induced hydatids. Experiment III tested the infectivity of eggs produced in gravid proglottids of experimentally induced adults of *E. oligarthrus*, and provided information on the development and fertility of second-passage hydatids in laboratory intermediate hosts.

Diagnostic Procedure

During the course of the work it became evident that in heavily infected animals primary hydatidosis could be detected by palpation of the body muscles and cavity. Detection of hydatid cysts, however, usually required a careful autopsy technique, involving the musculature as well as the internal organs. The autopsy included (*a*) skinning of the animal, to detect small subcutaneous cysts and to enable inspection to be made of the somatic musculature; (*b*) palpation and dissection of main body muscles, followed by transverse cuts made 1 cm. apart to cover the length of the muscle; (*c*) exposure and inspection of the viscera after opening the body cavities through the mid-ventral line; (*d*) examination and fixation of tissues.

Liver, spleen, pancreas, lungs, heart and kidneys were separated, and cuts were made at 1-cm. spacing; blocks of tissues were made from these organs, as well as from the brain, diaphragm and skeletal muscle. These tissues were fixed in 10 per cent. neutral formalin, and stained by standard haematoxylin and eosin procedures. In the case of positive tissues, other staining techniques were used, such as PAS and trichrome stains. Whole mounts of germinative membranes, hydatid sand and adult worms were fixed in formalin (10 per cent.), in warm alcohol-formalin-acetic acid solution, or in Bouin's fluid, followed by staining procedures with borax carmine or Mayer's carmalum. General measurements were obtained as described by Thatcher and Sousa (1966). The formalin-ether concentration technique was used to examine faecal material of experimental animals exposed to infection with hydatid *E. oligarthrus* material. The egg-counting technique of Stoll was used to determine daily egg-production of adult *Echinococcus*.

Animals used for experimental purposes were bred and reared at the Gorgas Memorial Laboratory in Panama, except for some wild carnivore species, such as the coati (*Nasua narica* L.), the tayra (*Tayra barbara* Goldman), and the margay (*Felis wiedii* Schinz), which were captured as juveniles and kept in the laboratory under observation before use as experimental animals. Laboratory-reared animals included the following species: spiny rat (*Proechimys semispinosus* Tomes), Panamanian climbing rat (*Tylomys panamensis* Gray), agouti (*Dasyprocta punctata* Gray), and cotton rat (*Sigmodon hispidus* Say and Ord). These were colonized from wild stock, native to Panama. Other experimental animals used were Wistar rats, CFW white mice, golden hamsters, gerbils, cats, dogs, rhesus monkeys, and a white-faced monkey (*Cebus capucinus* L.).

TABLE I

Showing the results obtained in six species of animals following the ingestion of proglottids of *E. oligarthrus* from a naturally infected puma

Animal	No. exposed	No. infected	Days under observation	Organs parasitized
Spiny rat (*Proechimys semispinosus*)	2	1	133	Lung
Panamanian climbing rat (*Tylomys panamensis*)	2	1	225–396	Body muscles, diaphragm, mesentery
CFW mouse (*Mus musculus*)	7	0	134–261	—
White rat (*Rattus rattus*)	4	0	133–268	—
Golden hamster (*Mesocricetus auratus*)	6	0	134–261	—
Brown agouti (*Dasyprocta punctata*)	3	3	512	Body muscles, heart, diaphragm, kidney
Totals	24	5	133–512	

RESULTS

Experiment I. Induced Primary Hydatidosis

Twenty-four laboratory-reared animals belonging to six species were exposed to infection with *E. oligarthrus*. Mature and gravid proglottids from a naturally infected puma were administered orally either through gastric intubation or with a water dispenser. Two spiny rats, two climbing rats, seven laboratory mice (CFW strain), four Wistar rats, six golden hamsters, and three agoutis were used in this experiment.

Hydatids of *E. oligarthrus* were recovered from the spiny rat (1 out of 2), the climbing rat (1 out of 2) and the agouti (3 out of 3) (see Table I).

Infection in the climbing rat. An adult male climbing rat was observed to develop superficial cysts at the base of the front and hind legs on the right side. These enlargements became noticeable after three months of development. The animal was killed 225 days after the ingestion of the infective material. The autopsy revealed a generalized hydatidosis, with five large cysts in the body musculature. The largest hydatid (3·0 × 2·5 cm.) was found in the right-flank muscles of the hind leg. The smallest cyst (2·0 cm. diameter) was found in the right cervical region (Plate XIII, fig. 1). In total, there were two cysts on the right hind quarter, and one cyst each on the left hind flank, on the right axillary region and on the right cervical region. All hydatids seen in the somatic muscles were of the simple vesicular type, with a thin hyaline cuticular layer and an active germinal layer. The cysts were fertile, with numerous mature scoleces, some of which promptly evaginated (fig. 2). Many small brood capsules and proliferating buds could be detected on the germinal layer of the cysts. The rostellar hooks ranged in size from 31·3 to 35·0μ (average 33·3μ) for the large hooks, and from 25·9 to 29·2μ (average 27·3μ) for the small hooks.

In the abdominal cavity a large irregular-shaped cyst was found fixed to the peritoneal wall on the left side (fig. 1). Septation was evident, dividing the cyst into three chambers. This cyst was also fertile. It measured 2·4 cm. in length, with a 1·7 cm. diameter at the base, and 0·7 cm. in diameter towards the smaller chamber at the apex. Two cysts developed in the diaphragm muscles; they were vesicular in nature (1·0–2·5 cm. in diameter) and bulged into both pleural and abdominal cavities. A multilocular cystic mass developed in the mesentery proper; it presented many chambers (fig. 3). Although most of the chambers were sterile, some development of scoleces was detected in histological sections (fig. 4).

No cysts were detected in the liver, kidneys, lungs or brain. The heart, however, showed development of a hydatid on the surface of the left auricle, which extended into the left dorsal wall imbedded in fatty tissue. This cyst was vesicular and contained fertile scoleces.

Infection in the spiny rat. An adult male rat was found dying 133 days after exposure to infection. On autopsy the animal weighed 375·7 gm. and showed no abnormalities in the abdominal cavity, mesenteries, urinary bladder or intestinal wall. The liver, spleen and diaphragm appeared normal and free of parasites. The right lung was parasitized with five vesicular hydatid cysts ranging in size from 0·9 to 2·0 cm. in diameter (Plate XV, fig. 14). Although the borders of these cysts were irregular, they were not septate or multichambered. The germinal layers showed evidence of active proliferation of scoleces. All cysts were fertile, although approximately 60 per cent. of the scoleces were not yet fully matured. Active mature invaginated scoleces with fully formed rostellar hooks were studied. The scoleces varied in size from 218·0 to 230·0μ, with numerous calcareous bodies and a rostellar crown of 34–42 hooks, easily differentiated into small and large rostellar hooks. Small hooks ranged in length from 24·6 to 29·2μ (average 25·8μ); large hooks varied in length from 30·9 to 35·0μ (average 33·3μ). Another spiny rat showed no evidence of hydatid cysts when autopsied 133 days after exposure to infection.

Infection in the agouti. The local agouti proved to be highly susceptible to infection with the eggs of *E. oligarthrus*. Of three animals exposed to infective material, all developed hydatid cysts. Two of them showed evidence of cystic growths by palpation of the body

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EXPLANATION OF PLATE XIII

Experimental primary hydatids of *E. oligarthrus* in the climbing rat, *T. panamensis*

FIG. 1. Generalized primary hydatidosis, showing abdominal, somatic and cervical cysts. (Half natural size.)

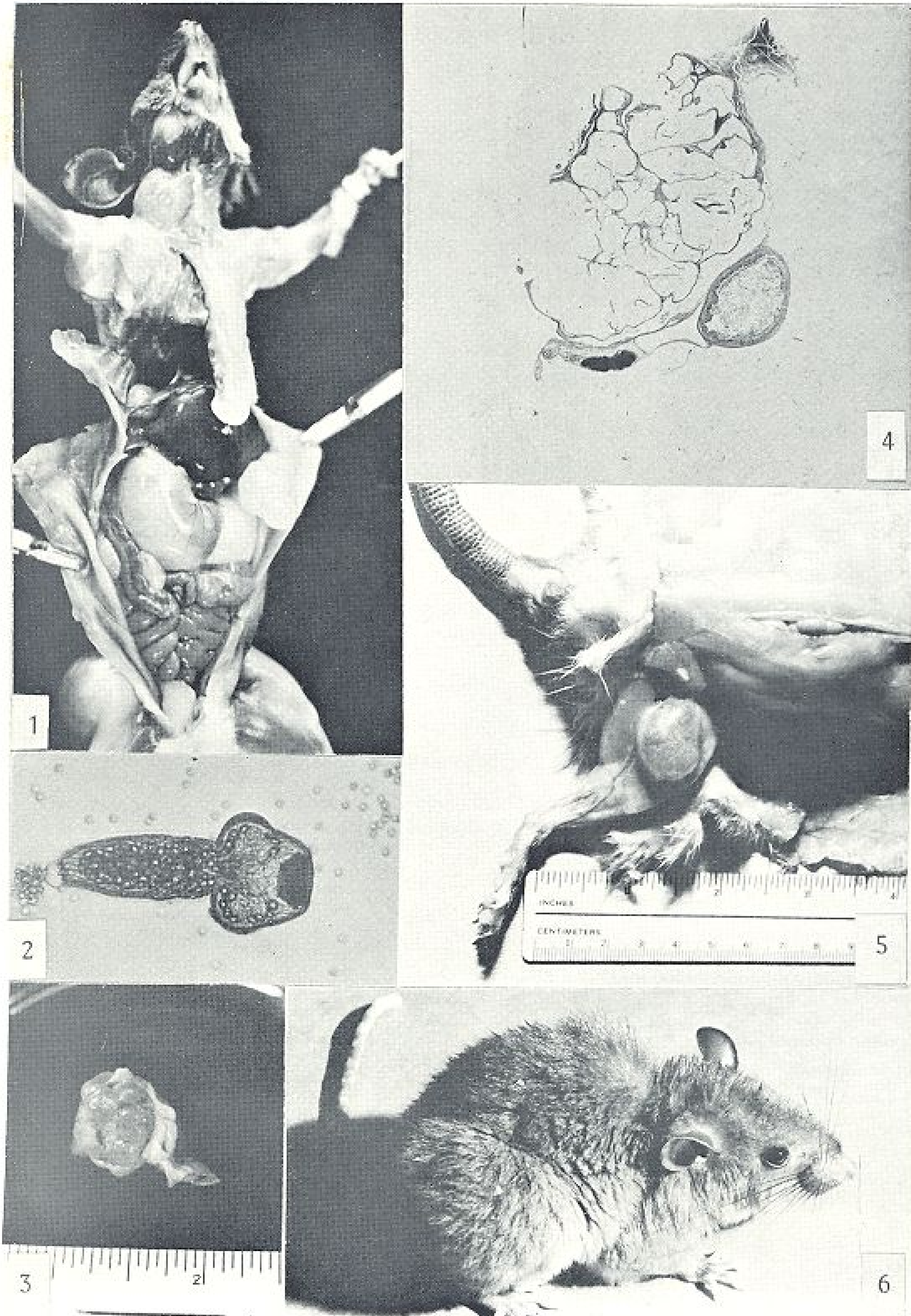
FIG. 2. Evaginated scolex of *E. oligarthrus* from an experimentally induced hydatid in *T. panamensis*. (×150.)

FIG. 3. Multilocular macrovesicular cyst developed in the mesentery proper of *T. panamensis* fed on eggs of *E. oligarthrus*. (9/10 natural size.)

FIG. 4. Histological section of the cyst in fig. 3, showing multiple chambers adjoining cross-section of the small intestine. (×3·3.)

FIG. 5. Primary hydatid in leg muscle. (Half natural size.)

FIG. 6. Adult male *Tylomys*, showing large hydatid cyst in right hind leg. (1/3 natural size.)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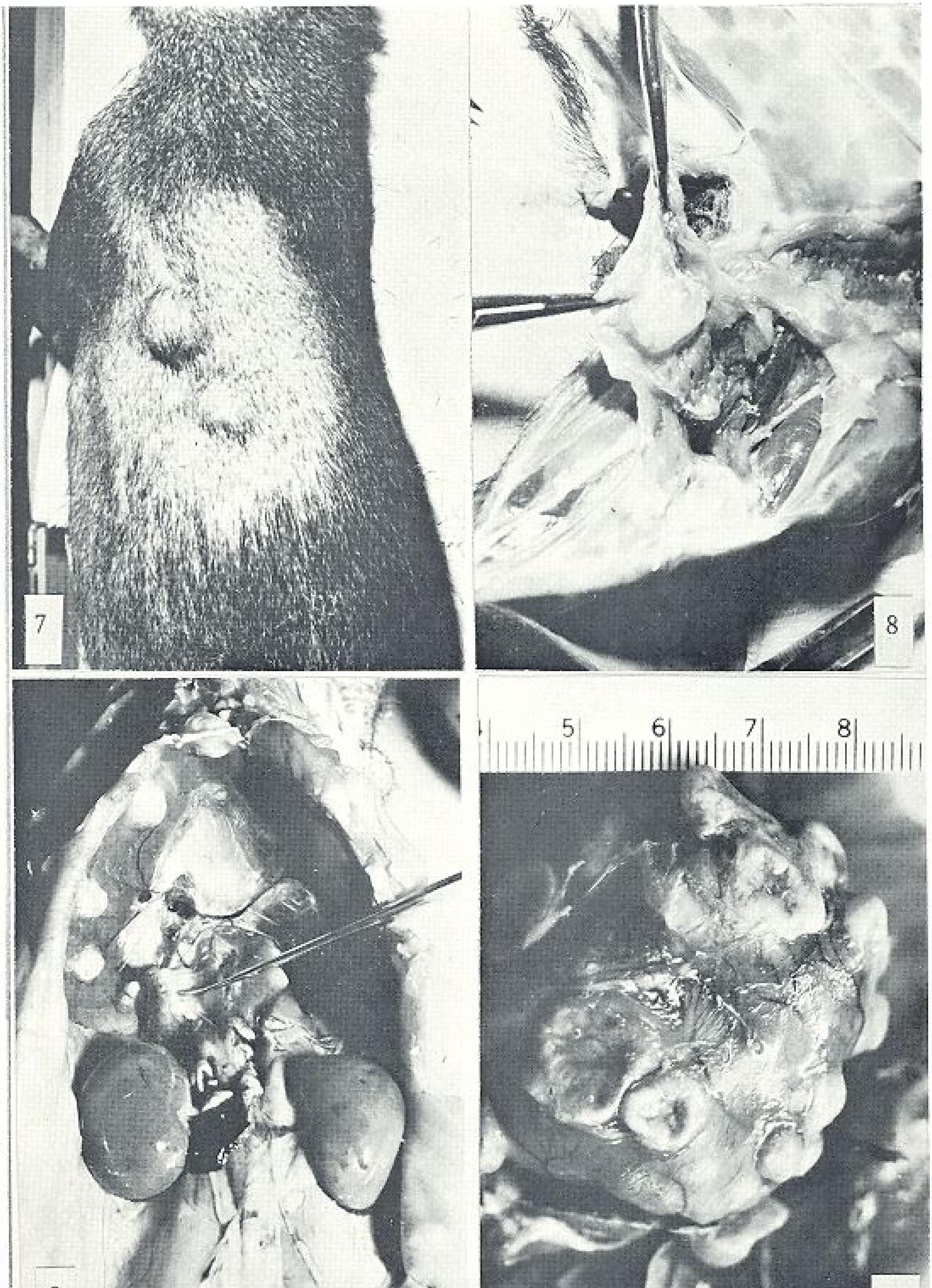
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musculature seven months after infection. One of them showed 12 subcutaneous cysts following a routine superficial examination. This animal was kept under observation for 17 months, during which time the hydatidosis became generalized, with many cysts detectable on the body surface (Plate XIV, fig. 7). Some of the cysts ruptured upon scratching, leaving an open ulcer-like wound that soon healed. Except for weight loss and dyspnoea, this animal appeared normally active when it was killed for autopsy.

On the ventral surface alone 30 cysts (0·5–3·0 cm.) had developed in the subcutaneous muscles. The deeper muscles of the legs, the intercostals and lumbar muscles were also parasitized (fig. 8).

TABLE II

Showing the results obtained in experimental hosts fed on cysts of *E. oligarthrus* obtained from various intermediate hosts

Experimental animal (definitive host)	Infective material			Results		
	No. of cysts given	Intermediate host	Location of hydatid	Time of observation	Eggs passed in faeces	Adults recovered
Domestic cat no. 1	4	Spiny rat	Lung	6 days	–	40 juveniles
Domestic cat no. 2	3	*Tylomys*	Muscles	115 days	None	3,000
Domestic cat no. 3	2	Agouti	Muscles	126 days	+	Several 1,000s
Domestic cat no. 4	3	Agouti	Muscles	142 days	+	Several 1,000s
Margay	1	*Tylomys*	Muscles	120 days	None	None
Dog no. 1	4	*Tylomys*	Muscles	71 days	None	3
Dog no. 2	2	Agouti	Muscles	151 days	None	None
Raccoon (*Procyon lotor*)	20	Agouti	Muscles	76 days	None	None
Coatimundi (*Nasua narica*)	2	Agouti	Muscles	66 days	None	None

Examination of internal organs revealed hydatid cysts in the kidneys and pancreas. The heart was heavily parasitized. Both simple vesicles and multilocular polycystic growths were seen imbedded in the myocardium. Seven cysts, some septate, developed in the muscles of the diaphragm (figs. 8, 9, 10). One large cyst from the dorsal base of the diaphragm extended into the liver parenchyma. Although the liver was not greatly involved, small cysts were located in the lungs. No hydatids were recovered from the mesentery proper, intestines, spleen or brain.

Experiment II. Experimental Echinococcosis: Development of Adult E. oligarthrus

Four domestic cats, one margay, two domestic dogs, one raccoon and a coatimundi were induced to ingest infective hydatid material from various intermediate hosts (see Table II). After a period of observation of 66–151 days, no development of adults could be

EXPLANATION OF PLATE XIV

Experimentally induced primary hydatids of *E. oligarthrus* in the agouti, *D. punctata*

FIG. 7. Two subcutaneous hydatid vesicles. (Half natural size.)
FIG. 8. A fertile hydatid vesicle embedded in the deeper muscles of the hind leg. (9/10 natural size.)
FIG. 9. Septate cysts in the diaphragm. (Half natural size.)
FIG. 10. Multiple cysts in the heart. (Natural size.)

detected in the margay, raccoon, coatimundi and one of the domestic dogs. The second dog, which had received a muscle hydatid from a *Tylomys*, was killed 71 days after infection; only three adult worms were recovered from the animal's intestine. One of the specimens was almost mature, with two segments; the other two worms had not developed a second proglottid. The development of the adults was abnormal, with no gravid proglottids produced by the low proportion which matured.

The domestic cat was found to be a good host for the development of adult *E. oligarthrus*. Of four cats given infective hydatid material from spiny rat, climbing rat or agouti, all showed evidence of infection and development of adult *Echinococcus*. Although one cat (no. 1), given hydatid material from a lung infection in a spiny rat, died only six days after ingestion of the infective meal, it was found to harbour over 40 active juvenile worms. Cat no. 2, given three hydatid cysts from the muscles of a climbing rat, was found to harbour over 3,000 well-developed adults of *E. oligarthrus* in the small intestine 115 days after exposure to infection. Both mature and gravid proglottids were seen in some specimens; yet all faecal examinations of cat no. 2, performed at 48-hour intervals, had given negative results, no eggs being detected in the faeces. Domestic cats (nos. 3 and 4), given infective hydatid material from an agouti, showed *E. oligarthrus* eggs in the faeces 86 and 87 days following ingestion of the infective meal. Daily counts of 100–600 eggs per gm. of faeces were recorded for these experimentally induced infections until the animals were killed for autopsy 126 and 142 days after infection. Adult *Echinococcus* were detected in the duodenum 16–18 inches from the pyloric sphincter. The greatest parasite load was detected in the intestinal wall 24–30 inches from the pylorus. Up to four segments, including the gravid proglottid, could be detected in some specimens. Adult morphology and characteristics of the eggs were comparable to our *E. oligarthrus* material of puma origin (Plate XV, fig. 11).

Experiment III. Experimental Hydatidosis, Second Passage

Twenty animals of seven species were exposed to infection by oral administration of infective *E. oligarthrus* material derived from experimentally infected house cats no. 3 and 4. The animals included spiny rats, climbing rats, cotton rats, gerbils, agoutis, one rhesus monkey and a white-faced monkey. Table III summarizes the results of the experiment. Hydatid cysts developed in the climbing rat (4 out of 4), the cotton rat (4 out of 6), the gerbil (2 out of 4) and the agouti (2 out of 2). After an observation period lasting 310–411 days, no hydatids were recovered in the spiny rats or the monkeys.

Infections in the climbing rat produced large hydatid cysts in the somatic musculature which could easily be detected by palpation (Plate XIII, fig. 6). The hydatids measured from 2·3 to 5·0 cm. in length. They were either simple or septate polycystic macrovesicles, with numerous scolcces and brood capsules in the germinal layer (fig. 5).

EXPLANATION OF PLATE XV

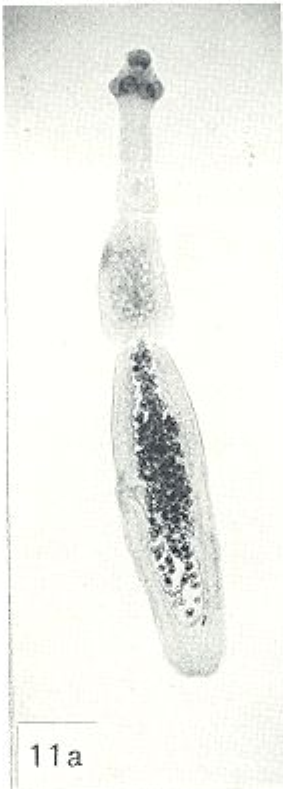
Experimental *E. oligarthrus*

FIG. 11. a, Adult worm with gravid proglottid, from a natural infection in a Panamanian puma. (×32.) b, Egg passed in the faeces of an experimentally infected domestic cat. (×600.)

FIG. 12. Fertile primary hydatid cyst developing in the mesentery of an experimentally infected cotton rat, 455 days after infection. (Half natural size.)

FIG. 13. Somatic hydatid cysts induced in a gerbil, 80 days after ingestion of eggs. (×1·2.)

FIG. 14. Pulmonary hydatid vesicles developed in the spiny rat. (Half natural size.)



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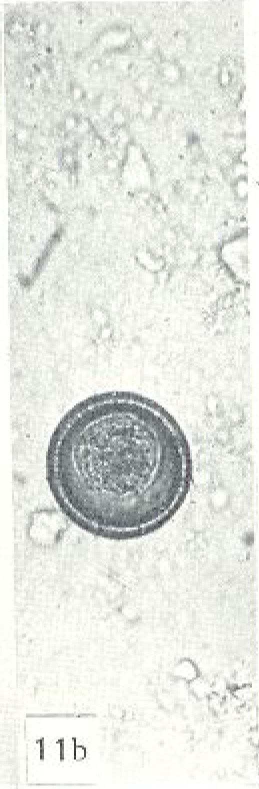

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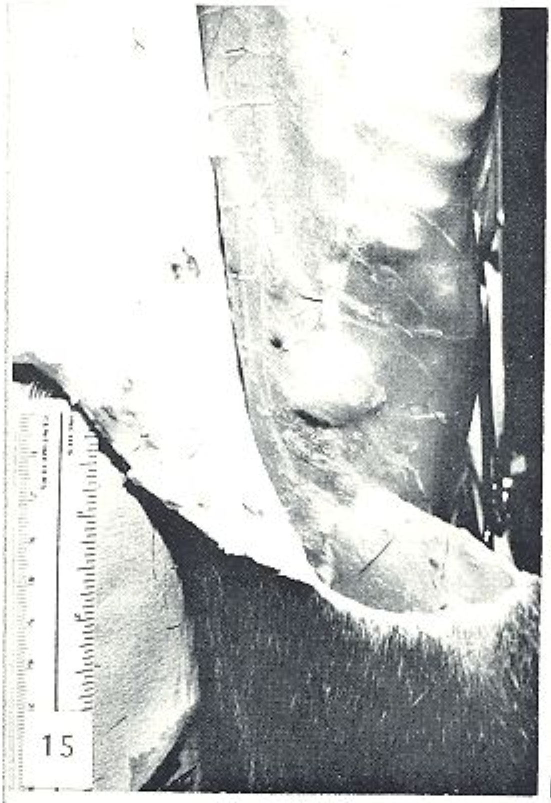

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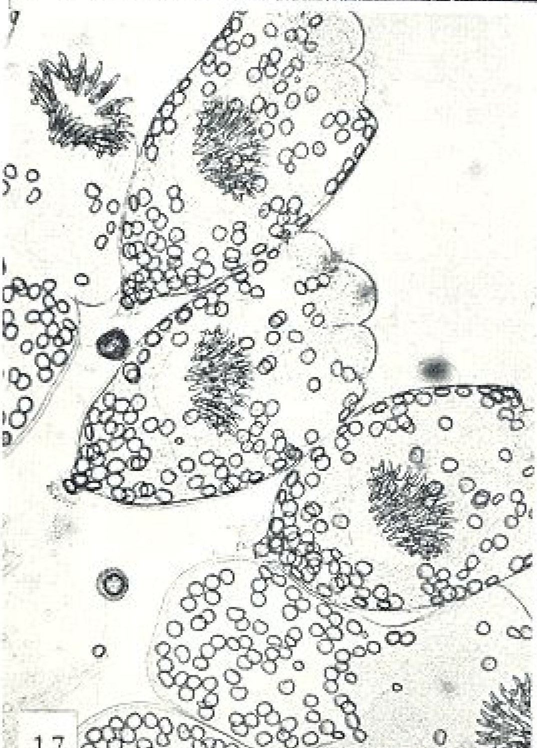

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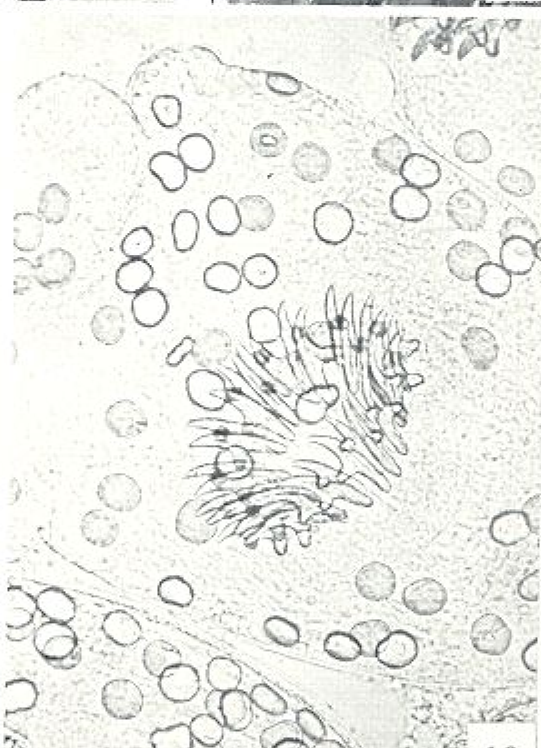

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In the cotton rat, hydatids could not easily be detected by external palpation. Although a small (0·9 cm.) hydatid vesicle was found on the muscles of the right anterior extremity of one animal, larval development was found more frequently in the body cavity. A septate multilocular cyst (2·2 × 1·4 cm.) was seen in the mesentery proper of one cotton rat (Plate XV, fig. 12); vesicular cysts developed at the base of the heart, and in one case two calcifying cysts were located in the pleural wall of the left lung.

TABLE III

Showing the results obtained in seven species of animals following the oral administration of gravid proglottids of *E. oligarthrus*

Host	No. exposed	No. infected	Days under observation	Tissue parasitized
Spiny rat (*Proechimys semispinosus*)	2	0	370	—
Panamanian climbing rat (*Tylomys panamensis*)	4	4	450	Muscles
Cotton rat (*Sigmodon hispidus*)	6	4	103–455	Pleural sac, muscles, mesenteries, heart
Gerbil (*Meriones unguiculatus*)	4	2	47–164	Muscles, lung, kidney
Rhesus monkey (*Macaca mulatta*)	1	0	310	—
White-faced monkey (*Cebus capucinus*)	1	0	411	—
Brown agouti (*Dasyprocta punctata*)	2	2	432–450	Muscles, heart, lungs, skin
Totals	20	12	47–455	

Infections in the agouti were more generalized than in the other experimental animals used. Fertile vesicular hydatids developed in the subcutaneous tissues, the somatic muscles, the lungs and heart. In the heart, the cyst developed as a small septate macrovesicle (1·0 cm. diameter) located in the wall of the right ventricle. No hydatid growth developed in the liver, spleen or pancreas. Infection in the gerbil involved the somatic muscles and the kidneys (Plate XV, fig. 13).

NATURAL HYDATID INFECTIONS IN PANAMANIAN WILD RODENTS

From the area of Achiote, Colon Province, where *E. oligarthrus* is known to occur in wild felids, 47 spiny rats, 15 climbing rats and 39 agoutis were examined for hydatid cysts. None of the spiny rats or climbing rats were found to harbour natural hydatid infections. Three agoutis (7·7 per cent.) showed natural infections with the larval stage of *Echinococcus*. In every case the hydatids were found in the subcutaneous muscle layers or deeper within the greater muscles of the extremities. From one to four cysts were detected in the muscles of the infected wild-caught agoutis. The cysts were fertile, with many active scoleces which readily evaginated (Plate XVI, fig. 17). The general morphology of the cysts and of the sco-

EXPLANATION OF PLATE XVI

Natural hydatid infection in the agouti, *D. punctata*

FIG. 15. Surface view of hydatid bulging from the body wall on the right lumbar region. (Half natural size.)

FIG. 16. Dissection and internal view of the cyst shown in fig. 15. (Half natural size.)

FIG. 17. Active and evaginating scoleces from a naturally acquired hydatid. (×200.)

FIG. 18. Hooks, their arrangement and morphology, in a mature scolex. (×400.)

leces was similar to that of the hydatids of *E. oligarthrus* experimentally induced in laboratory-reared agoutis. The number (32–36), size (large hooks 32–40μ) and shape of the rostellar hooks were compatible with those characterizing the hydatids of the species. Up to 100 round-to-ovoid calcareous corpuscles were usually seen in mature scoleces. The cyst wall presented a thin cuticular layer, at times delaminating or septating. The germinal layer, with scattered calcareous corpuscles, proliferated brood capsules containing 12–20 scoleces. The length of the scoleces varied from 112·0 to 126·0μ, and their width from 82·0 to 84·0μ.

DISCUSSION

Although *E. oligarthrus* was first recognized by Diesing in 1863, it is only recently that experimental observations have been made on the species. The adults have been recorded from at least three species of wild felids in tropical America. The intermediate host was unknown, even though the hydatid described by Brumpt and Joyeux (1924) from a Brazilian agouti (*D. agouti*) has often been regarded as the larval stage of the species. There has been a lack of direct evidence either that *E. oligarthrus* is capable of developing in agoutis or that naturally occurring hydatids of the agouti will develop into the adult of *E. oligarthrus*. Thatcher and Sousa (1966) regarded previous assignments of intermediate hosts as speculative.

Several other South American rodents have been reported as infected with natural hydatids. Smyth and Smyth (1964) and Rausch (1953) called attention to the natural occurrence of the larval stage of an *Echinococcus* sp. in a large South American rodent (*Myocastor* sp.). Vogelsang and Barnola (1956) reported a natural infection in *D. rubrata* of Venezuela. Bustos (1963) reported a hydatid infection in one of 6,773 *Octodon degus* examined in Chile. Cameron and Webster (1961) referred to the presence of hydatids in *Microcavia* sp. and suggested a possible relationship to *E. oligarthrus*.

The present report demonstrates that in Panama the eggs of *E. oligarthrus* of puma origin are capable of developing into fertile primary hydatid cysts in various rodent species, including the gerbil. The larval stage of this *Echinococcus* has developed in laboratory-bred agoutis (*D. punctata*), spiny rats (*P. semispinosus*), cotton rats (*S. hispidus*), and climbing rats (*T. panamensis*). So far, only the agouti has been demonstrated to be a natural intermediate host for *Echinococcus* in the Panama area.

The experimentally induced hydatids of *E. oligarthrus* and those from naturally acquired infections in the agouti (*D. punctata*) show similar morphology and localization in the host. They are considered conspecific, but await confirmation until adults of *E. oligarthrus* are shown to be produced in laboratory animals following the ingestion of naturally acquired hydatids.

Development of the larval stage is relatively slow, requiring 3–5 months to produce cysts measuring 1–2 cm. The cysts are vesicular, with a tendency to become septate and to form multichambered growths. A striking characteristic of the local strain is the tendency to develop in the muscle tissue. In 17 experimentally infected rodents belonging to five species, only one (*P. semispinosus*) failed to show development of hydatids in the muscles. According to Perez Fontana (1963), this is indicative of a peripheral localization of the larval stage, in contrast to the central (visceral) localization of the hydatids in *E. granulosus* and *E. multilocularis*. General somatic and cardiac muscles, as well as the muscles of the diaphragm, have been found parasitized in experimentally infected rodents. Natural infections in the agouti also showed hydatids in the somatic muscles.

Infection of the lungs, kidneys, pancreas and mesentery proper were recorded in some experimental animals, but localization in the visceral organs was less frequent than in the muscles. None of the infected animals showed marked involvement of the liver or spleen.

Active fertile hydatidosis in the agouti has been observed to extend over a period of 17 months. In other animals, such as the cotton rat and the climbing rat, active hydatidosis has been maintained for periods up to 15 months after infection.

The characteristically thin cuticular layer, the active proliferating germinal layer with many calcareous corpuscles, the large number of brood capsules, the morphology of the scolex and the size of large and small hooks all resemble the characters described for the hydatids from Brazilian agoutis (*E. cruzi*). The morphology of the larval stage, as of the adult worms, is intermediate between *E. granulosus* and *E. multilocularis*.

The adults of *E. oligarthrus* can develop to maturity in the domestic cat (*F. catus*). Viable eggs have been recovered in the faeces of experimentally infected cats some 86–87 days after infection. It is generally recognized that patency of infection is evident after 48 days in *E. granulosus* and earlier in *E. multilocularis*.

With the exception of *E. g. felidis* Ortlepp, 1937, all other strains of *E. granulosus* develop mainly in canine hosts. According to Verster (1965), *E. granulosus* could be maintained in cats for only up to 48 days, being lost at 75 days and thereafter. Although adults of *E. oligarthrus* may develop in the dog, only a few (three) non-gravid specimens have been recovered from an animal fed with fertile hydatids from a climbing rat.

Whereas *E. multilocularis* can develop both in dogs and in the domestic cat, *E. oligarthrus* develops principally in feline hosts.

The experimental *E. oligarthrus* infection in the domestic cat produces infective eggs capable of developing into hydatid cysts if ingested by appropriate intermediate hosts. Second-passage cysts have been produced experimentally in *Tylomys*, *Sigmodon*, *Dasyprocta* and *Meriones*. The house cat may play an important role as host of *E. oligarthrus* and as a potential risk to man.

It is evident that *E. oligarthrus* is a valid species, with distinct morphological and biological characters separating it from *E. granulosus* and *E. multilocularis*.

It is well known that *E. granulosus* may occur in sylvatic and domestic life-cycles, and Magath (1954) has pointed out the significance of the variety of sylvatic intermediary and final hosts for the species. Only canids and ungulates, however, have been involved in the natural life-cycle of *E. granulosus*. Rodents do not seem to play a role as natural hosts of the species. Nelson and Rausch (1963), while studying echinococcosis in man and animals in Kenya, examined a large number of rodents; of 1,674 rodents and miscellaneous small mammals examined, none were infected with hydatids. Although Webster and Cameron (1961) provided evidence that *E. granulosus* oncospheres may develop in the liver and lung of some rodents, it is still generally accepted that rodents play an insignificant role in the life-cycle of *E. granulosus*. This criterion has been used in differentiating *E. granulosus* from *E. multilocularis*. The latter species is well known for its domestic and sylvatic cycles involving canids and microtine rodents. There is also good evidence that the domestic cat may be found naturally infected with *E. multilocularis*. Rausch and

Yamashita (1957) indicated that experimental infection of the domestic cat with this species may produce viable eggs that are capable of development into the larval hydatid stage in voles.

E. oligarthrus seems to be biologically closer to *E. multilocularis* than to *E. granulosus*. Its life-cycle is sylvatic, involving wild felids (puma, jaguar, jaguarundi) as definitive hosts, and the agoutis (*Dasyprocta* spp.) and possibly other rodents as intermediate hosts. There is at present no evidence of the occurrence of natural infections in domestic animals.

SUMMARY

1. The life-cycle of *Echinococcus oligarthrus* is demonstrated experimentally, with several rodent species used as possible intermediate hosts and the domestic cat as an experimental definitive host.

2. Although spiny rats (*Proechimys semispinosus*), climbing rats (*Tylomys panamensis*), cotton rats (*Sigmodon hispidus*) and agoutis (*Dasyprocta punctata*) are shown to be susceptible to infection with the larval stage of *E. oligarthrus*, only the agouti was found naturally infected with *Echinococcus* (hydatids) in Panama.

3. *E. oligarthrus* is characterized by distinct biological and morphological characters that distinguish it from *E. granulosus* and *E. multilocularis*.

4. The natural life-cycle of *E. oligarthrus* involves wild felids (puma, jaguar, jaguarundi) as definitive hosts, and the agouti, and possibly other rodents, as intermediate hosts.

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