1965

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Onderstepoort J. Vet. Res. (1965), *Vol.* 32 (1), 7–118

Printed in the Republic of S. Afr. by the Government Printer, Pretoria

REVIEW OF *ECHINOCOCCUS* SPECIES IN SOUTH AFRICA*

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* Submitted in fulfilment of the requirements for the Degree of Doctor of Philosophy in the Department of Zoology in the University of South Africa (1 June, 1964).

Received for publication on 4 January, 1965.—Editor.

Introduction

Because the genus *Echinococcus* Rudolphi, 1801 is of economic importance from both the veterinary and public health point of view, it is not surprising that it has been the subject of attention of many helminthologists. To date, 12 species belonging to this genus have been described, four of these have been recorded from South Africa.

In South Africa the sexual stage has been recorded from the black-backed jackal [*Canis* (*Thos*) *mesomelas*] (Gough, 1908; Viljoen, 1937); the lion (*Panthera leo*) (Ortlepp, 1937) and the Cape hunting dog (*Lycaon pictus*) (Cameron, 1926; Ortlepp, 1934). Hydatid cysts have been recorded by Verster (1962) from the warthog (*Phacochoerus aethiopicus*), the blue wildebeest (*Gorgon taurinus*) and the zebra (*Equus burchelli*).

In Southern Africa there are relatively few records of the sexual stage in the domestic dog (Ortlepp, 1934) or wild carnivores, and it would appear that this genus is not very widespread. Verster (1961, 1962), however, found the cystic stage widespread in domestic livestock. The incidence of hydatidosis varies considerably in species and between different abattoirs. It was generally high in all species in the Eastern Province, e.g. King William's Town had a 28·6 per cent, 13·4 per cent and 13·5 per cent incidence in cattle, sheep and pigs respectively. At Welkom in the Orange Free State 25·6 per cent of the sheep, and at Worcester in the Western Province 32·1 per cent of the pigs, were infested. Verster's findings indicate that *Echinococcus* spp. are not only of economic importance but are also of real danger to man, and therefore warrant intensive study.

Experimental infestation of wild carnivores with hydatid cysts of bovine origin resulted in specimens which resembled *E. granulosus* (Batsch, 1786) as described by Rausch (1953). These parasites, however, differed from *E. granulosus* in three aspects of the life-cycle as quoted by Lapage (1956).

(*a*) The cystic stage is fertile in cattle.

(*b*) The Cape hunting dog is more susceptible to infestation than is the domestic dog.

(*c*) A small percentage established themselves and attained sexual maturity in the cat (Verster, 1961).

It was therefore necessary to determine whether there was any correlation between their host preferences and morphology and to compare them with *E. granulosus* (Batsch, 1786) from its type locality Europe, Germany.

From the literature it was apparent that the morphology of species of this genus is influenced by various factors. Rausch (1953), investigating the reliability of structures used in the taxonomy of the genus, showed that some characters, e.g. length of the strobila, were dependent on the host-species, and that others, e.g. the number of segments and size of rostellar hooks were subject to geographical variation. Leuckart (1863) had found that the rostellar hooks increase in size after ingestion by the definitive host. This finding was confirmed by Rausch (1953), Yamashita *et al.* (1956) and Vogel (1957). It was thus necessary to establish criteria which are not influenced by the species of the definitive host, nor by the age of the infestation. Such criteria could only be established on material originating from experimental infestations, of known age, from different species of carnivores. It is known that the increase in size of the rostellar hooks of *E. granulosus*, as the worm ages, is due to the development of the handle (Leuckart, 1881; Rausch, 1953); therefore it was decided to investigate the possibility of using the length of the blade instead of the total length of the hook for taxonomic purposes.

The purpose of these investigations was three-fold: (*a*) to evaluate the variability of characters used in their taxonomy; (*b*) to diagnose the specificity of the parasites indigenous to the Republic; (*c*) to determine the role of domestic and wild carnivora in their life-cycle.

PART I

VARIABILITY OF STRUCTURES

1. *Review of the Literature*

The variability of structures used in the taxonomy of this genus was investigated by Rausch (1953). Vogel (1957) gave data regarding the variability of certain characters which are of value in distinguishing between *Echinococcus granulosus* (Batsch, 1786) and *E. multilocularis* Leuckart, 1863. Yamashita *et al.* (1958b) confirmed Vogel's observations.

The characters most commonly used heretofore for the diagnosis of species are:—

(i) The length of the rostellar hooks (Cameron, 1926; Ortlepp, 1934, 1937; Vogel, 1957; Rausch & Nelson, 1963).
(ii) The shape of the rostellar hooks (Cameron, 1926; Ortlepp, 1934, 1937; Rausch, 1953; Vogel, 1957).
(iii) The number and arrangement of the segments (Ortlepp, 1934, 1937; Vogel, 1957).
(iv) The number and distribution of the testes (Rausch, 1953; Vogel, 1957; Rausch & Nelson, 1963).
(v) The form of the gravid uterus (Rausch, 1953; Vogel, 1957).
(vi) The position of the genital pore (Vogel, 1957; Rausch & Nelson, 1963).
(vii) The size of the cirrus sac (Rausch, 1953; Rausch & Nelson, 1963).
(viii) Host specificity of the adult stage (Ortlepp, 1934, 1937; Rausch, 1953; Vogel, 1957).
(ix) Host specificity of the cystic stage (Rausch, 1953; Vogel, 1957).

Sweatman & Williams (1963) differentiate subspecies of *E. granulosus* on the basis of:—

(i) The length of cystic and of adult rostellar hooks.
(ii) The number and arrangement of the segments.
(iii) The size and shape of the seminal receptacle.
(iv) The size, shape and position of the cirrus sac.
(v) The position of the genital pore.
(vi) The number and distribution of the testes.
(vii) The ratio of the length of the mature to that of the gravid segment.
(viii) Host preferences of the cystic stage.

Vogel (1957) differentiates *E. multilocularis sibiricensis* Rausch & Schiller, 1954 from *E.m. multilocularis* on the basis of differences in the length of both the cystic and the adult hooks, host preferences of the cystic and the adult stage and preferences in localization of the cystic stage.

Size of the strobila.—The length of the strobila varies markedly, and is dependent on the species of the definitive host (Rausch, 1953; Vogel, 1957).

Scolex, rostellum and suckers.—The scolex, rostellum and suckers are larger in *E. granulosus* than in *E. multilocularis* (Vogel, 1957). Yamashita *et al.* (1958b) found that the rate of growth of the rostellum was in the same proportion in both species; but the relative growth of the suckers was greater in *E. multilocularis* than in *E. granulosus*. Vogel (1957) noted that the size of the scolex of *E. multilocularis* is independent of the host species.

Number of segments.—According to Rausch (1953) this is uniform in any given species and may be of value when it is used in conjunction with other characters in sexually active individuals. In both *E. granulosus* and *E. multilocularis* the number of segments is subject to geographical variation (Rausch, 1953; Vogel, 1957).

Position of the sexually mature segment.—The position of the sexually mature segment has been used in conjunction with other structures by some authors. The sexually mature segment is penultimate in *E. granulosus* (Vogel, 1957), but antepenultimate in *E. lycaontis* (Ortlepp, 1934), *E. cameroni* (Ortlepp, 1934), *E. felidis* (Ortlepp, 1937) and *E. multilocularis* (Vogel, 1957). Sweatman & Williams (1963) found in *E. granulosus* the position of this segment dependent on the number of segments constituting the strobila, but it may differ in four-segmented specimens of the same subspecies.

Rostellar Hooks: (*a*) *Number.*—Rausch (1953) considers the number of hooks worthless for taxonomic purposes. In *E. multilocularis* the number of rostellar hooks is dependent on the age of the cyst and on its location, as well as on the species and variety of the intermediate host (Lubinsky, 1960). Sweatman & Williams (1963) found the range of the number of hooks to be the same in their four subspecies of *E. granulosus*. They show significant differences in the number of hooks is "*E. g. granulosus*" from abnormal intermediate hosts; in *E. g. equinus* there is a considerable variation in the number of hooks from different cysts. The scolicen may have uneven numbers of hooks since large and small hooks do not necessarily alternate, but may be grouped in pairs. Uneven numbers of hooks were found in all four of their subspecies of *E. granulosus*.

(*b*) *Arrangement.*—The hooks are usually arranged in two rows. Accessory or supernumerary hooks, smaller than those of the second row, occur in *E. granulosus*. They are approximately two-thirds the size of the small hook and their position alternates with those of the second row (Vogel, 1957; Rausch & Nelson, 1963; Sweatman & Williams, 1963; Williams & Sweatman, 1963).

(*c*) *Size.*—Cameron (1926) and Ortlepp (1934, 1937) use the size of the rostellar hooks, in conjunction with other structures, for specific identification. Rausch (1953) concluded that this character is of value provided only gravid specimens are considered and due account is taken of geographical variation.

Sweatman & Williams (1963) found highly significant differences in the cystic hooks from different host-species, in individual hosts as well as in different cysts. The adult hooks from different species of carnivores did not show any differences in size. They conclude that the ultimate size of the hook is determined in the cystic stage. These authors use the size of the cystic and adult hooks in conjunction with other characters to create subspecies of *E. granulosus*.

(*d*) *Growth.*—Krabbe (1865) and Leuckart (1881) drew attention to the fact that the length of the hook of *E. granulosus* increases in the definitive host.

The hooks of *E. granulosus* increase in length up to 375 days after infestation (Yamashita *et al.*, 1956); in *E. multilocularis* they increase up to 290 days after infestation (Yamashita *et al.*, 1958a). Vogel (1957) found that *E. granulosus* shows a 30 per cent increase in hook size, while *E. multilocularis* shows a 13 per cent increase, by the time the worms are gravid. Hutchinson & Bryan (1960) found no increase in hook size of *E. granulosus* at eight weeks after infestation.

(*e*) *Shape.*—Cameron (1926) considered the shape a reliable criterion for specific identification. Rausch (1953) found the shape subject to minor variations but considered these constant for a given species. Sweatman & Williams (1963) found that the shape of the adult hook is subject to extreme variation even in hooks on the same scolex.

Position of the genital pore.—Vogel (1957) demonstrated a difference in the position of the genital pore in *E. granulosus* and *E. multilocularis*. Sweatman & Williams (1963) found that the position of this structure in *E. g. canadensis* Cameron 1960 differs from that in their other subspecies of *E. granulosus*.

Male genitalia: (*a*) *Number of testes.*—Rausch (1953) and Vogel (1957) consider the number of testes an important criterion for specific diagnosis. Sweatman & Williams (1963) use this character for sub-specific diagnosis in *E. granulosus*. On the other hand, Hutchinson & Bryan (1960) state: " Because the number of testes varies with the age of the worm, this character cannot be relied upon for species identification ".

(*b*) *Testes distribution.*—Both Rausch (1953) and Vogel (1957) consider the testes distribution relative to the genital pore reliable for species identification. Williams & Sweatman (1963) also use the number of rows of testes posterior to the vitellaria for the differentiation of the subspecies *E. g. equinus*.

(*c*) *Cirrus sac.*—Rausch (1953) found that the size of the cirrus sac may be of value if it is used in conjunction with other characters. Its shape and position both relative to the genital pore, and to the longitudinal axis of the mature and gravid segment, are regarded as a valid criterion for creating subspecies of *E. granulosus* (Sweatman & Williams, 1963).

Female genitalia: (*a*) *Ovary.*—The structure of the ovary is of importance in differentiating between *E. granulosus* and *E. multilocularis* (Vogel, 1957).

(*b*) *Seminal receptacle.*—The size and shape of the seminal receptacle may differ in the subspecies of *E. granulosus* (Sweatman & Williams, 1963).

(*c*) *Uterus.*—Rausch (1953) and Vogel (1957) use the structure of the uterus to differentiate *E. granulosus* from *E. multilocularis*.

Host specificity.—Although much experimental work has been done on the host preferences of the hydatid cyst, little has been done on that of the sexual stage. Apart from a few experiments, most of our information regarding the host specificity of the sexual stage, is based on natural infestations.

E. granulosus has been recorded from a wide range of carnivora:—

Canis familiaris, the domestic dog, by Krabbe, 1865; Leuckart, 1886; Hall, 1919; Ross, 1929; Ortlepp, 1934; Rausch, 1953; Yamashita *et al.*, 1956; Vogel, 1957; Lubinsky, 1959; Nelson & Rausch, 1963; Sweatman & Williams, 1963; Williams & Sweatman, 1963.

C. dingo, the Australian dingo by Durie & Rick, 1952; Gemmell, 1959a.

C. latrans, the coyote, by Sweatman, 1952.

C. lupus, the wolf, by Riley, 1933; Erikson, 1944; de Vos & Allin, 1949; Sweatman, 1952; Rausch, 1953; Rausch & Williamson, 1953; Cameron, 1960; Rausch & Nelson, 1963; Sweatman & Williams, 1963.

C. (Thos) mesomelas, the black-backed jackal, by Gough, 1908; Viljoen, 1937; Nelson & Rausch, 1963.

C. (Thos) aureus, the golden jackal, by Witenberg (1933) and Dissanaike & Paramananthan (1960).

Crocuta crocuta, the spotted hyaena, by Nelson & Rausch, 1963.

There is disagreement regarding the recovery of *E. granulosus* from the domestic cat and from the fox. In experimental infestations Southwell (1927), Lörincz (1933), Nosik (1954) and Gemmell (1959a) found that although this parasite may establish itself in the dometic cat, it does not attain patency. In contrast to this it has been recovered from a lion in Zoological Gardens; Porter (1943) in London and Badinin (1947) at Samarkand.

Rausch (1953) recorded *E. granulosus* from *Vulpes* sp. and *Alopex* sp. in North America. Malczewski (1961) succeeded in infesting 14 of 19 *V. vulpes* with *E. granulosus* but found 31 *Alopex lagopus* refractory to infestation with this species.

Material from a natural infestation of a fox, *Vulpes vulpes*, in England, was considered a new species, *E. cameroni* Ortlepp, 1934, but Rausch (1953) considers it to be synonymous with *E. granulosus*. Matoff & Jantscheff (1954) and Gemmell (1959a, b), in experimental infestations, found that *E. granulosus* does not attain sexual maturity in the fox; Gemmell (1960) was therefore inclined to accept the specific separation of *E. cameroni.*

Vogel (1957) found that not only the dog, but also the fox (*Vulpes* sp. and *Alopex* sp.) and the domestic cat may be experimentally infested with *E. multilocularis.*

Two species have been described from naturally infested felines: *E. oligarthrus* (Diesing, 1863) Cameron, 1926 from the puma *Felis concolor*, and the jaguar, *F. yaguarondi*, and *E. felidis* Ortlepp, 1937 from the lion, *Panthera leo*. Rausch & Nelson (1963) consider *E. oligarthrus* a valid species, but the status of *E. felidis* uncertain.

2. *Materials and Methods*

Experimental design

This is summarized in Table 1*. The strains refer to the infestation of definitive hosts with scolices collected at the same time from intermediate hosts of the same species.

* For Tables 1 and 3 to 26 see pages 94 to 118.

Source of infestive scolices

Hydatid cysts of bovine and porcine origin were collected at the Pretoria, and the ovine cysts at the Johannesburg Municipal Abattoirs.

The hydatid cyst of human origin was surgically removed from a Bantu patient at the Pretoria General Hospital.

In the bovine and ovine strains, scolices from hydatid cysts from a number of animals of the same species were collected and pooled. The scolices of porcine origin for the three porcine strains originated from a single liver in each case. Ova from specimens removed from the dog infested with the Porcine II strain and examined on the 48th day, were used to infest various intermediate hosts. A pig infested with this material was slaughtered eleven months later. Scolices present in the hydatid cysts in the liver of this animal were used to infest dogs and jackals, thus yielding a second generation for further study.

Experimental infestations

The scolices were not counted, but the carnivores in each experiment were given the same volume of scolices.

The carnivores were killed at various intervals after infestation and the intestinal tract removed.

Collection and fixation

The gut was split open; immersed in 1 per cent trypsin in saline and placed in an incubator at 37° C for two hours. The mucosa of the gut was stripped, the trypsin solution replaced with warm saline and incubated for a further six hours, followed by refrigeration overnight. The worms were fixed in 4 per cent formalin while still immobilized by the low temperature.

Number of worms recovered from each host

The scolices in two one-tenth aliquots were counted and the total number estimated. If the total did not exceed an estimated 1,000 worms, all the scolices present were counted.

Preparation of specimens for microscopical examination

(*a*) *Hooks*.—The rostella were detached and mounted *en face* in Hoyer's modification of Berlese Mounting Medium. The hooks were measured under oil-immersion phase-contrast with screw micrometer.

A maximum of 5 large hooks per rostellum and, where possible, 50 large hooks from each host, was measured. A few small hooks were also measured. The measurements carried out on the hooks (Figure 1) are as follows: total length A to F and B to E; ventral blade length D to E; dorsal blade length C to E and handle length B to C.

(*b*) *General morphology*.—The specimens were stained with Lacto-Carmine, Aceto-Carmine, Mayer's Haemalum and Lillie-Mayer's Haemalum. When sufficient material was available at least 20 to 25 specimens from each host were examined. However, this was not always possible, e.g. when few worms were recovered; or they were refractory to staining; or their genitalia were not well developed.

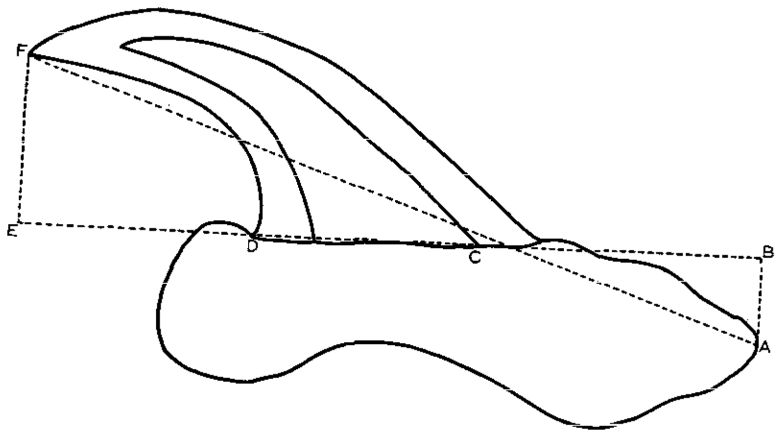

FIG. 1.—Measurements carried out on rostellar hooks
Total length: A to F, and B to E
Ventral Blade length: D to E
Dorsal Blade length: C to E
Handle length: B to C

(*c*) *Size of the ova*.—The ova were freed from the surrounding tissue and mounted in glycerine-alcohol. Three drops of Gurr's Glyceel were placed on a coverslip and allowed to dry before it was inverted over the ova.

(*d*) *Oncosphere hooklets*.—Terminal segments containing mature ova were mounted in Hoyer's Berlese Mounting Medium. Pressure was exerted on the coverslip to flatten the hooklets, which were measured under oil-immersion phase-contrast with a screw micrometer.

3. *Rostellar Hooks*

Number (cf. Table 2)

The number of rostellar hooks is based on the number of large and small hooks. Accessory hooks, both anterior to the large hooks and posterior to the small hooks, are not taken into consideration.

TABLE 2.—*Number of rostellar hooks*

Strain	Number examined	Range	Mean
Bovine I	7	32–36	34
Bovine II	43	28–38	32·5
Ovine I	1	32	32
Ovine II	5	26–34	30·8
Porcine I	15	32–38	34·9
Porcine II	5	32–40	36
Human	2	34–36	35

Discussion.—Rausch (1953) does not consider the number of rostellar hooks of any value for specific identification. Sweatman & Williams (1963) found that scolices of " *E. g. granulosus* " from abnormal intermediate hosts have a greater number of hooks than those from domestic animals. Williams & Sweatman (1963) reported that the number of hooks varies from cyst to cyst in *E. g. equinus*. Lubinsky (1960) working with *E. multilocularis*, showed that the number of hooks is dependent on the age and location of the cyst as well as on the species and variety of the intermediate host.

In the present investigation the author is unable to draw any conclusion regarding the variability of the number of rostellar hooks, as counts could be carried out on only a negligible number of specimens. However, from the above authors' findings it appears improbable that the number of hooks would be of taxonomic value.

Size

Figure 1 illustrates the measurements taken: the total length was measured in two ways, viz. A to F and B to E; the ventral blade length, D to E; the dorsal blade length, C to E and the handle length, B to C.

Cystic hooks.—The various measurements are summarized in Table 3. In these the total length, BE only, was measured.

Total length: The frequency distributions of the total length AF (Fig. 1) in the various strains are given in Figures 2 to 9; while that of total length BE (Fig. 1) are given in Figures 10 to 17. Range, arithmetic mean and standard deviation of these lengths for each host are given in Table 4 and that for each strain in Table 8 (*a*).

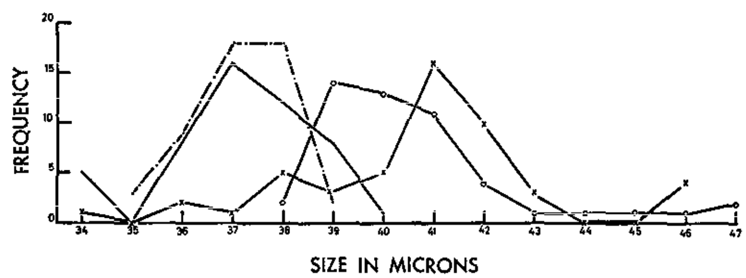

FIG. 2.—Frequency distribution of the total length, AF, of the large hooks of the Bovine I strain. All specimens 48 days old.

-o- Cape hunting dog, No. 1
-x- Cape hunting dog, No. 2
-·- Dingo
— Dog

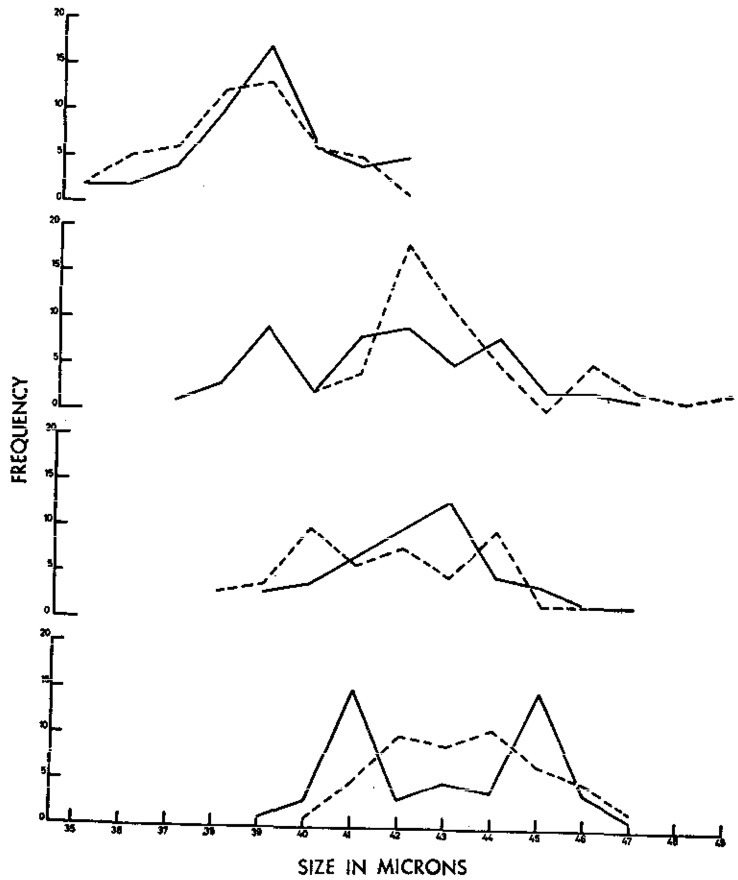

FIG. 3.—Frequency distributions of the total length, AF, of the large hooks of the Bovine II strain. From top to bottom the frequency distributions represeent that of material 35, 76, 118 and 135 days old respectively.

—— Dog
---- Jackal

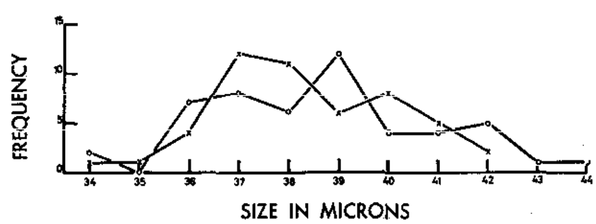

FIG. 4.—Frequency distribution of the total length, AF, of the large hooks of the Ovine I strain. All specimens 48 days old.

–o– Cape hunting dog, No. 1
–x– Cape hunting dog, No. 2

6403300–2

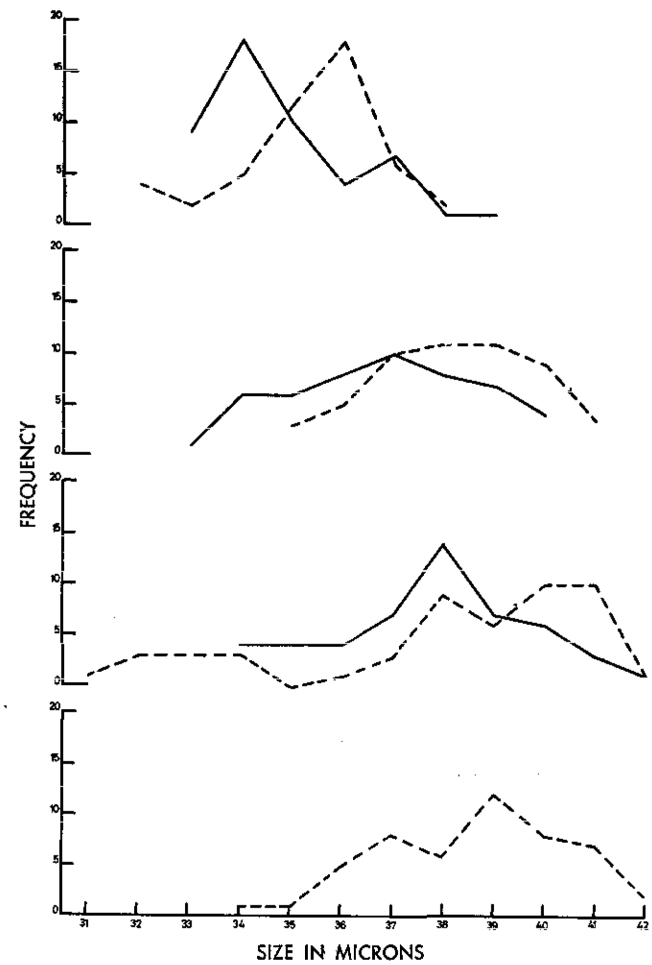

FIG. 5.—Frequency distributions of the total length, AF, of the large hooks of the Ovine II strain. From top to bottom the frequency distributions represent that of material 35, 76, 95 and 118 days old respectively.

—— Dog
- - - - Jackal

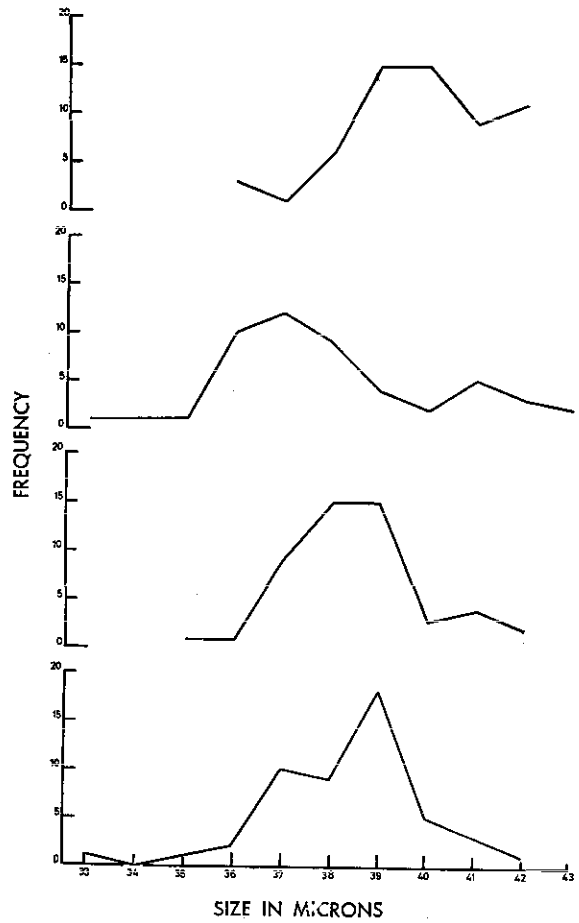

FIG. 6.—Frequency distributions of the total length, AF, of the large hooks of the Porcine I strain. Dogs only were infested. From top to bottom the frequency distributions represent that of material 48, 60, 109 and 135 days old respectively.

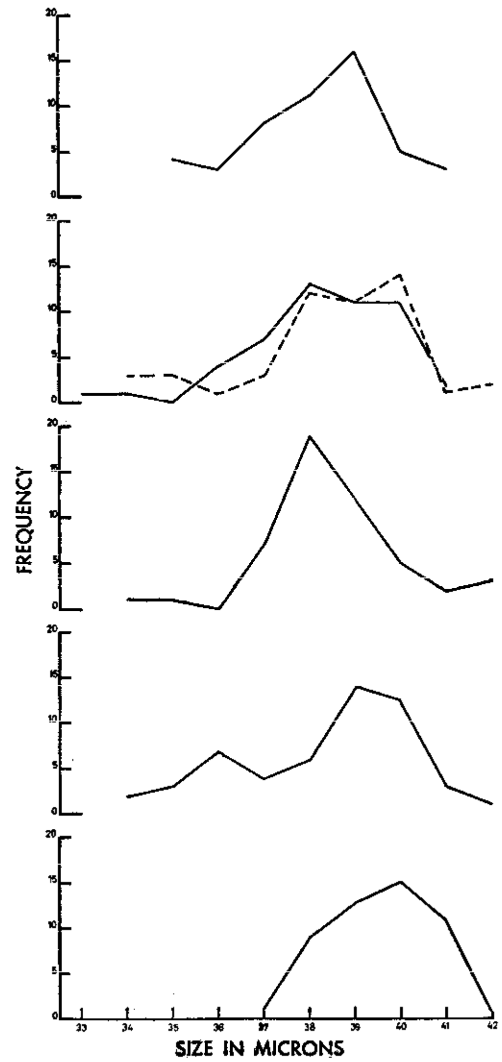

FIG. 7.—Frequency distributions of the total length, AF, of the large hooks of the Porcine II strain, first generation. From top to bottom the frequency distributions represent that of material 48, 76, 95, 118 and 135 days old respectively.

—— Dog
---- Jackal

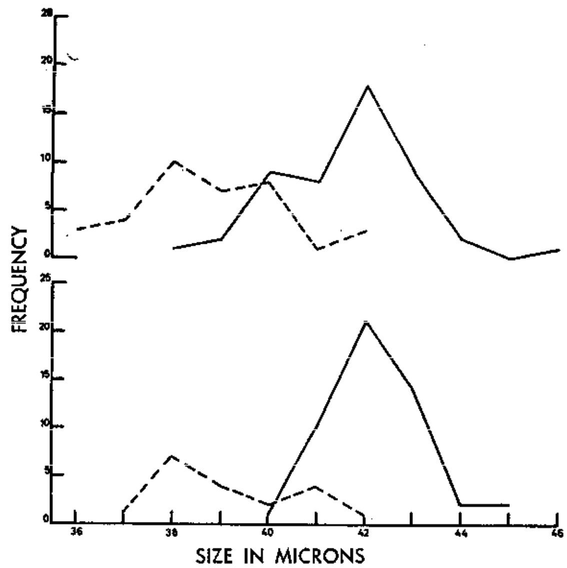

FIG. 8.—Frequency distributions of the total length, AF, of the large hooks of the Porcine II strain, second generation. From top to bottom the frequency distributions represent that of material 48 and 95 days old respectively.

—— Dog
- - - - Jackal

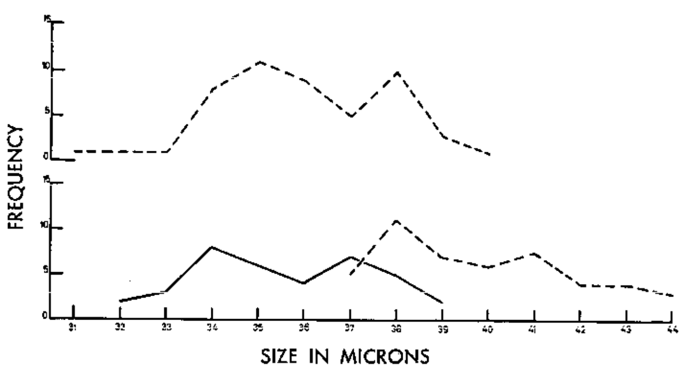

FIG. 9.—Frequency distributions of the total length, AF, of the large hooks of the Human strain. From top to bottom the frequency distributions represent that of material 35 and 76 days old respectively.

—— Dog
- - - - Jackal

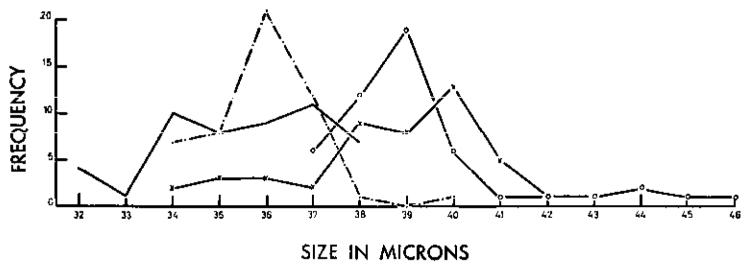

FIG. 10.—Frequency distribution of the total length, BE, of the large hooks of the Bovine I strain. All specimens 48 days old.

-o- Cape hunting dog, No. 1
-x- Cape hunting dog, No. 2
-·- Dingo
— Dog

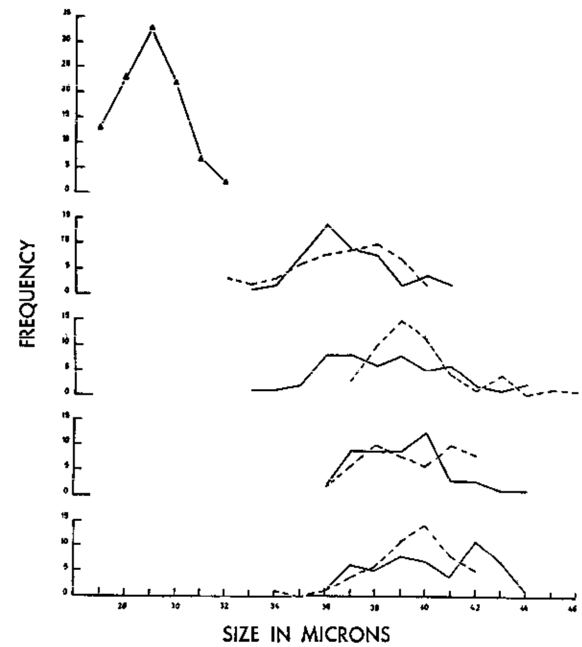

FIG. 11.—Frequency distribution of the total length, BE, of the large hooks of the Bovine II strain. From top to bottom the frequency distributions represent that of the cystic hooks, and adult hooks of material 35, 76, 118 and 135 days old respectively.

-△- Hydatid cysts
— Dog
---- Jackal

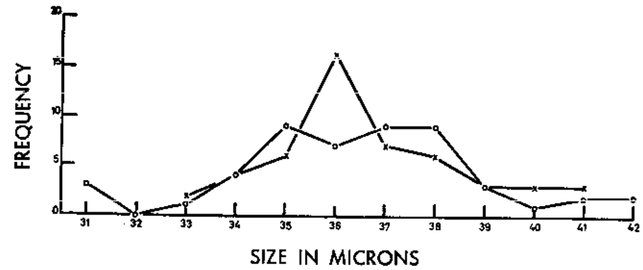

FIG 12.—Frequency distributions of the total length, BE, of the large hooks of the Ovine I strain. All specimens 48 days old.

-o- Cape hunting dog, No. 1
-x- Cape hunting dog, No. 2

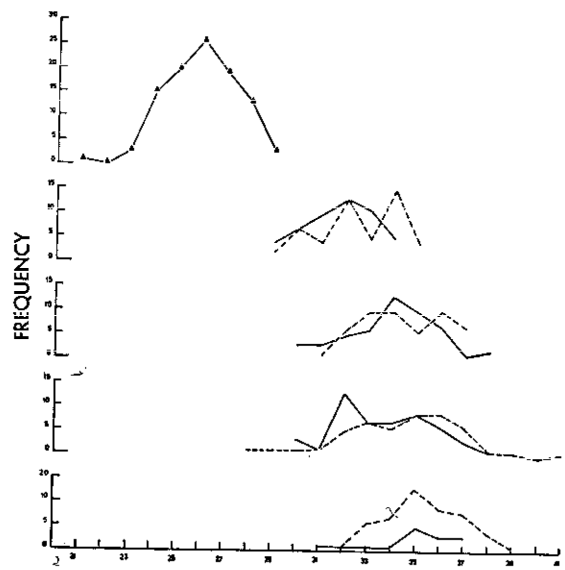

FIG. 13.—Frequency distributions of the total length, BE, of the large hooks of the Ovine II strain. From top to bottom the frequency distributions represent that of the cystic hooks, and adult hooks of material 35, 76, 95 and 118 days old respectively.

-△- Hydatid cysts
—— Dog
- - - - Jackal

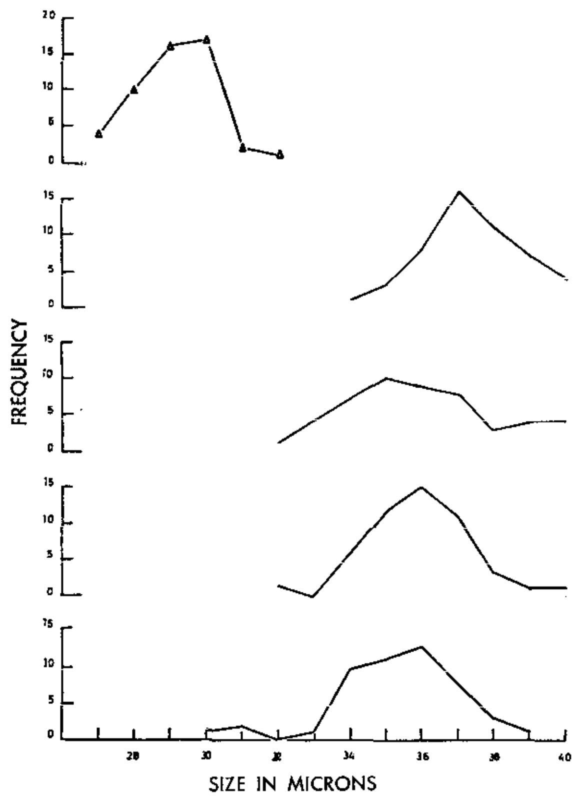

FIG. 14.—Frequency distributions of the total length, BE, of the large hooks of the Porcine I strain. Dogs only were infested. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 48, 60, 109 and 135 days old respectively.

–△–Hydatid cysts
—— Dog

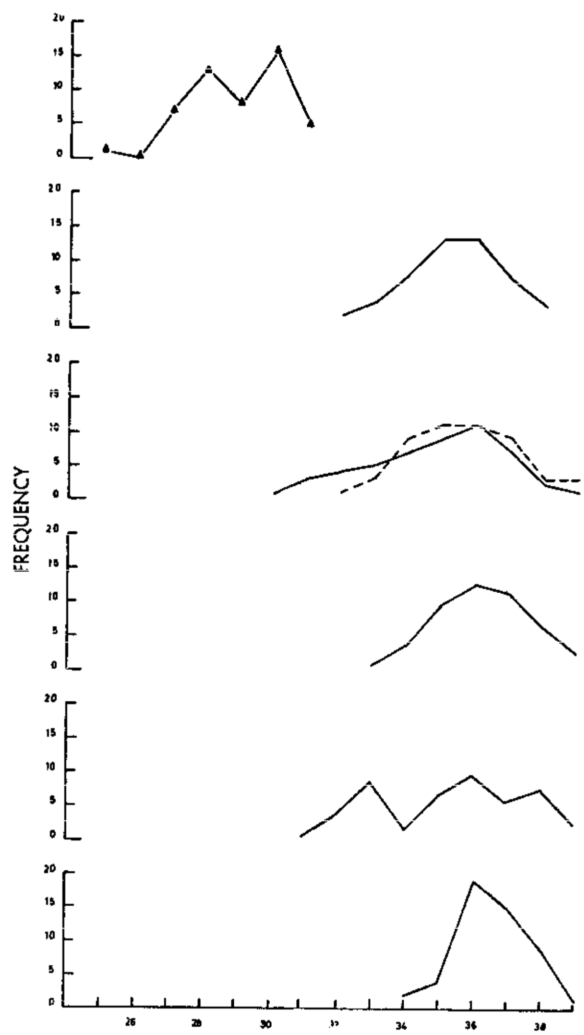

FIG. 15.—Frequency distributions of the total length, BE, of the large hooks of the Porcine II strain, first generation. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 48, 76, 95, 118 and 135 days old respectively.

-△- Hydatid cysts
—— Dog
- - - - Jackal

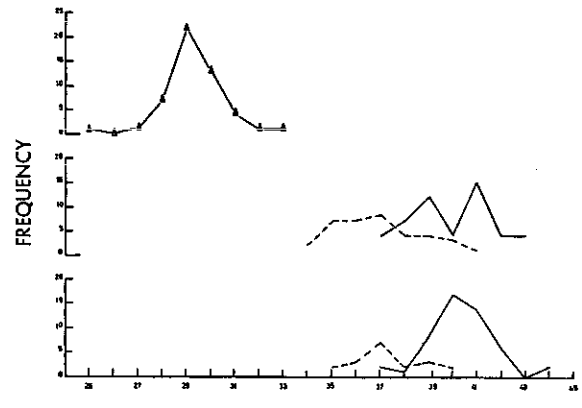

FIG. 16.—Frequency distributions of the total length, BE, of the large hooks of the Porcine II strain, second generation. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 48 and 95 days old respectively.

-△- Hydatid cysts
—— Dog
- - - - Jackal

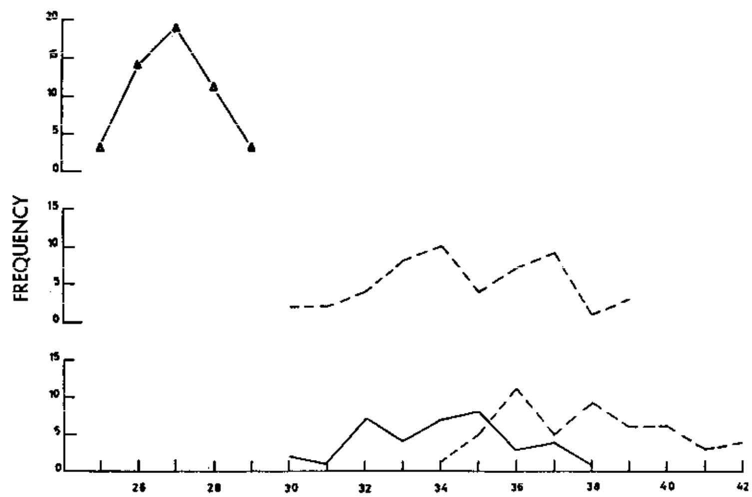

FIG. 17.—Frequency distributions of the total length, BE, of the large hooks of the Human strain. From top to bottom the frequency distributions represent that of cystic hooks, and the adult hooks of material 35 and 76 days old respectively.

-△- Hydatid cysts
—— Dog
- - - - Jackal

Ventral blade length: The frequency distributions of this length (DE in Fig. 1) in various strains are given in Figures 18 to 25. Range, arithmetic mean and standard deviation are given in Tables 5 and 9 (*a*).

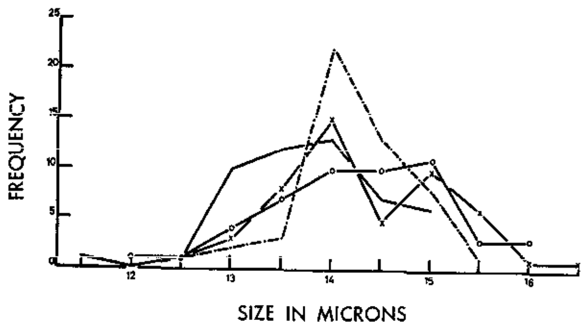

FIG. 18.—Frequency distributions of the ventral blade length, DE, of the large hooks of the Bovine strain. All specimens 48 days old.

-o- Cape hunting dog, No. 1
-x- Cape hunting dog, No. 2
-·- Dingo
— Dog

FOR FIG. 19 SEE PAGE 28.

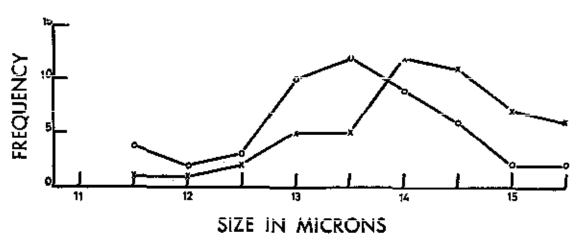

FIG. 20.—Frequency distributions of the ventral blade length, DE, of the large hooks of the Ovine I strain. All specimens 48 days old.

-o- Cape hunting dog, No. 1
-x- Cape hunting dog, No. 2

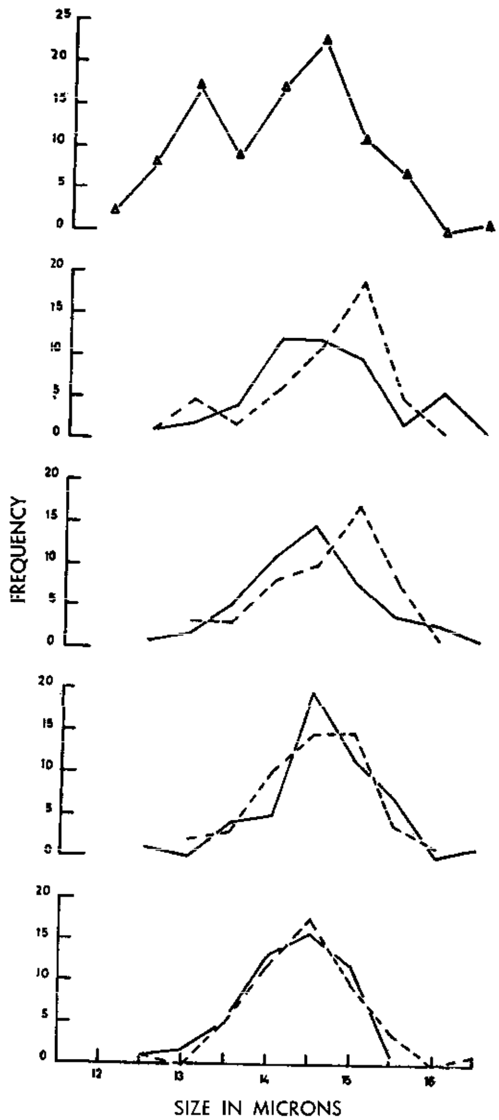

FIG. 19.—Frequency distributions of the ventral blade length, DE, of the Bovine II strain. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 35, 76, 118 and 135 days old respectively.

-△- Hydatid cysts
—— Dog
- - - - Jackal

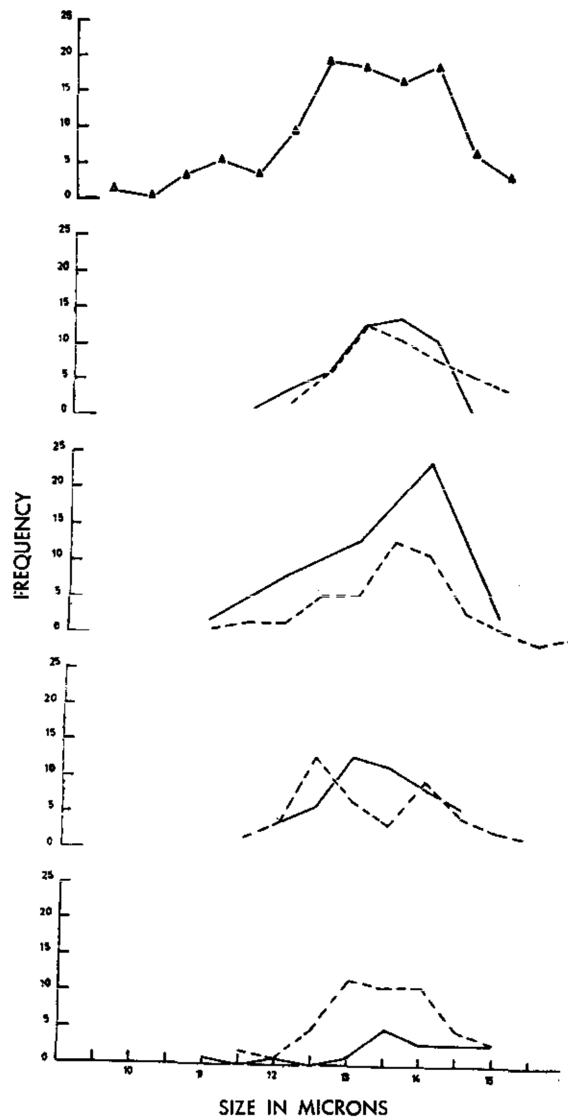

FIG. 21.—Frequency distributions of the ventral blade length, DE, of the large hooks of the Ovine II strain. From top to bottom the frequency distributions represent that of cystic hooks, and of adult hooks of material, 35, 76, 95 and 118 days old respectively.

-△- Hydatid cysts
—— Dog
- - - - Jackal

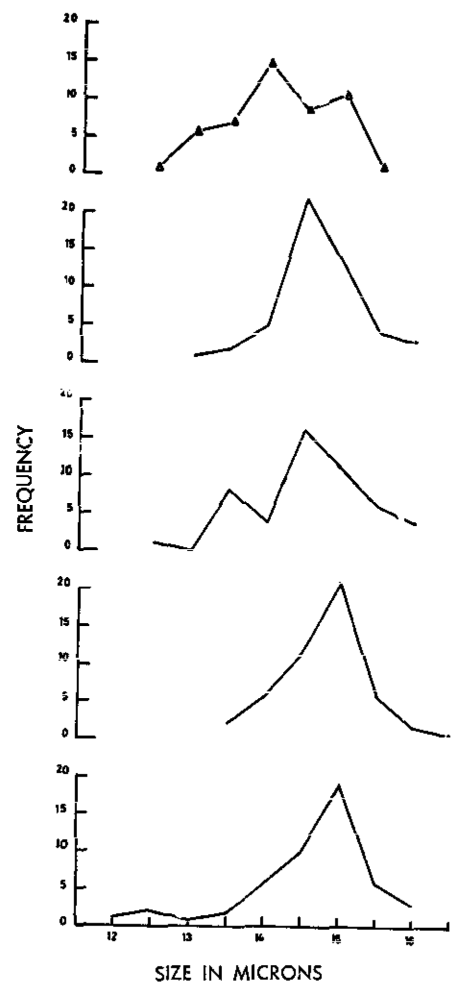

FIG. 22.—Frequency distributions of the ventral blade length, DE, of the large hooks of the Porcine I strain. Dogs only were infested. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 48, 60, 109 and 135 days old respectively.

-△- Hydatid cysts
—— Dog

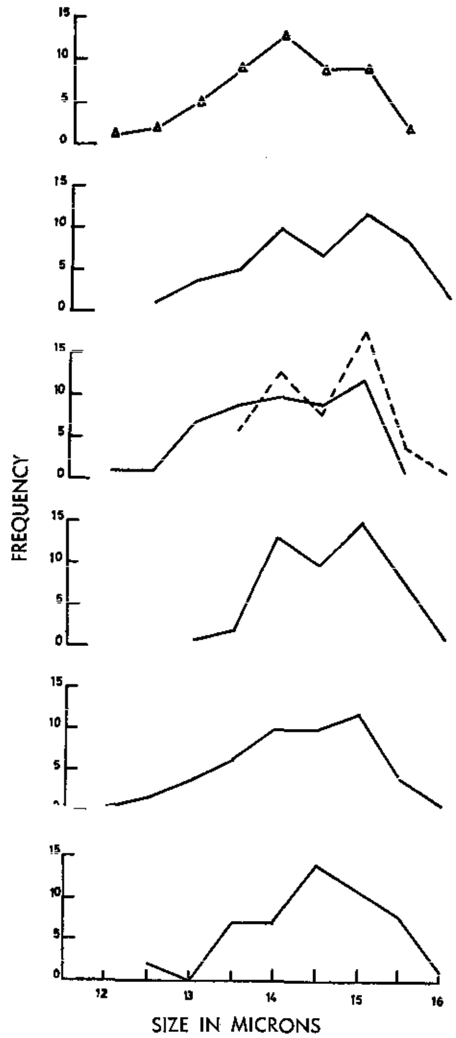

FIG. 23.—Frequency distributions of the ventral blade length, DE, of the large hooks of the Porcine II strain, first generation. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 48, 76, 95, 118 and 135 days old respectively.

-△- Hydatid cysts
—— Dog
- - - - Jackal

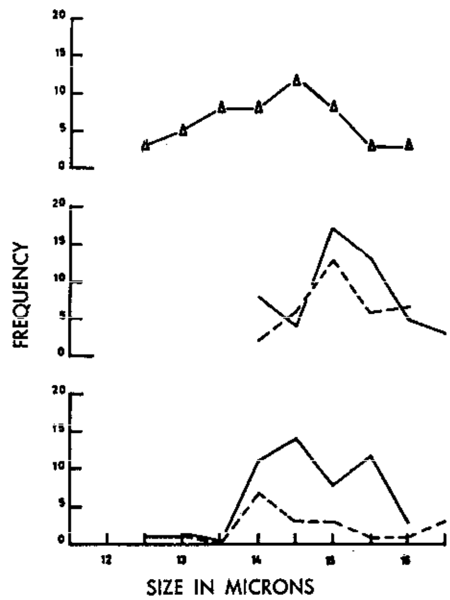

FIG. 24.—Frequency distributions of the ventral blade length, DE, of the large hooks of the Porcine II strain, second generation. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 48 and 95 days old respectively.

-△- Hydatid cysts
—— Dog
---- Jackal

Dorsal blade length.—The frequency distributions of this length (CE in Fig. 1) in the various strains are given in Figures 26 to 33. Range, arithmetic mean and standard deviation are given in Tables 5 and 9 (*a*).

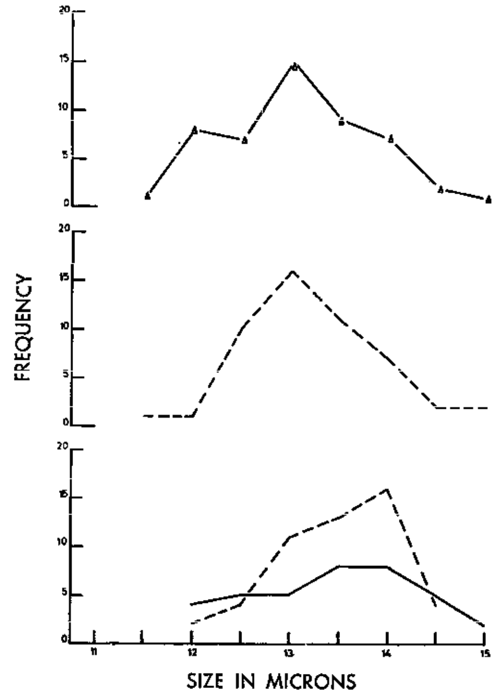

FIG. 25.—Frequency distributions of the ventral blade length, DE, of the large hooks of the Human strain. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 35 and 76 days old respectively.

-△- Hydatid cysts
—— Dog
- - - - Jackal

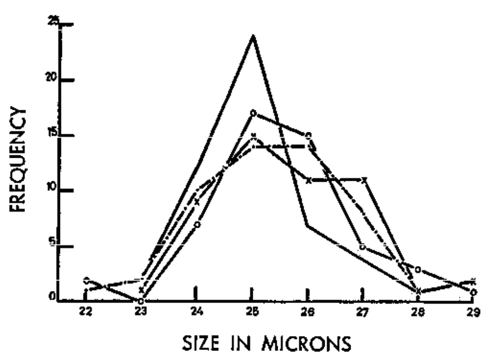

FIG. 26.—Frequency distributions of the dorsal blade length, CE, of the large hooks of the Bovine I strain. All specimens 48 days old.

-o- Cape hunting dog, No. 1
-x- Cape hunting dog, No. 2
-·- Dingo
—— Dog

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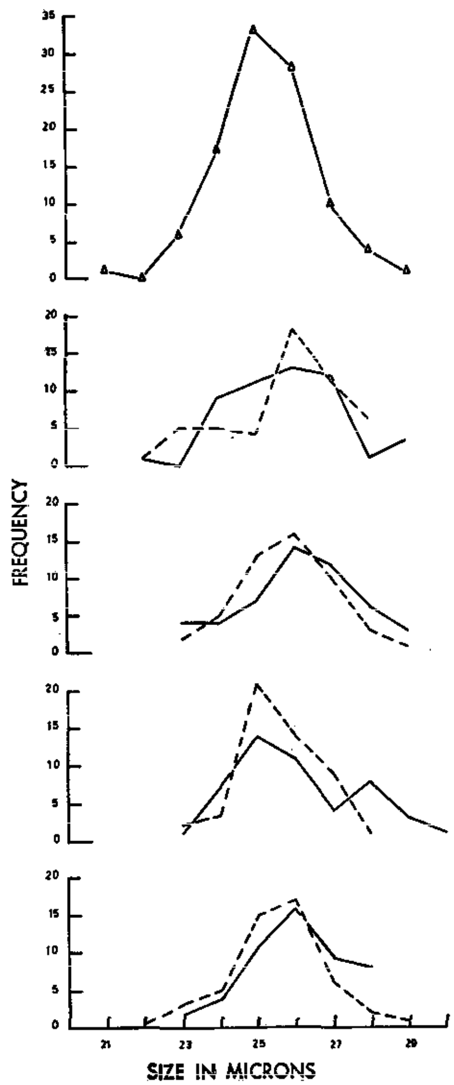

FIG. 27.—Frequency distributions of the dorsal blade length, CE, of the large hooks of the Bovine II strain. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 35, 76, 118 and 135 days old respectively.

-△- Hydatid cysts
—— Dog
---- Jackal

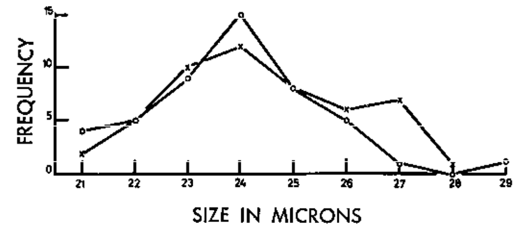

FIG. 28.—Frequency distributions of the dorsal blade length, CE, of the large hooks of the Ovine I strain. All specimens 48 days old.

–o– Cape hunting dog, No. 1
–x– Cape hunting dog, No. 2

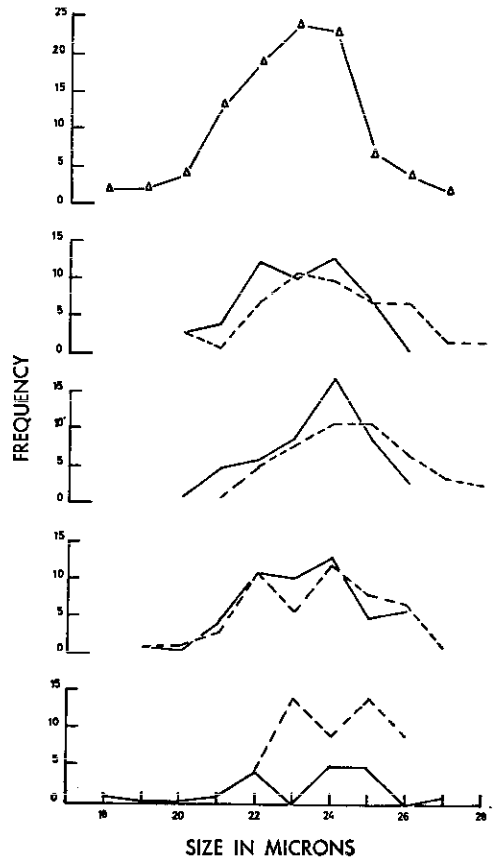

FIG. 29.—Frequency distributions of the dorsal blade length, CE, of the large hooks of the Ovine II strain. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 35, 76, 95 and 118 days old respectively.

–△– Hydatid cysts
—— Dog
- - - - Jackal

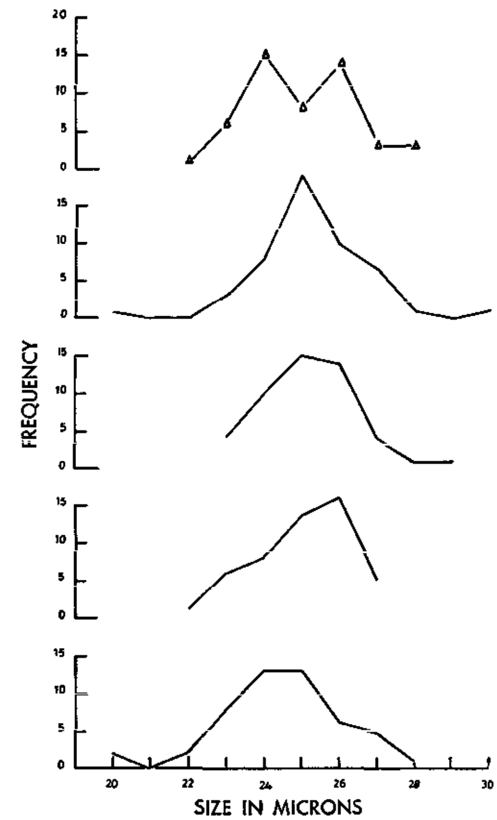

FIG. 30.—Frequency distributions of the dorsal blade length, CE, of the large hooks of the Porcine I strain. Dogs only were infested. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 48, 60, 109 and 135 days old respectively.

-△- Hydatid cysts
—— Dog

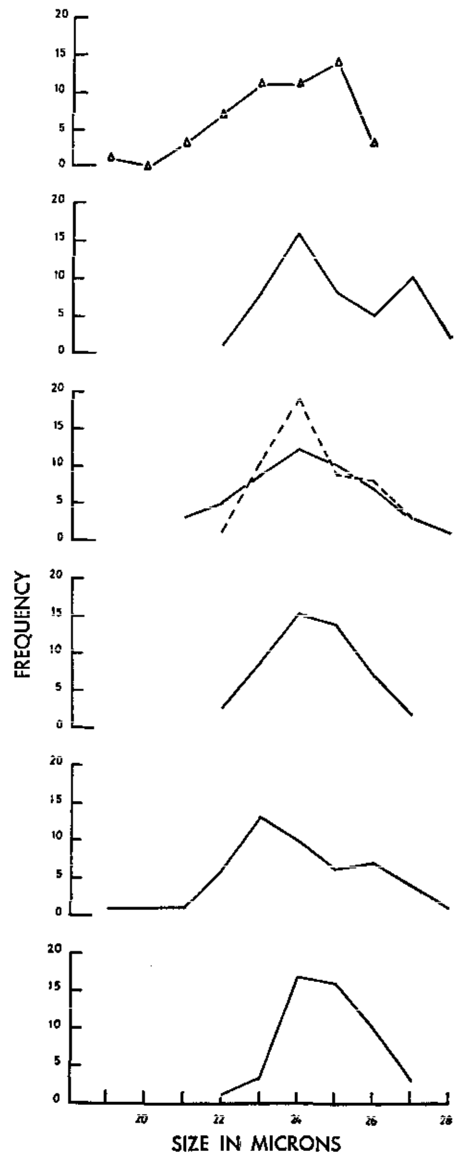

FIG. 31.—Frequency distributions of the dorsal blade length, CE, of the large hooks of the Porcine II strain, first generation. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 48, 76, 95, 118 and 135 days old respectively.

-△- Hydatid cysts
—— Dog
---- Jackal

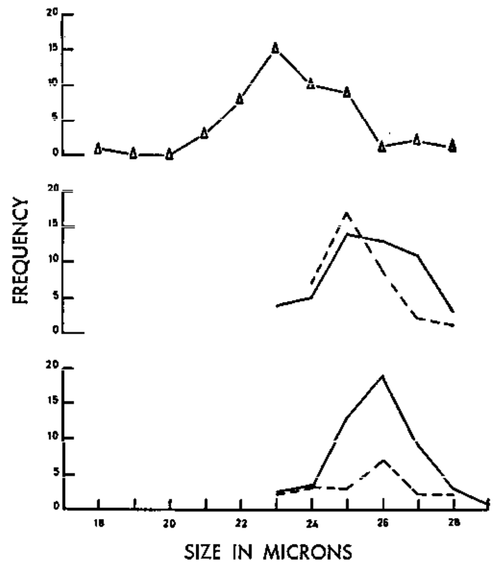

FIG. 32.—Frequency distributions of the dorsal blade length, CE, of the large hooks of the Porcine II strain, second generation. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 48 and 95 days old respectively.

-△- Hydatid cysts
—— Dog
---- Jackal

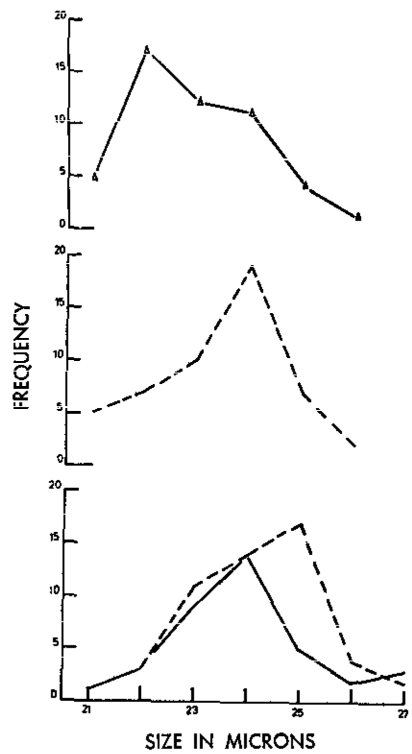

FIG. 33.—Frequency distributions of the dorsal blade length, CE, of the large hooks of the Human strain. From top to bottom the frequency distributions represent that of cystic hooks, and adult hooks of material 35 and 76 days old respectively.

-△- Hydatid cysts
—— Dog
---- Jackal

Handle length: Range, arithmetic mean and standard deviation of this length (BC in Fig. 1) are given in Tables 5 and 9 (*a*).

Statistical analyses: The results of the analyses of variance applied to the above data may be summarized as follows:—

Total length: Growth of the hooks: It is not possible to determine the age at which the growth of the hook is complete. When the total length, both AF and BE, of specimens from dogs infested with the Bovine II strain and examined at 35, 76 118 and 135 days, is subjected to an analysis of variance, it shows highly significant differences between ages. The data of the 76, 118 and 135 days old infestations (i.e. the 35 days old material is not included), also show highly significant differences. In the jackal, however, analyses show highly significant differences for all age groups, but no significant differences if only 76, 118 and 135 days old infestations are considered. Analyses of variance of the total length of Ovine II from the dogs examined at 35, 76 and 95 days show highly

significant differences; but when the 35 days old material is excluded, there is no significant difference. The material from the jackals infested with this strain, also shows highly significant differences when all the age groups are analysed together; at 76 and 95 days the significance of differences persists. The analysis of variance when applied to the Porcine I data (all age groups) shows highly significant differences. These data were not analysed further as the mean length of the hooks is smaller in the older infestations (i.e. 37·8, 36·5, 36·3 and 35·9 microns at 48, 60, 109 and 135 days respectively). Analysis of variance of the data of Procine II from the dogs (all age groups) shows highly significant differences; when the 48 days old material is excluded, the significance of differences persists. Highly significant differences were also shown by 35 and 76 days old material from the jackals infested with the Human strain.

Influence of host species: Analyses of the data from infestations of the same origin (i.e. strain) and the same age, but from different species of definitive hosts, give inconsistent results. Comparison of the total length of the Bovine I strain at 48 days from the dog and the dingo shows no significant difference. Analyses of the total length of the Bovine II strain give inconsistent results when the dog is compared with the jackal: at 35 days no significant difference; at 76 a highly significant difference; at 118 days no significant difference and at 135 days a significant difference.

The Ovine II strain also yields inconsistent results: at 35 days a significant difference; at 76 days no significant difference and at 95 days a significant difference.

The human strain shows a highly significant difference when data from the dog and jackal at 76 days are compared.

In contrast to the above, a comparison of the data from the two Cape hunting dogs infested with Bovine I, examined on the 48th day, shows no significant difference of total length. A similar result is obtained on the data from two Cape hunting dogs infested with the Ovine I strain.

Successive generations: An analysis on the total length of the large hook in successive generations of the same strain could only be carried out with Porcine II. In both generations the intermediate host was the pig. An analysis of variance of the total length (BE) of the hooks of the hydatid cysts, used as infestive material for the two generations, shows no significant difference; but analyses of the total lengths, BE and AF, of specimens 48 and 95 days old from the dogs infested with the first and second generation respectively, show highly significant differences.

Adult hooks of the same genotype: The parasites derived from the human strain originate from a single hydatid cyst. An analysis of variance of the total length of the large hooks from the three definite hosts, viz. jackal/35 days; dog, jackal/76 days, shows highly significant differences. The total length of material from the jackals shows highly significant differences between age groups. The 76 days old material from the two host species also shows highly significant differences.

Ventral and dorsal blade lengths: Analyses of variance on the dorsal blade length of hooks from hosts infested with Bovine I and Ovine I show no significant differences when material from hosts belonging to the same or different species is compared. The dorsal blade lengths of the other five strains show highly significant differences. The ventral blade lengths show highly significant differences in all the strains.

The highly significant differences obtained with the analyses of variance of these two blade lengths, are probably due to the small variability shown by the length of the blade.

Handle length: Analysis of variance of the handle length of the hooks in the different strains corresponds with that of the total length, BE; thus indicating that this is the part of the hook which increases in length.

Small hooks: In view of the obvious variation in size of these hooks only a few from each host were measured.

The total lengths, AF and BE, are summarized in Tables 6 and 8 (*b*); dorsal and ventral blade and handle lengths are summarized in Tables 7 and 9 (*b*).

Discussion: Sampling method: The data presented may be questioned in that the sampling method is biased and the size of the sample from each host possibly inadequate. Only the largest intact specimens from each host were selected and only those hooks lying in profile measured.

To determine the number of hooks to be measured to give reliable results, initially 100 cystic hooks of the Bovine II and Ovine II strains were examined (Table 3). One hundred cystic hooks of Bovine II varied in length from 27·1 to 32·5 (mean 29·4 ± 1·2) microns; the first 50 hooks varied from 27·5 to 31·5 (mean 29·2 ± 1·1) microns. One hundred cystic hooks of Ovine II varied from 21·5 to 29·5 (mean 26·3 ± 1·5) microns; the first 50 hooks showed the same range, but the mean was 26·7 ± 1·6 microns. Obviously no useful purpose could be served by examining more than 50 hooks from each host.

Rausch (1953) advocated that hook size should be determined only on specimens with mature ova in the uterus. In natural infestations such a selection would ensure that only sexually mature specimens are compared. Under experimental conditions it was found that selection could not be done on this basis. The absence of mature ova in the uterus of the worms when the animal is autopsied, does not necessarily mean that the infestation was not patent in the past. This is demonstrated clearly by Porcine II, first generation: the percentage of gravid specimens from dogs examined on the 48th, 76th, 95th, 118th and 135th days post-infestation was 66·7 per cent, 17·4 per cent, 23·3 per cent, 73·9 per cent and 16·3 per cent respectively. The total length of the large hooks of specimens from the 135 days old infestation is greater than that from younger infestations.

Further evidence of the unimportance of the presence of mature ova is provided by Porcine II, second generation/jackal material. Unfortunately most of the specimens from these hosts had lost their rostellar hooks; it was possible to examine only 36 and 19 hooks from the two animals autopsied on the 48th and 95th day post-infestation respectively. The 48 days old specimens were extremely small and consisted of one or two segments only; neither mature nor developing ova were present in any of the specimens. The majority of the specimens of the 96 days old material contained ova in the uterus. Despite this marked difference in the stage of development and the age of infestation, there was very little difference either in the range of variation or in the arithmetic means of the large hooks.

Growth: Yamashita *et al.* (1956; 1958a) found that the large and small hooks of both *E. granulosus* and *E. multilocularis* continue increasing in length up to the 375th and 290th day post-infestation respectively. Vogel (1957) showed that the hooks of *E. granulosus* increase in size between 51, 64 and 81 days. Hutchinson & Bryan (1960), however, found that there was no increase in the size of the hooks of *E. granulosus* after eight weeks, i.e. 56 days.

The present data show such extreme variation that it is difficult to determine when the hooks have completed their growth. In some strains the arithmetic means of the hooks of the older specimens from the same host species increased as the infestation became older, e.g. Bovine II/dog. Other strains, however, did not show such a direct relationship between length and age. The lower limits of the range in the different strains was usually higher in older infestations; the upper limits of the range did not show the same tendency. From this, and the results of the analyses of variance, it would appear that the large hook has not completed its development 35 days after infestation of the definite host, but it is not possible to determine at what age, if any, the hooks cease their growth.

Influence of the host species: Sweatman & Williams (1963) found that the species of the definitive host did not have any influence on the total length of the large hook. This finding was not confirmed in the present experiments; on the contrary, the size of the large hook was found to be dependent on the species of the definitive host. When the same infestive material was administered to more than one animal of the same host species and examined at the same age, the size of the large hooks did not show any significant differences as is instanced in material originating from Cape hunting dogs infested with Bovine I and Ovine I respectively (Table 4). The size of the large hooks of specimens from the dingo and dog infested with Bovine I (Table 4) did not show any significant difference, but when the size of the large hooks from the latter two hosts was compared with those of the Cape hunting dogs, highly significant differences were found. Bovine II and Ovine II from dogs and jackals gave inconsistent results (Table 4): large hooks originating from the same infestive material and of the same age from these two host species showed no difference, significant difference or highly significant difference in the total length (both BE and AF).

The difference in the size of the large hook in different host species does not appear to be due to " crowding ". The Cape hunting dogs infested with Bovine I harboured more worms than either the dog or the dingo; yet the hooks of the worms in the Cape hunting dogs were larger than those from either the dog or the dingo.

Successive generations: Due to the slow development of this parasite in the intermediate host, a second generation of only one experimental strain was available, viz. Porcine II (cf. Materials and Methods). Two dogs and two jackals were infested; one of each pair was necropsied on the 48th and 95th day after infestation. The total length, BE and AF, of the large hooks of specimens from the dogs showed a highly significant difference when hooks of the same age, but of successive generations were compared. The hooks in the second generation were larger than those of the first generation (Table 4). Furthermore, with one exception (AF—48 days old), the lower limit of the range of the second generation exceeded the mean of the first generation. In so far as the total length of the cystic hooks from the first and second generation did not show any significant difference, this discrepancy in the adult hook is unexpected.

Same genotype: The size of the large hook shows the same variability in material derived from the same genotype (Human strain) as from pooled scolices from a number of hydatid cysts originating from a single host (Porcine I and II) or originating from a number of individuals of the same host species (Bovine I and II; Ovine I and II).

It has been found that the size of the rostellar hooks is dependent on a number of factors: geographical variation (Rausch, 1953); age (Vogel, 1957 and Yamashita *et al.*, 1956, 1958a, b). Despite these findings, taxonomic value has been and is still being attached to these structures.

Sweatman & Williams (1963) contend that the ultimate size of the rostellar hook is fixed in the cystic stage. This was not confirmed. The size of the cystic hooks in the first and second generation of Porcine II did not differ, but the adult hooks, in the same host species and of the same age, did differ markedly in their size. Furthermore, material with the same genetic constitution (Human strain) is subject to influence by the host species.

Sweatman & Williams (1963) recorded a wide range in the length of the adult large hooks in their different subspecies. In " *E. g. granulosus* " it varies from 25 to 40 (mean 34·2) microns; in individual dogs the mean length varies from 29·4 to 37·0 microns, while the mean length in their various subspecies shows the same range, the extremes being 34·2 microns in " *E. g. granulosus* " and 41·8 microns in *E. g. borealis*. It would therefore appear that the mean length in " *E. g. granulosus* " in different hosts shows variations of the same magnitude as that between subspecies. Despite the intra- and inter-subspecific variations, and the fact that the respective ranges of their subspecies overlap, these workers attach significance to the size of these structures.

The data presented above show that the identity of the definitive host also affects hook size, and further that hook size is not constant in successive generations. It would therefore appear to be extremely undesirable that taxonomic significance be attached to the size of the rostellar hooks.

Blade length: The present experiments show that both the ventral and dorsal blade lengths appear to remain constant throughout the life of the parasite. It is unlikely that variations in this structure are of taxonomic significance; the variations within and between strains are small and there is an overlap between different strains.

Shape

Large hook: The shape of the large hook shows its greatest variation in the handle and guard.

The blade also shows a certain variation in shape. The dorsal aspect of the blade is occasionally notched a short distance above the point at which it joins the handle. This notch may be present or absent in the hooks of a single host. The large hooks of the one Cape hunting dog infested with the Ovine I strain show such a variation (Fig. 34). The lower part of the dorsal aspect of the blade is slightly concave in the top and bottom hook, but in the middle hook this same area is convex.

Variation in the curvature of the blade is illustrated in Ovine II where hooks from different hosts are compared (Fig. 35). Furthermore it may vary in the same host (Fig. 34, 36).

Small hook: As in the case of the large hook, the small hook shows a similar variation in the size and shape of the handle. Both size and shape may vary to such an extent that small hooks may on occasion only be identified as such by their position on the rostellum and by the ventral blade length (Fig. 37). Variation in shape and size on a single specimen is illustrated in Fig. 38a and b. Similar variations in shape may be found in small hooks adjacent to each other (Fig. 39).

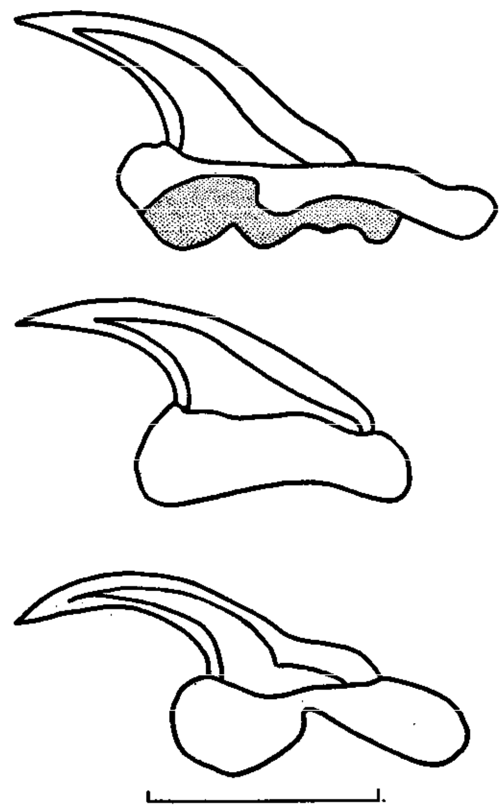

FIG. 34.—Variation in the shape of the large hook. Ovine I/Cape hunting dog, 48 days.

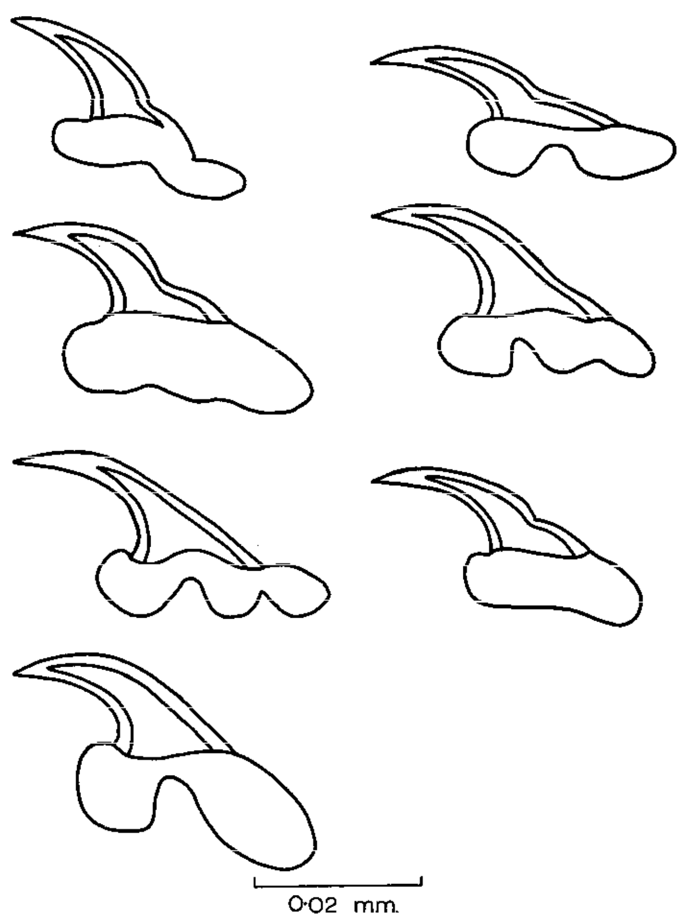

FIG. 35.—Variation in the shape of the large hook of Ovine II, from the jackal (left) and the dog (right).
The hooks from the top to the bottom are 35, 76, 95 and 118 days old respectively.

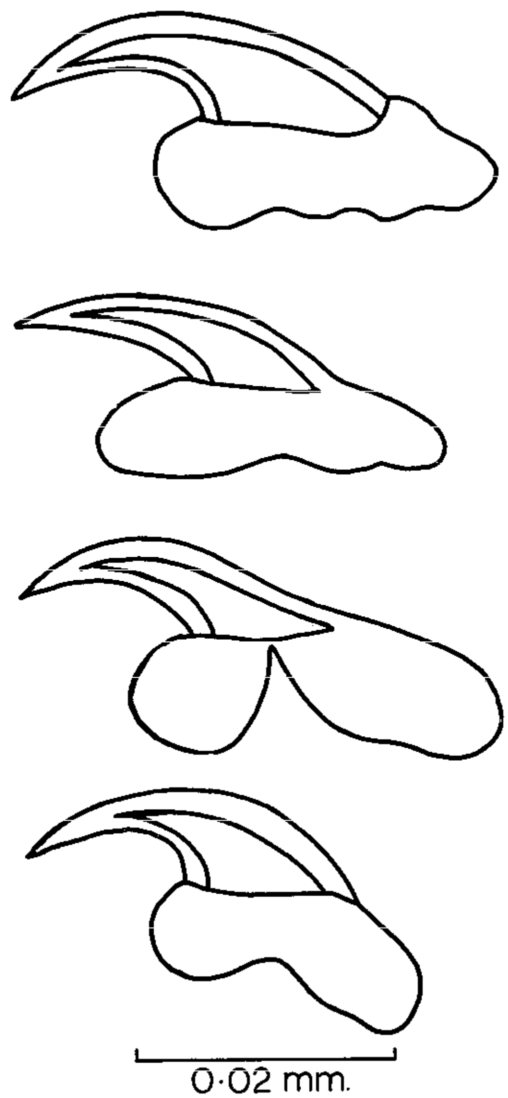

FIG. 36.—Variation in the shape of the large hook. Human/dog, 76 days.

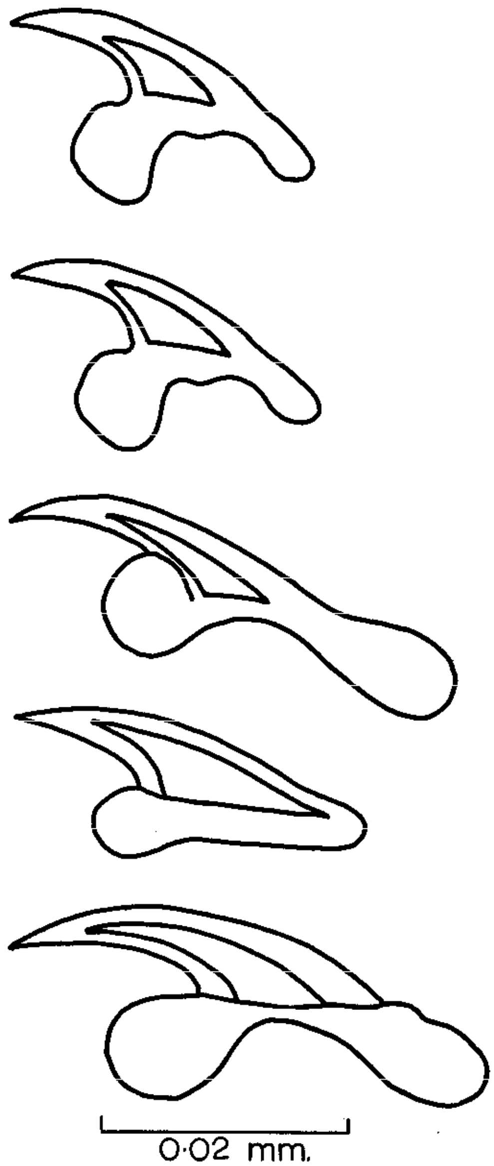

FIG. 37.—Variation in the shape of the small hook. Bovine I/Cape hunting dog, 48 days.

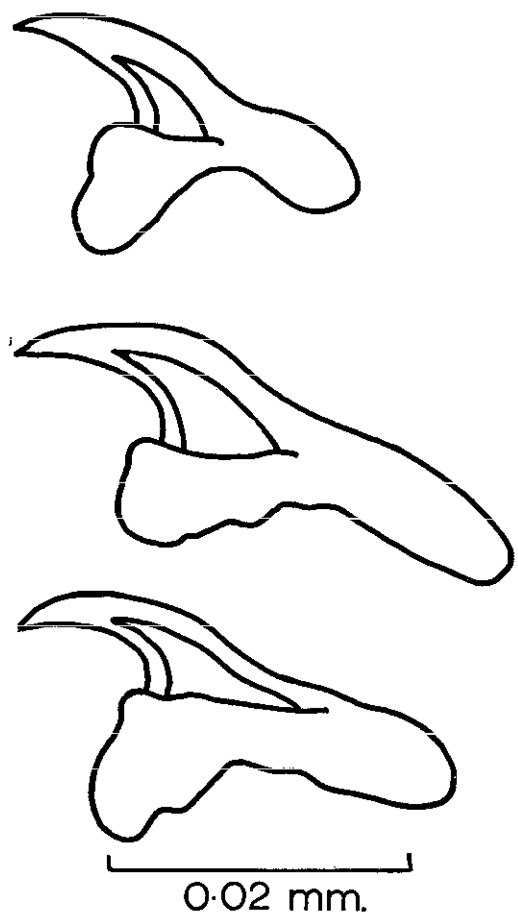

FIG. 38 (*a*).—Variation in the shape and size of the small hooks on the scolex of a single specimen. Ovine I/Cape hunting dog, 48 days.

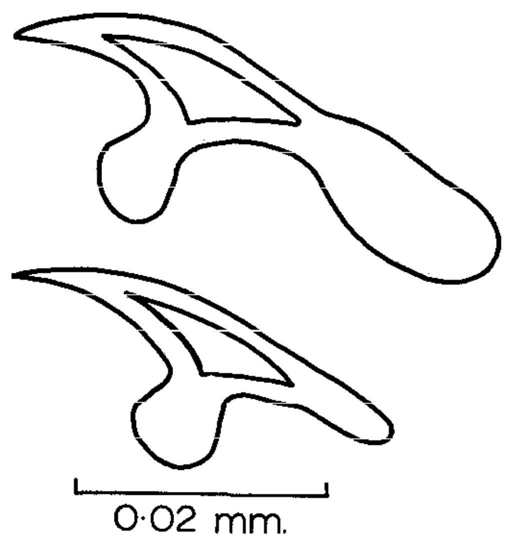

FIG. 38 (*b*).—Variation in the shape of the small hooks on the scolex of a single specimen. Bovine II/dog, 76 days.

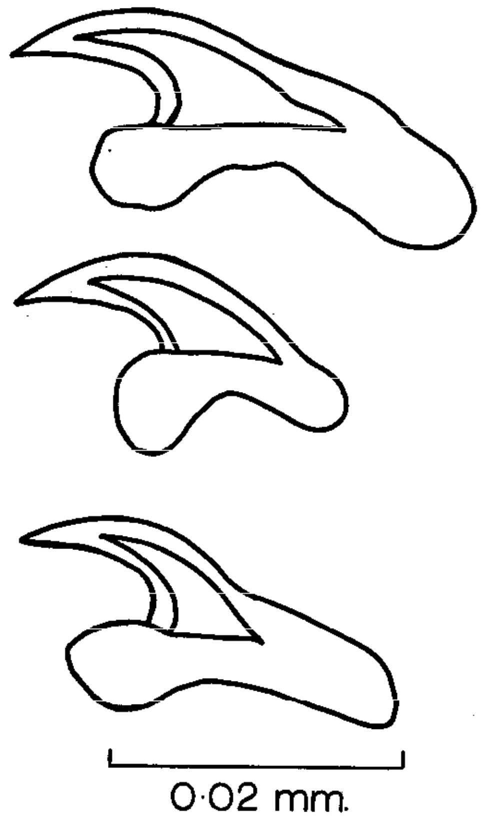

FIG. 39.—Variation in the shape of adjacent small hooks. Human/dog, 76 days.

Discussion: Cameron (1926), Rausch (1953) and Vogel (1957) consider the shape of the large hook to be characteristic for a given species. Vogel (1957) found that the shape of the base of the large hooks shows specific variations: *E. multilocularis* forms a concavity where the handle joins the guard, this is less developed or absent in *E. granulosus*. The small hook of both species resembles that of the large hook in *E. multilocularis*. Yamashita *et al.* (1958b) concluded that these wo species show only slight differences in the shape of the large hook.

In the present experiments the shape and degree of development of the handle and of the guard is inconsistent and shows extreme variation in both large and small hooks. These findings therefore agree with those of Sweatman & Williams (1963) who found that extreme variation in the shape of the large hook may be encountered on the same scolex.

Accessory hooks

The commonest type of accessory hook is smaller than, and posterior to, the small hooks with which they alternate (Fig. 40). The total length (AF) and ventral blade length (DE) of these hooks are summarized in Table 10; Fig. 41 (*a*) and (*b*) illustrate the variation in the shape of these hooks.

The accessory hooks anterior to and alternating in position with the large hooks were found in three hosts only, viz. dogs infested with Porcine II, 76 and 116 days; the jackal infested with the Human strain, 36 days. These hooks differ from the large hooks in that they have a longer blade and a very weakly developed handle (Fig. 42).

Discussion: The small accessory hooks were described by Vogel (1957) in *E. granulosus* and by Sweatman & Williams (1963) in " *E. g. granulosus* ". The latter authors also described accessory large hooks from " *E. g. granulosus* ". The present investigation confirms the findings of these authors.

Conclusion: The number, size and shape of the rostellar hooks are not reliable criteria for taxonomic purposes.

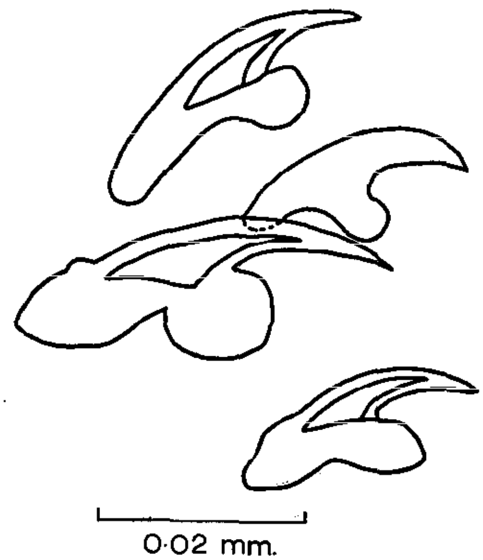

FIG. 40.—Position of the accessory hook relevant to that of the large and small hook. Human/dog, 95 days.

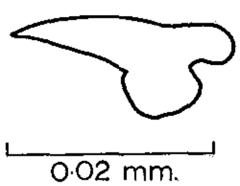

FIG. 41 (*a*).—Small accessory hook. Ovine I/Cape hunting dog, 48 days.

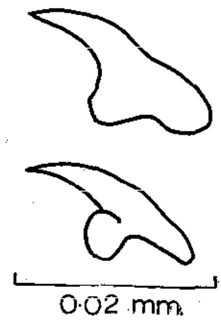

FIG. 41 (*b*).—Small accessory hook. Human/jackal, 95 days.

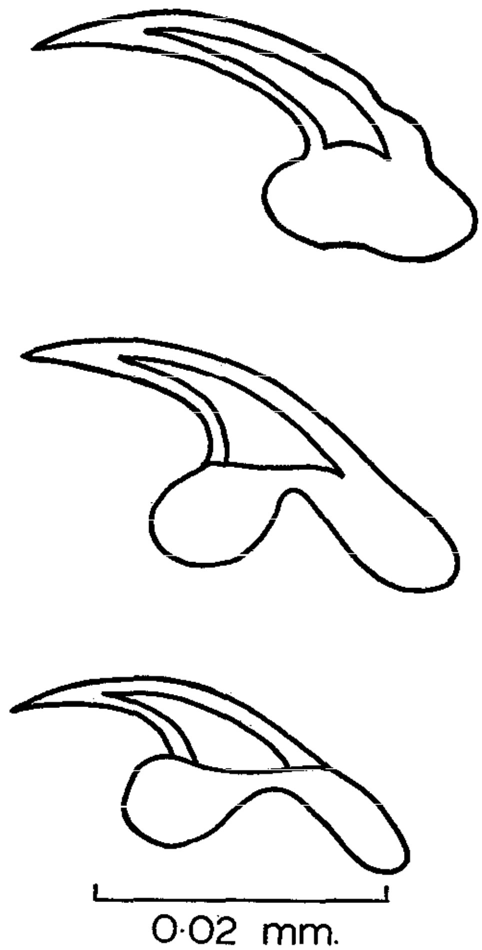

FIG. 42.—Comparison of the structure of an accessory large hook (top) with that of a normal large hook (middle) and normal small hook (bottom). Porcine II/dog, 76 days.

4. *Number and Arrangement of the Segments*

Number of segments (cf. Table 11)

The number of segments, with the exception of Ovine I strain (*vide infra*), varies from two to four, most have three. Two-segmented worms are in the majority in six hosts; four-segmented ones in one host only. If gravid specimens only are considered, three-segmented worms are again in the majority; in one host four-segmented worms outnumber those of three segments (Table 11).

The Ovine I strain is not included in Table 11 as its number of segments varies from four to six. Twenty-nine specimens were examined: 13·8 per cent consist of four, 82·8 per cent of five and 3·4 per cent of six segments. Eighteen specimens were gravid, of these: 5·6 per cent consist of four, 88·8 per cent consist of five and 5·6 per cent of six segments.

Discussion: Rausch (1953), Vogel (1957) and Yamashita *et al.* (1958b) found the number of segments constant in *E. granulosus* and *E. multilocularis*.

With the exception of the Ovine I strain, all the worms have two to four segments. In these strains the majority of the gravid specimens consist of three or four segments. Most of Ovine I consist of five segments.

It is apparent from the present experiments that the number of segments is dependent on the age of the infestation and also on the rate of development in a particular host species. The variation due to the age of the infestation is shown by Porcine I: the majority of the 49, 60 and 109 days old specimens consist of three segments, but the majority of the 135 days old specimens consist of only two segments. The effect of the host species on this character is illustrated by Bovine I where the majority of the specimens from all the hosts consist of three segments; whereas in the dingo, dog and silver fox a fairly large number consist of only two segments, and no four-segmented worms occur in them.

Arrangement of the sexually mature segments (cf. Table 12)

As the specimens consist of varying numbers of segments, the position of the sexually mature segment, for the sake of clarity, is designated from the posterior end.

In the majority of the specimens the penultimate segment is sexually mature but this is dependent on the degree and therefore the rate of development within the particular host. In Ovine I (48 days), the antepenultimate segment is sexually mature.

Discussion: Vogel (1957) found the penultimate segment of *E. granulosus* to be sexually mature, while in *E. multilocularis* it is the antepenultimate segment. Sweatman & Williams (1963) reported that in "*E. g. granulosus*", the position of the sexually mature segment may be penultimate or antepenultimate depending on the number of segments present.

The present findings show that when only gravid specimens are considered, it is usually the penultimate segment that is sexually mature. Ovine I resembles *E. multilocularis* in that there it is the antepenultimate segment that is sexually mature. The position of the sexually mature segment shows only slight variation in gravid specimens; rather more variation is shown in specimens not yet gravid.

Conclusion: The number of segments constituting the strobila, and the position of the sexually mature segment, appear to be valid criteria for specific and subspecific diagnosis.

5. *Size of the Strobila*

Total length (cf. Tables 13, 14)

The Ovine I strain consists of four to six segments. Eighteen specimens have ova in the uterus; the four-segmented worm is 4·69 mm long; the 16 five-segmented worms vary from 4·38 to 7·54 (mean 5·72 ± 0·64) mm, while the six-segmented specimen is 6·06 mm long. A total of 29 specimens was examined: the four four-segmented specimens vary from 4·12 to 5·33 (mean 4·78) mm; the 24 five-segmented worms from 4·38 to 7·54 (mean 5·70 ± 0·84) mm, while the six-segmented specimen is 6·06 mm long.

The data of the remaining strains are summarized in Tables: Table 13 those of the gravid specimens and Table 14 all the specimens examined.

The mean length of all the specimens examined is usually less than that of the gravid worms alone. There are three exceptions viz. Cape hunting dog No. 2 (Bovine I, 48 days); jackal (Ovine II, 95 days) and dog (Porcine I, 135 days).

The total length of the specimens of the same strain and age varies in the different host species. The animals infested with the Bovine I strain were all autopsied on the 48th day. The mean length and the upper limit of the range of the worms from the Cape hunting dogs are higher than in the dingo, dog or the silver fox.

Discussion: The total length in the same host species, varies with the age of the infestation and the stage of development of the specimens. This confirms Vogel's (1957) observations on *E. granulosus* and *E. multilocularis.*

The length of the strobila of the same strain and age, varies in hosts of different species. This is most noticeable in Bovine I, in which the specimens from the Cape hunting dog are larger than those from other hosts. Cape hunting dogs are not only more susceptible to infestation but the worms are larger and their development is more advanced than in other hosts. Variation in the rate of development in different host species is also apparent in Bovine II. At 76 days, three-segmented specimens from the jackal are larger than those from the dog; at 95 and 118 days the opposite applies.

Rausch (1953) states: " In general, the larger individuals occur in the relatively large host species (e.g. wolf and dog), and the smaller worms occur in foxes (both *Vulpes* and *Alopex*) ". The present experiments do not confirm Rausch's observations, for although the Cape hunting dog is larger than any of the other carnivores used and shows the largest worms, the blackbacked jackal is smaller than the majority of domestic dogs and yet may have larger worms. Thus the total length is more closely correlated with the susceptibility of the host species, and with the rate of development of the worms within these hosts, rather than with the physical size of the definitive host.

Size of segments (cf. Tables 15, 16, 17)

The length of the terminal segment, and its length expressed as a percentage of the total length of the strobila, is given in Table 15. The width of the last and second last segment is summarized in Table 16. The ratio of the length of the mature to the length of the gravid segment is summarized in Table 17.

Discussion: Both the length of the terminal segment and its ratio to the length of the strobila show a greater range of variation than do those given by Vogel (1957) for *E. multilocularis* and for *E. granulosus*. The average length of the terminal segment is above one millimetre, but the lower limits of the range may be under one millimetre; the ratio of the terminal segment to strobilar length shows extreme variation even in specimens from the same host.

The width of the last two segments also shows a wide range of variation in the specimens from any one host. The mean width of the ultimate segment is greater than that of the penultimate, but when these measurements are compared, they are seen to overlap. The difference in the width of these two segments is greater than that given by Vogel (1957) for *E. granulosus* or *E. multilocularis*.

Sweatman & Williams (1963) recognize differences in the ratio of the length of the mature to that of the gravid segment for the distinction of their subspecies of *E. granulosus*. This feature, in the present experiments, is subject to extreme variations not only in the different strains, but also in a single host.

Size of the scolex, rostellum and suckers (cf. Table 18)

The size of these structures is summarized in Table 18.

Discussion: The scolex, rostellum and suckers also show a greater range of variation than was reported by Vogel (1957). These variations are probably due to differences in the reaction of individual worms to fixation.

Conclusion: The size of the strobila and its constituent parts is subject to extreme variation, and hence must be treated with reserve in species and subspecies differentiation.

6. *Position of the Genital Pore* (cf. Tables 19, 20)

In this investigation the distance of the genital pore from the anterior margin of the segment is expressed as a percentage of the length of the segment; results are summarized in Tables 19 and 20.

The Ovine I strain consists of four or more segments; the antepenultimate segment is usually sexually mature and in the penultimate segment the genitalia have not completely degenerated nor have the ova completed their development. These penultimate segments are hereafter referred to as post-mature segments. The position of the genital pore in the mature segment (29 specimens) is from 38·9 to 63·5 per cent (mean 55·0 per cent); the post-mature (29 specimens) from 47·8 to 67·4 per cent (mean 60·6 per cent) and in 24 gravid segments from 51·4 to 65·5 per cent (mean 58·4 per cent) of its length from the anterior margin. In the 18 gravid specimens the position of the genital pore in the mature segment is 38·9 to 62·5 per cent (mean 54·5 per cent); the post-mature 47·8 to 66·7 per cent (mean 60·3 per cent) and the gravid segment 51·4 to 69·5 per cent (mean 58·8 per cent) of its length from the anterior margin.

Discussion: The distance of the genital pore from the anterior margin of the gravid segment shows a greater variability in the different strains than has been recorded for either *E. multilocularis* (Vogel, 1957; Yamashita *et al.* 1958a) or for *E. granulosus* (Nelson & Rausch, 1963). However, the usual position is at, or just posterior to, the midpoint of the segment in all the experimental strains. This corresponds with the position of this structure in *E. granulosus* as given by Nelson & Rausch (1963).

Conclusion: The position of the genital pore appears to be of value only at the species level.

7. *Male Genitalia*

Testes number and distribution (cf. Table 21)

The number of testes and their distribution relative to the genital pore is summarized in Table 21.

Bovine I strain (Fig. 43): The range and arithmetic mean is higher in the material originating from the two Cape hunting dogs than in material from the other hosts.

In 92 specimens (85·2 per cent) there are more testes in the anterior than in the posterior half of the segment; in 10 specimens (9·2 per cent) the testes are approximately equally distributed in the two halves of the segment; in six specimens (5·6 per cent) there are more testes in the posterior than in the anterior half of the segment. The usual testes distribution in this strain is illustrated in Fig. 43.

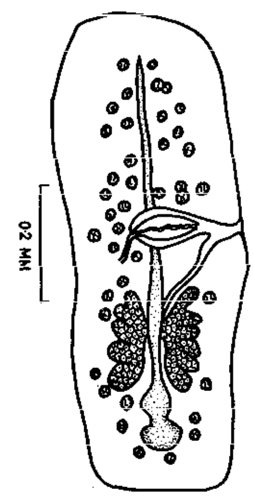

FIG. 43.—Sexually mature segment showing number and distribution of testes. Bovine I.

Analyses of variance show highly significant differences in the number of testes anterior to and posterior to the genital pore.

Bovine II strain (Fig. 44): In 195 specimens examined, all but one have more testes anterior than posterior to the genital pore.

Bovine II differs from Bovine I in that testes are absent posterior to the vitellaria (Fig. 44); in one specimen (0·5 per cent), however, one testicle is present in this part of the segment.

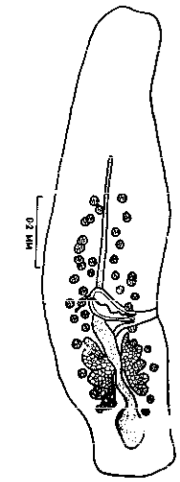

FIG. 44.—Sexually mature segment showing number and distribution of testes. Bovine II.

Analyses of variance show similar results to those obtained for Bovine I.

Ovine I strain (Fig. 45): There are more testes in this strain than in any of the others. Furthermore, the lower limit of the range is higher than the higher limit in any other strain. The number varies from 58 to 80 (mean $68 \cdot 4 \pm 7 \cdot 1$); the greatest number of testes in any other strain is 55 (Human/dog, 76 days).

The greater number of testes are situated in the anterior half of the segment (Fig. 45). In one instance (4 per cent) the testes are equally distributed in the two halves of the segment.

An analysis of variance shows a highly significant difference in the number of testes anterior to and posterior to the genital pore.

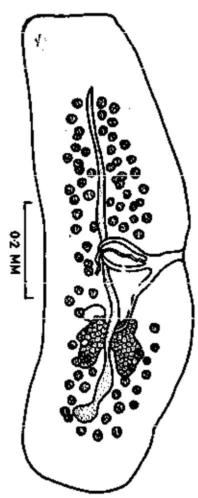

FIG. 45.—Sexually mature segment showing number and distribution of testes. Ovine I.

Ovine II strain (Fig. 46): In all these specimens the majority of the testes are n the anterior half of the segment (Fig. 46). They differ from Bovine I in that the mean number of testes is greater than in Bovine I. The range of the total number and that of those anterior and posterior to the genital pore do not differ markedly from Bovine I.

This strain also shows highly significant differences in the distribution of the testes relative to the genital pore.

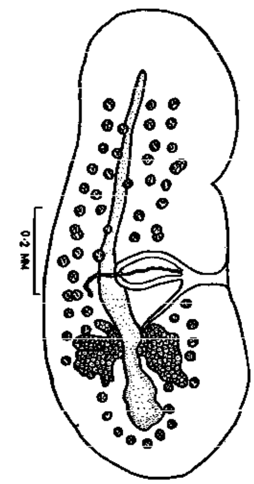

FIG. 46.—Sexually mature segment showing number and distribution of testes. Ovine II.

Porcine I strain (Fig. 47): With the exception of four specimens (9·8 per cent), the testes are either equally divided in the two halves of the segment or the greater number is in the posterior half (Fig. 47). In 9·8 per cent of the specimens the majority of the testes are in the anterior half of the segment.

An analysis of variance of the testes distribution in this strain as a whole shows significant differences. However, the individual hosts gave inconsistent results. The 49 days old specimens show no significant difference in the number of testes anterior and posterior to the genital pore. The 60 and 109 days old specimens show highly significant differences; in the 60 days old specimens this is due to them having a greater number posterior to the genital pore; in the 109 days old specimens it is due to four specimens having more testes anterior to the genital pore.

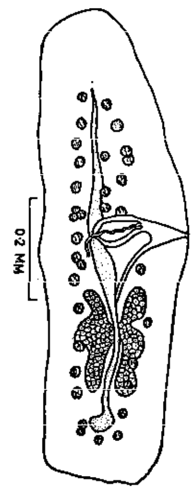

FIG. 47.—Sexually mature segment showing number and distribution of testes. Porcine I.

Porcine II strain. First generation (Fig. 48): With the exception of two specimens (2·9 per cent) the distribution of the testes resembles that of Porcine I. In two specimens the majority of the testes are in the anterior half of the segment.

The 118 days old specimens of this strain show a significant difference in the testes distribution due to two specimens having a greater number of testes in the anterior half. The remaining five hosts show no significant difference. When the strain is analysed as a whole, significant differences are obtained, due to the majority of the specimens having the greater number of testes in the posterior half of the segment.

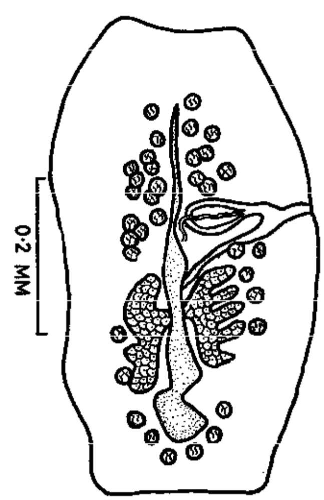

FIG. 48.—Sexually mature segment showing number and distribution of testes. Porcine II, first generation.

Second generation (Fig. 49): These specimens correspond with those of the first generation in the number and distribution of the testes. In all the specimens examined the testes were either equally distributed in the two halves of the segment, or there were more testes in the posterior than the anterior half (Fig. 49).

The testes distribution in this generation shows significant differences. The 95 days old specimens show no significant difference, but the 48 days old specimens show a highly significant difference which is due to a greater number of testes in the posterior half of the segment.

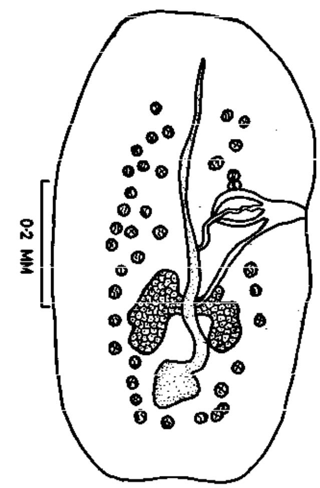

FIG. 49.—Sexually mature segment showing number and distribution of testes. Porcine II, second generation.

Human strain (Fig. 50): Six specimens (12·5 per cent) have more testes in the anterior than in the posterior half of the segment. The distribution of the testes in the remaining specimens (Fig. 50) resembles that of the two porcine strains.

An analysis of variance of this strain as a whole shows no significant difference in the testes distribution in the two halves of the segment. The 35 days old specimens, however, show a highly significant difference. The 76 days old specimens from the dog show no significant difference, but that of the same age from the jackal shows a significant difference. The significant differences in the testes distribution are due to the greater number of testes in the posterior half of the segment.

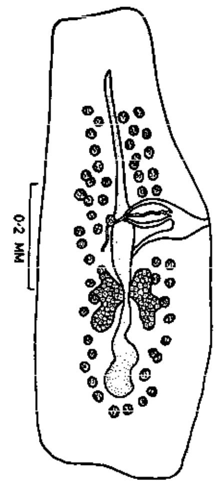

FIG. 50.—Sexually mature segment showing number and distribution of testes. Human strain.

The data suggest the following divisions on the basis of testes distribution:—

(*a*) *Testes equally distributed:* This applies to the Human and Porcine I and II strains. Only 12 specimens (6·1 per cent) of all the worms examined in these strains have more testes in the anterior than in the posterior half of the segment. It is accepted that in some species of *Echinococcus* the testes in the posterior half of the segment develop before those in the anterior half, therefore the testes posterior may outnumber those anterior at a certain stage of development. Thus it is to be expected that within limits this criterion may be subject to some variability.

(*b*) *More testes anterior than posterior:* The remaining four strains have this distribution and may be divided into three subgroups:—

(i) Bovine I and Ovine II with the majority of the testes anterior, about one third being posterior. Only 16 specimens (7·8 per cent) of these two strains do not conform.

(ii) Bovine II with no testes posterior to the vitellaria.

(iii) Ovine I with more testes than the other strains.

Discussion: The number of testes is considered to be relatively constant by both Rausch (1953) and Vogel (1957). These authors concluded that the number of testes in both *E. granulosus* and *E. multilocularis* is not dependent on the host-species. This conclusion is confirmed by Bovine I, in which the ranges overlap in the different host-species.

Hutchinson & Bryan (1960) consider the number of testes worthless as a specific character. Those authors state: " Because the number of testes varies with the age of the worm, this character cannot be relied upon for species identification ". If by the age of the worm, these authors refer to its chronological age, this is not in agreement with the findings of Vogel (1957) or of the present investigation. The results (Table 21) prove that the mean number of testes may vary but that the range shows only slight variability despite differences in the age of the worm.

Testes distribution is regarded as constant by both Rausch (1953) and Vogel (1957). The testes in the anterior and posterior halves of the segment are approximately equal in *E. granulosus* (Rausch, 1953), while in *E. multilocularis*, few of the testes are situated anterior to the genital pore (Rausch, 1953; Vogel, 1957). Testes distribution is one of the characters used by Sweatman & Williams (1963) for the differentiation of their subspecies of *E. granulosus*.

The present experiments show that the testes distribution remains constant for any given strain; it is neither affected by host-species nor by successive generations, and shows only a slight dependency on the degree of development. Thus it is a reliable character for both species and subspecies differentiation.

Size of the cirrus sac (Table 22)

The results are summarized in Table 22. The range of the length of the cirrus sac in the mature segment overlaps that of the gravid segment. With three exceptions, the arithmetic mean is greater in the gravid than in the mature segment.

The increase in the length of the cirrus sac from the mature to the gravid segment is particularly clear in Ovine I. (Data not included in the above table). The cirrus sac in 22 mature segments varies in length from 92·7 to 197·4 (mean 158·9 $\pm$ 14·2) microns, in width from 44·8 to 108·1 (mean 78·2 $\pm$ 14·2) microns. In 22 post-mature segments it varies in length from 154·0 to 225·0 (mean 194·6 $\pm$ 18·8) microns, in width from 67·2 to 98·7 (mean 85·6 $\pm$ 6·9) microns. In 12 gravid segments its length varies from 182·0 to 294·0 (mean 217·9 $\pm$ 30·2) microns, and its width from 50·4 to 94·0 (mean 79·0 $\pm$ 13·5) microns.

The width of the cirrus sac is also usualy greater in the gravid than in the mature segment, but this difference is not as great or as clearly marked as it is in the length.

Discussion: The size of the cirrus sac is generally considered of some value in the taxonomy of cestodes. Rausch (1953) states: "Cirrus sac dimensions may have value in combination with other characters". Sweatman & Williams (1963) used its size, shape and position relative to the genital pore, and the extent to which it overlaps the midline in the mature and in the gravid segment in the differentiation of the subspecies of *E. granulosus*.

The present experiments show the length of the cirrus sac to be subject to considerable variation. Althoutgh the range of variation of this organ in the mature overlaps that of the gravid segment, the mean length of the latter is usually the greater.

Conclusion: The testes distribution and number are reliable criteria for species and subspecies differentiation. The size of the cirrus sac for taxonomic purposes, is of doubtful value.

8. *Female Genitalia*

The ovary and the seminal receptacle

The ovary is usualy a compact bilobed structure, but in some Bovine I the lobes have radiating branches.

The seminal receptacle is a slight dilation of the vagina in all the strains.

Discussion: Sweatman & Williams (1963) found the structure of the ovary variable in "*E. g. granulosus*" and in *E. g. borealis*. In both these subspecies it may be either compact or provided with radiating branches. In *E. g. canadensis* it is always compact.

Sweatman & Williams (1963) reported that the seminal receptacle in " *E. g. granulosus* " is a large, round structure; in the remaining subspecies merely a dilation of the vagina.

The gravid uterus

The specimens of the present series have sacculations proximally but branches distally.

Discussion: Rausch (1953) and Vogel (1957) point out that this structure is of value at the specific level. In the present experiments no differences could be observed in the various strains.

Size of ova and oncosphere hooklets

The greatest and smallest diameters of the ova, as well as the size of the oncosphere hooklets, are summarized in Table 23; the lengths of the three pairs of oncosphere hooklets in a single ovum are listed in Table 24.

Discussion: The summary of the measurements shows that the size of the ova and that of the oncosphere hooklets are variable. The variation in the size of the ovum is greater than that recorded by Vogel (1957) for *E. multilocularis.*

Conclusion: Should any variations in the structure of the ovary, seminal receptacle and uterus be found, they would be reliable criteria.

9. *Host Specificity* (cf. Tables 25, 26)

The number of worms recovered from the different hosts is summarized in Table 25 and the percentage of worms with ova in the uterus in Table 26.

Bovine I strain

The different carnivores showed a marked difference in their susceptibility to infestation, the Cape hunting dog being the most susceptible, the cat the least.

Sixty-three excysted scolices were recovered from a cat which died three days after infestation. The other cat, examined 48 days after infestation, only had six worms of which one was intact. Those worms contained immature ova (Fig. 51).

The percentage of worms which became gravid in 48 days varied in the different hosts, in the two Cape hunting dogs 88·6 per cent and 50·0 per cent; in the dog 29·4 per cent; in the dingo 13·3 per cent and in the silver fox 12·5 per cent.

Bovine II strain

The animals in this group were examined at different infestive ages. The total number of worms recovered from the dogs was 22,002 and from the jackals 28,981. The number of worms per individual recovered from the five dogs varied from 324 to more than 16,000; only two had less than 1,000 worms.

Four cats each dosed with the same number of scolices yielded two worms in the cat examined on the 35th day; the other three animals were negative.

The percentage of worms which attained patency did not differ markedly in dogs and jackals. In the 118 days old infestations the percentage patency in the jackal exceeded that in the dog by 26 per cent; in the 135 days old infestations, however, the percentage patency in the dog exceeded that in the jackal by 20 per cent.

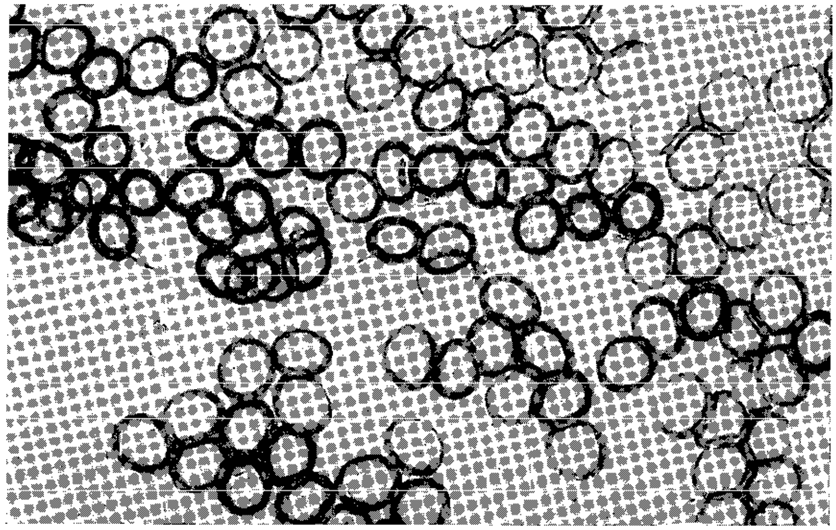

FIG. 51.—Ova: 48 day old specimen from cat. Bovine I.

Ovine I strain

With the exception of two of the three Cape hunting dogs, which showed heavy infestations, few or no worms were recovered from the other carnivora.

Ovine II strain

A striking feature is the large number of worms at all ages recovered from jackals when compared with dogs. The count for the jackal killed on the 95th day should be ignored, however, as this animal was accidentally given an overdose of scolices. Two cats were negative but two worms were recovered from the cat killed on the 35th day.

Porcine I strain

The five dogs infested with this material showed extreme variation in their susceptibility. These animals were not bred at the Institute and their ages were unknown. The negative animal was extremely old, which may have influenced the result.

The percentage of patent worms in the 48, 60 and 109 days old infestations was fairly uniform at about 50 per cent. At 135 days, however, only 12·5 per cent of the specimens recovered were patent.

Porcine II strain

First generation: The five dogs showed some variation in the number of worms recovered, but the take was more uniform than in Porcine I.

The dogs infested with this strain show a marked fluctuation in the percentage of gravid worms at different ages of infestation.

Second generation: The scolices used for this experiment were removed from the liver of an experimentally infested pig (cf. Materials and Methods p. 13–15). As relatively few scolices were available, these carnivores yielded fewer worms than those infested with the first generation. As in the first generation the percentage of gravid worms fluctuated markedly.

Human strain

Only a few scolices were available; jackals appear to be rather more susceptible than are dogs.

Discussion

The number of scolices used to infest each animal could not be accurately counted as the scolices adhered to the glass containers used for making the necessary dilutions. The only practical method was to give the animals in each experimental group the same number of scolices by volume. The possible slight inaccuracy of the scolex dosage alone could not account for the difference in the numbers of worms recovered from the different hosts (Table 25).

As the number of carnivores available was limited, the results obtained cannot be subjected to a statistical analysis. However, it is seen that carnivores of different species as well as those of the same species differ in their susceptibility to infestation with the various strains.

Echinococci were recovered from cats infested with three of the four strains used; Ovine I did not establish itself. One of the specimens recovered from the cat infested with Bovine I contained ova in the terminal segment; these, however, were not yet fully mature. Despite the fact that a few worms were capable of establishing themselves and attaining sexual maturity in cats, they did not appear able to maintain themselves in this host for any length of time, being present only up to 48 days and absent at 75 days and thereafter.

These findings for the cat therefore partially confirm those of Nosik (1954) and Gemmell (1959a) who found that very few worms were recovered from cats after four weeks. The observation that ova may develop in specimens from the cat, however, differs from the findings of Southwell (1927), Lörincz (1933), Nosik (1954) and Gemmell (1959a).

Conclusion

It is clear from these experiments that some of the strains do exhibit a marked degree of host specificity; that the number of patent worms is related to the rate of development in a particular host species and therefore also to the age of infestation; that the more susceptible host yields not only larger numbers of worms, but as a general rule, more of these are patent at any particular time.

10. *Summary*

It is clear that no one character alone may be used for the specific identification of *Echinococcus*.

Strobila

(i) The number of segments and the position of the sexually mature segment are relatively constant. These characters may be used in conjunction with other characters.

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(ii) The size of the strobila and its constituent parts, as well as the ratio of these parts to one another, are subject to extreme variability. It is dependent not only on the fixation methods employed, but also on the age of the parasite and the identity of the definitive host. It is therefore inadvisable that taxonomic significance be attached to it.

Rostellar hooks

The size of the rostellar hooks is dependent on the age of the infestation and the identity of the definitive host and further shows variability in successive generations as well as in material of the same genotype. It is therefore undesirable that taxonomic significance be attached to either the size or the shape of these structures.

Genital pore

This appears to be of value, but mainly at the species level.

Male genitalia

(i) The number and distribution of the testes show but slight variability; these characters may be used in conjunction with other characters.

(ii) The actual size of the cirrus sac differs in the mature and gravid segment; therefore it is not of value in the taxonomy of this genus.

Female genitalia

The structure of the female genitalia in the present experiments does not differ in parasites showing other morphological differences. Variations in the structure of the female genitalia would therefore be of taxonomic significance.

Host specificity

The degree of host specificity exhibited by those parasites varies, being marked in some strains, but less so in others.

Host specificity may be used in conjunction with the number and arrangement of the segments, as well as the number and distribution of the testes.

PART 2

Identification of Material

1. *Review of the literature*

The cystic stage of this parasite was described by Goeze in 1782 as *Taenial socialis granulosa* (Braun, 1894). Batsch (1786) subsequently identified similar material from the liver of a sheep as *Hydatigena granulosa*. In 1800 Zeder united hydatid cysts of human origin with coenuri of ovine origin in the genus *Polycephalus*. The genus *Echinococcus* was erected by Rudolphi in 1801; in 1808 he separated the genus *Coenurus* from *Echinococcus*. Laennec in 1804 created the genus *Acephalocystis* for sterile hydatid cysts, but Wilson in 1845 showed it to be synonymous with *Echinococcus* Rudolphi, 1801 (Braun, 1894). Other synonyms are *Liococcus* Bremser, 1819; *Splanchococcus* Bremser, 1819; *Discostoma* Goodsir, 1844; and *Echinococcifer* Weinland, 1858; (Stiles & Stevenson, 1905).

Hartmannus in 1694 was the first to observe adult echinococci in a dog (Braun, 1894). Rudolphi in 1808 identified these parasites from a dog as young *Taenia cucumerina* (Leuckart, 1881); Röll working in Vienna in 1852 identified them as young *Taenia serrata* (von Siebold, 1852; Braun, 1894); while von Siebold (1852), working in Breslau, found that *Echinococcus veterinorum* developed into small, three-segmented tapeworms in the dog. He proposed that the name of this parasite be changed to *Taenia echinococcus* with the diagnosis: " Corpus triarticulatum. Caput subglobosum. Rostellum rotundatum corona duplici uncinularum 28–36 brevium armatum. Collum longiusculum in posteriore parte stricturem gerens. Ambo articuli androgyni oblongi et apertura genitali marginali alternante instructi. Longitud. $1\frac{1}{2}$ lin. Habitat in intestino tenui Canis familiaris ". This parasite had been described by van Beneden in 1850 as *Taenia nana*, but as the description was published only in 1858, *Taenia echinococcus* Siebold, 1852 has precedence (Leuckart, 1886).

In 1863 two other species belonging to this genus were described: *E. multilocularis* Leuckart, 1863 from hydatid cysts occurring in the liver of man (Leuckart, 1886; Braun, 1894), and the adult stage of *Taenia oligarthrus* Diesing, 1863 from *Felis concolor* (Braun, 1894; Cameron, 1926).

In 1882 Huber pointed out that the 56 known cases of *E. multilocularis* all originated from southern Bavaria, Württemburg and northern Switzerland; he also raised the point as to whether or not the sexual stage of *E. multilocularis* was identical with *Taenia echinococcus*. In 1892 Mangold drew attention to the difference between the shape of the adult rostellar hooks of specimens derived from the artificial infestation of dogs with cysts of *E. multilocularis*, and those of adult *Taenia echinococcus* (Braun, 1894). Mangold's finding, however, was not generally accepted by his contemporary or by subsequent workers. Some of them adopted the unitarian view maintaining that the cyst of *E. multilocularis* was merely another form of an *E. granulosus* cyst; others adopted the dualistic view as indicated by Mangold maintaining that two different species gave rise to the two types of cystic stage. It was not until 1955 that Vogel confirmed Mangold's finding and showed that the sexual stage derived from an *E. multilocularis* cyst differed from that derived from an *E. granulosus* cyst.

In 1926 Cameron transferred *Taenia oligarthrus* Diesing, 1863 to the genus *Echinococcus* Rudolphi, 1801; he also described two species, *E. minimus* from *Canis lupus* in Macedonia and *E. longimanubrius* from *Lycaon pictus*, as well as *E. granulosus* from the fox, *Vulves vulpes*, in England. Ortlepp (1934) considered Cameron's specimens from *V. vulpes* a new species, *E. cameroni*. In the same year he described: *E. lycaontis* from *L. pictus* and in 1937 *E. felidis* from *Panthera leo*. Rausch & Schiller (1954) described *E. sibiricensis* from *Alopex lagopus* from St. Lawrence Island, Alaska.

Recently this genus has been reviewed by Rausch (1953), Vogel (1957) and Rausch & Nelson (1963).

Rausch & Nelson (1963) accept the validity of three species: *E. granulosus* (Batsch, 1786); *E. multilocularis* Leuckart, 1863; *E. oligarthrus* (Diesing, 1863), They consider four species, *E. cameroni* Ortlepp, 1934, *E. lycaontis* Ortlepp, 1934, *E. intermedius* Lopez-Neyra and Soler Planas, 1943, and *E. ortleppi* Lopez–Neyra and Soler Planas, 1943, synonymous with *E. granulosus* leaving the status of *E. felidis* Ortlepp, 1937 and *E. patagonicus* Szidat, 1960 uncertain.

Vogel (1957) created the first subspecies of this genus when he sank *E. sibiricensis* Rausch and Schiller, 1954 to *E. multilocularis sibiricensis*; differentiating it from the nominate subspecies on the size of the rostellar hooks, on differences in host preferences of the cystic and the adult stages and on the predilection sites of the cystic stage.

E. granulosus canadensis Cameron, 1960 was originally distinguished on serological differences of hydatid material from reindeer in Canada as compared with material originating from domestic animals in New Zealand (Cameron, 1960), and on differences in its host preferences (Cameron, 1960; Sweatman & Williams, 1963). The diagnosis for the sexual stage of this subspecies was only given subsequently by Sweatman & Williams (1963). In 1963 Sweatman & Williams and Williams & Sweatman described three further subspecies of *E. granulosus*, basing their subspecies diagnosis on differences in the size of the rostellar hooks, on the distribution and the number of the testes and on host preferences.

The nominate subspecies *E. granulosus granulosus* of Sweatman & Williams, 1963 utilizes sheep, bovids and domestic pigs as intermediate, and dogs as definitive hosts; the type locality is New Zealand. *E. g. canadensis* Cameron, 1960 utilizes reindeer (*Rangifer tarandus*) as intermediate and dogs as definitive hosts; the type locality is Aklavik, N.W.T., Canada. *E. g. borealis* Sweatman and Williams, 1963 utilizes moose (*Alces alces*) and other cervids as intermediate hosts; the sexual stage occurs in the timber wolf (*Canis lupus*), the coyote (*C. latrans*), and the domestic dog; the type locality is Northern Ontario, Canada. *E. g. equinus* Williams & Sweatman, 1963 is derived from the experimental infestation of dogs with cysts from horses in Great Britain.

2. *Materials and methods*

Echinococcus spp. from Germany, Alaska, Australia, Canada and New Zealand were examined. The South African material was obtained from natural and from experimental infestations.

The material was prepared for microscopy as described on pages 13 to 15 in Part 1.

3. *Proposed taxa*

On the basis of criteria established as valid in Part 1, the definition of the two best known and most debated species of *Echinococcus* Rudolphi, 1801 may be modified to read as follows:—

Echinococcus granulosus (Batsch, 1786)

Cestodes varying in length up to 9·2 mm, consisting of two to seven segments. Genital pore near midpoint in both mature and gravid segment. Cirrus sac horizontal or tilted anteriorly. Testes 25 to 80; from slightly less than half to more than half anterior to genital pore. Uterus with lateral branches or sacculations.

Echinococcus multilocularis Leuckart, 1863

Cestodes varying in length up to 3·7 mm, consisting of two to five segments. Genital pore in anterior third of both mature and gravid segment. Cirrus sac tilted posteriorly. Testes 12 to 31; 0 to 6 anterior to genital pore. Uterus without lateral branches or sacculations.

On the basis of criteria established as valid in Part 1 (i.e. the number and arrangement of the segments, the number and distribution of the testes, and host specificity) it is possible to distinguish:—

A. *Valid species:*

Echinococcus granulosus (Batsch, 1786).
Echinococcus multilocularis Leuckart, 1863.

B. *Valid subspecies:*

E. g. borealis Sweatman and Williams, 1963.
E. g. canadensis Cameron, 1960.
E. g. newzealandensis Sweatman and Williams, 1963, nom. nov.

C. *Sink to subspecific rank:*

E. felidis Ortlepp, 1937.
E. lycaontis Ortlepp, 1934.
E. ortleppi Lopez-Neyra and Soler Planas, 1943.

D. *Create the subspecies:*

E. g. granulosus nominate subspecies novum.
E. g. africanus subsp. nov.

The South African subspecies which have been studied in detail are:—

E. g. granulosus nom. subsp. nov.
E. g. africanus subsp. nov.
E. g. felidis Ortlepp, 1937 n. comb.
E. g. lycaontis Ortlepp, 1934 n. comb.
E. g. ortleppi Lopez-Neyra and Soler Planas, 1943 n. comb.

Available comparative material from countries other than South Africa is:—

E. g. granulosus nom. subsp. nov. from Germany.
E. g. borealis Sweatman & Willams, 1963 from Canada.
E. g. canadensis Cameron, 1960 from Canada and Alaska.
E. g. newzealandensis Sweatman & Williams, 1963, nom. nov.

E. multilocularis sibiricensis Rausch & Schiller, 1954 from Alaska.
E. oligarthrus (Diesing, 1863) Cameron, 1926 from South America. (As only four specimens were available, this is considered a *species inquirendae*).

Species and subspecies not studied are:—

E. g. equinus Sweatman & Williams, 1963.
E. cameroni Ortlepp, 1934.
E. intermedius Lopez-Neyra and Soler Planas, 1943.
E. longimanubrius Cameron, 1926.
E. minimus Cameron, 1926.
E. patagonicus Szidat, 1960.

4. *South African material*

Echinococcus granulosus granulosus nominate subspecies novum

(Nec: *E. g. granulosus* Sweatman & Williams, 1963)

In the assumed absence of type specimens, the nominate subspecies is represented by specimens from dogs placed at my disposal by Prof. Vogel, Hamburg, Germany. The South African specimens were derived from the experimental infestation of dogs and jackals [*C.* (*T.*) *mesomelas*] with scolices of porcine and human origin. This material is fully described in Part 1.

Neotype (German material)

Thirty-seven specimens were examined; seven of these are 50 days old, the remaining 30 being of unknown age.

The *strobila* varies in length from 1·70 to 2·92 mm (mean 2·51 ± 0·9 mm). The segments are three in number, the second being sexually mature. The ratio of the length of the mature to that of the gravid segment varies from 1: 2·9 to 1: 4·2 (mean 1: 3·5). The gravid segment varies from 1·008 to 1·872 (mean 1·600) mm and constitutes from 59·1 to 70·3 per cent (mean 63·1 per cent) of the total length.

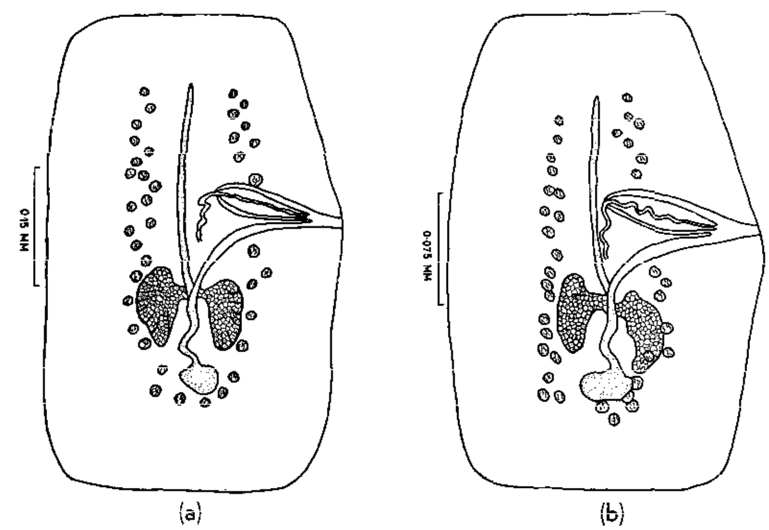

FIG. 52.—Sexually mature segment of *Echinococcus granulosus granulosus* nominate subspecies novum. Neotype, Europe.
(*a*) Testes equally divided in the two halves of thesegment.
(*b*) Majority of testes posterior to genital pore.

The position of the *genital pore* in the mature segment varies from 42·9 to 55·6 per cent (mean 48·4 per cent) of its length from the anterior margin; in the gravid segment it varies from 53·6 to 70·0 per cent (mean 58·0 per cent). The *testes* number 32 to 45 (mean 37·9 ± 3·2) and are present posterior to the vitellaria, extending forward to just behind the anterior margin of the segment. In 15 specimens the number of testes posterior to the genital pore is equal to the number anterior to it (Fig. 52a). In the remaining 22 specimens there are more testes posteriorly than anteriorly (Fig. 52b). The number anterior varies from 12 to 24 (mean 16·9 ± 2·3); and posterior from 17 to 27 (mean 21·0 ± 2·5). The *cirrus sac* in 33 mature segments is from 56·0 to 110·4 (mean 83·4 ± 11·6) microns long and from 33·6 to 59·8 (mean 43·4 ± 6·4) microns wide. In 11 gravid segments it is 92·0 to 138·0 (mean 111·7 ± 11·5) microns by 50·6 to 69·0 (mean 58·8 ± 5·7) microns.

Metatype (South African specimens)

The strobila varies in length from 2·62 to 6·41 mm (mean 3·53 ± 0·94 mm). The majority (82·5 per cent) consist of three, 6·7 per cent of two, and 10·8 per cent of four segments. The ratio of the length of the mature to that of the gravid segment varies from 1:2·0 to 1:3·2 (mean 1:2·5). The gravid segment varies from 0·850 to 2·380 (mean 2·140) mm in length and constitutes from 35·2 to 78·2 per cent (mean 56·5 per cent) of the total length.

The position of the *genital pore* in the mature segment is from 43·8 to 66·7 per cent (mean 51·0 per cent), in the gravid segment from 50·6 to 80·9 per cent (mean 67·4 per cent), of their length from the anterior margin. The *testes* number from 28 to 50 (mean 41·3 ± 5·7). The testes extend posterior to the vitelline gland; anterior to the genital pore they vary from 12 to 29 (mean 20·2 ± 3·1) and posterior from 12 to 30 (mean 21·1 ± 3·5) (Fig. 47, 48, 49, 50). The *cirrus sac* in the mature segment varies in length from 70·0 to 169·2 (mean 109·6 ± 18·8) microns and in width from 39·2 to 98·0 (mean 63·3 ± 9·8) microns; in the gravid segment its length varies from 103·6 to 224·0 (mean 132·0 ± 15·4) microns and its width from 50·4 to 98·0 (mean 67·8 ± 8·0) microns.

Discussion

The description of *Hydatigena granulosa* Batsch, 1786 is based on the hydatid cyst only. The type locality of this parasite is not given, but it is more than likely that it was collected near Batsch's home, i.e. Jena or Halle (Vogel, 1964). Furthermore, as the first description of the adult worm is based on material from Breslau (von Siebold, 1852), the type locality of *E. granulosas* (Batsch, 1786), by implication, is Europe (Germany).

Since the type of a species is also the type of its nominate subspecies [Article 61 (*a*) International Code of Zoological Nomenclature, 1958] the type locality of the species is also that of the nominate subspecies. It is generally accepted that the "first reviser" may designate the type locality where it is not given (Mayr *et al.*, 1953, p. 244). Such a designation is, however, subject to conditions laid down by Recommendation 72 E of the International Code of Zoological Nomenclature, 1958. This recommendation states:—

"An author who either designates or restricts a type locality should base his action on one or more of the following criteria:—

(1) the original description of the taxon;

(2) data accompanying the original material;

(3) collector's notes, itineraries, or personal communications; and

(4) as a last resort, localities within the known range of the species or from which specimens identified with the species have been taken.

If a type locality was erroneously designated or restricted, it should be corrected ".

It therefore follows that the type locality of the nominate subspecies of *Echinococcus granulosus* (Batsch, 1786) must be Europe (Germany) and cannot be New Zealand as designated by Sweatman & Williams (1963).

In the present investigation the specimens of German origin agree with the description given by Vogel (1957). The specimens are smaller than those described by Vogel, but have the same number and arrangement of segments. The mean number of testes is lower, but the range of variation of their number (33 to 45) does not differ significantly from that of Vogel (38 to 52). Vogel found that two-thirds of the testes are situated anterior to the ovary, the number anterior to the cirrus sac varying from 9 to 23. In the present investigation the distribution of the testes was determined taking the opening of the genital pore as the dividing line between the anterior and posterior halves of the segment. It is therefore difficult to compare the actual number in each half of the segment with the data given by Vogel. However, one of his illustrations shows the testes equally distributed in the two halves while the other illustration shows the greater number in the posterior half of the segment.

The South African specimens differ from those from Germany in that they show a greater variation in the length of the strobila and in the number of its segments. The number and the distribution of the testes correspond closely. The size of the cirrus sac in both the mature and the gravid segments shows a greater range of variation and mean in the South African material.

The material designated the plesiotypes of the nominate subspecies by Sweatman & Williams (1963) does not tally with *E. granulosus* from its type locality, i.e. Europe (Germany). They differ from the German material both in the number and arrangement of the segments and in the number and distribution of the testes. The New Zealand specimens usually consist of four segments, but vary from three to five, either the second or third being sexually mature; the number of testes varies from 40 to 70, the majority situated in the anterior half of the segment. This New Zealand material, hence, cannot be designated as the type of the nominate subspecies, and it is therefore proposed that *Echinococcus granulosus newzealandensis* nomen novum replace *Echinococcus granulosus granulosus* Sweatman & Williams, 1963.

Revised diagnosis of Echinococcus granulosus granulosus *nominate subspecies novum*

Strobila usually three segments, second segment sexually mature. Testes 32 to 52, either equally distributed anterior and posterior, or majority posterior, to the genital pore. Genital pore at midpoint of the mature segment, posterior to midpoint in gravid segment.

Host: Intermediate: Primarily sheep, pigs, goats and cattle.
Definitive: Dog and other Canidae.

Type locality: Europe (Germany).

Neotypes: Onderstepoort Helminthological Collection, and Helminthological Collection, Tropeninstitut, Hamburg.

Echinococcus granulosus africanus subsp. nov.

This subspecies is based on two of the experimental infestations viz. Bovine I/Canidae and Ovine II/dog, jackal, including specimens from a jackal [*Canis* (*Thos*) *mesomelas*] experimentally infested by Dr. N. Viljoen in Bloemfontein in 1936. A few representatives of this subspecies were also collected from a naturally infested dog, locality unknown. Bovine I/Canidae are selected as syntypes; these worms are given precedence over Ovine II/dog, jackal as they were collected from a larger number of host species. The specimens of the other two experimental infestations (Ovine II/dog, jackal and from the jackal infested by Dr. Viljoen) are regarded as metatypes.

Syntype

The *strobila* varies in length from 1·83 to 4·84 (mean 3·16 ± 0·2) mm; consists of two to four, but usually three, segments. Usually the penultimate is sexually mature, but in 3·5 per cent the antepenultimate is already sexually mature. The ratio of the length of the mature to that of the gravid segment varies from 1 : 1·6 to 1 : 4·5 (mean 1 : 2·7). The length of the gravid segment varies from 1·105 to 2·934 (mean 1·794) mm and constitutes from 43·3 to 72·4 per cent (mean 57·6 per cent) of the strobilar length.

The position of the *genital pore* in the mature segment varies from 38·6 to 61·5 per cent (mean 49·8 per cent); in the gravid segment from 38·5 to 63·0 per cent (mean 53·6 per cent) of their length from the anterior margin. The total number of *testes* varies from 25 to 49 (mean 34·3 ± 5·6). The testes extend posterior to the vitelline gland. Those anterior to the genital pore vary from 14 to 30 (mean 19·4 ± 3·4) and those posterior to it from 8 to 22 (mean 14·9 ± 3·1) (Fig. 53). The *cirrus sac* in the mature segment varies from 64·4 to 114·8 (mean 87·9 ± 12·2) microns in length and from 33·6 to 75·2 (mean 49·5 ± 8·1) microns in width; in the gravid segment it is 78·4 to 131·6 (mean 99·7 ± 12·9) microns by 39·2 to 84·6 (mean 55·6 ± 6·8) microns.

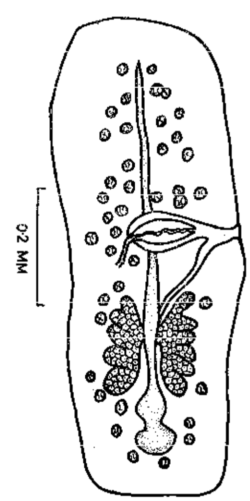

Fig. 53.—Sexually mature segment of *E. granulosus africanus* subspecies nov.

Metatype

The *strobila* varies in length from 2·12 to 6·13 (mean 4·12 ± 1·01) mm. The segments number from two to four, but usually three; the penultimate being sexually mature. The ratio of the length of the mature to that of the gravid segment varies from 1:1·5 to 1:3·1 (mean 1:2·1). The gravid segment varies in length from 1·152 to 3·658 (mean 2·088) mm and constitutes from 40·3 to 60·7 per cent (mean 50·5 per cent) of the total length.

The position of the *genital pore* in the mature segment varies from 45·5 to 64·5 per cent (mean 55·6 per cent), in the gravid segment from 47·1 to 69·7 per cent (mean 58·5 per cent), of the length from the anterior margin. The *testes* which extend posterior to the vitellaria, vary from 29 to 54 (mean 42·7 ± 4·5); from 17 to 37 (mean 27·2 ± 11·7) are anterior and from 10 to 25 (mean 15·5 ± 2·8) posterior to the genital pore (Fig. 46). The *cirrus sac* in the mature segment varies from 82·0 to 220·9 (mean 161·3 ± 30·3) microns in length and from 46·0 to 100·8 (mean 77·3 ± 9·1) microns in width; in the gravid segment it is 115·0 to 224·0 (mean 179·2 ± 9·0) microns by 59·8 to 108·1 (mean 83·9 ± 10·7) microns.

Natural infestation

Only four of the parasites from the naturally infested dog were complete. The *strobila* varies in length from 2·81 to 3·46 (mean 3·02) mm. It consists of three segments, the penultimate being sexually mature. The ratio of the length of the mature to that of the gravid segment varies from 1:1·9 to 1:2·6 (mean 1:2·1). The gravid segment varies in length from 1·440 to 1·728 (mean 1·594) mm and constitutes from 50·0 to 56·4 per cent (mean 53·0 per cent) of the total length.

The position of the *genital pore* in the mature segment varies from 52·0 to 58·8 per cent (mean 55·6 per cent), and in the gravid segment from 52·3 to 57·7 per cent (mean 55·4 per cent) of the length from the anterior margin. The *testes* (seven specimens) number from 32 to 47 (mean 39·4 ± 5·3). Those anterior to the genital pore vary from 19 to 28 (mean 23·0 ± 3·4) and those posterior from 13 to 21 (mean 16·4 ± 2·7). The *cirrus sac* could be measured in one mature segment only; it is 89·6 by 42·0 microns, in two gravid segments it varies from 117·6 to 123·2 (mean 120·4) microns by 61·6 to 70·0 (mean 65·8) microns.

Discussion

Although the number of testes in the syntype material differs from that of the metatype material and that of the natural infestation, the respective ranges do not differ markedly. Further, as all three show the same type of testes distribution, they can be considered conspecific. These specimens resemble " *E. g. granulosus* " Sweatman & Williams, 1963 in testes distribution, but differ in the number of testes and in the shape of the seminal receptacle.

Southwell (1927), Lorincz (1933,) Nosik (1954) and Gemmell (1959a) found that *E. granulosus* may establish itself in the domestic cat, but in no instance were ova produced. The results obtained with *E. g. africanus* differ from the above; six worms, 48 days old, were recovered from a cat infested with Bovine I; the ova in these specimens, although not yet fully mature, however, appear to be very close to maturity (Fig. 51). In view of the small numbers of worms recovered from the cats, these animals do not appear to be the normal hosts of this parasite. These animals may, however, play some role, at present still undetermined, in the dissemination of this parasite.

Diagnosis

Strobila two to four, but usually three, segments. Penultimate sexually mature, Genital pore at midpoint of mature-, but beyond midpoint of gravid-segment. Testes 25 to 54; majority anterior to genital pore. Seminal receptacle dilatation of vagina.

Host: Intermediate: cattle and sheep.
Definitive: Canidae.

Type locality: Transvaal, Orange Free State, South Africa.

Syn- and Metatype: Onderstepoort Helminthological Collection.

Echinococcus granulosus lycaontis Ortlepp, 1934. n.comb.
Syn: *E. lycaontis* Ortlepp, 1934.

This subspecies is based on the syntype specimens of *E. lycaontis* Ortlepp, 1934 and on Ovine I/Cape hunting dog; included are some specimens collected from a Cape hunting dog, Rustenburg district, Transvaal.

Syntype

The *strobila* is up to 5·29 mm long. It has from four to seven segments, the usual number being five. The third or fourth segment, i.e. the antepenultimate, is sexually mature. The ratio of the length of the mature to that of the gravid segment could be determined in two specimens only; this varies from 1:3·8 to 1:4·4 (mean 1:4·1); the length of the gravid segment (two specimens) is from 2·480 to 2·520 mm (mean 2·500 mm); it constitutes from 44·9 to 50·0 per cent (mean 47·5 per cent) of the total length.

The position of the *genital pore* (five specimens) in the mature segment varies from 52·6 to 60·0 per cent (mean 56·9 per cent) of its length from the anterior margin; in the post-mature segment (defined on p. 55, Part I) it varies from 53·3 to 66·7 per cent (mean 58·3 per cent), and in the gravid segment from 50·7 to 58·6 per cent (mean 54·6 per cent). The *testes* (six specimens) number from 41 to 44 (mean 42·5 $\pm$ 1·4). There are from 24 to 31 (mean 28·2 $\pm$ 2·3) anterior and from 13 to 17 (mean 14·3 $\pm$ 1·6) posterior to the genital pore (Fig. 54). The *cirrus sac* in the mature segment (seven specimens) varies from 95·2 to 110·4 (mean 100·7 $\pm$ 5·5) microns in the length and from 55·2 to 69·0 (mean 60·2 $\pm$ 5·3) microns in width; in the post-mature segment (four specimens) it is 92·0 to 128·8 (mean 113·9) microns by 59·8 to 69·0 (mean 65·5) microns. In the gravid segments the size could not be determined.

Homotype

The *strobila* varies in length from 4·12 to 7·54 (mean 5·68 $\pm$ 0·80) mm. There are from four to six, usually five, segments, the antepenultimate being sexually mature. The ratio of the length of the mature to that of the gravid segment varies from 1:1·6 to 1:3·3 (mean 1:2·1). The gravid segment varies in length from 1·334 to 2·667 (mean 2·055) mm and constitutes from 22·3 to 45·2 per cent (mean 36·4 per cent) of the strobilar length.

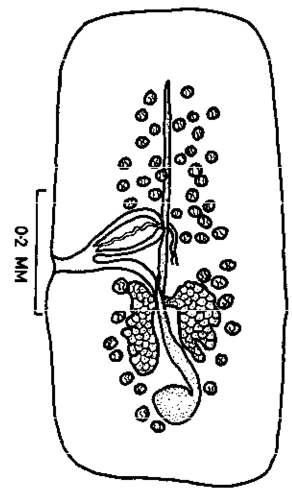

FIG. 54.—Sexually mature segment of *E. g. lycaontis* Ortlepp, 1934 n. comb. Syntype.

The position of the *genital pore* in the mature segment varies from 38·9 to 62·5 per cent (mean 54·5 per cent) of its length from the anterior margin; in the post-mature segment from 47·8 to 66·7 per cent (mean 60·3 per cent) and in the gravid segment from 51·4 to 69·5 per cent (mean 58·8 per cent). The number of *testes* varies from 58 to 80 (mean 69·4 ± 7·1), the majority are situated anterior to the genital pore. Those anterior vary from 34 to 53 (mean 41·5 ± 5·1); those posterior from 21 to 34 (mean 26·9 ± 4·1) (Fig. 54). The *cirrus sac* in the mature segment varies in length from 92·7 to 197·4 (mean 158·9 ± 14·2) microns and in width from 44·8 to 108·1 (mean 78·2 ± 14·2) microns. In the post-mature segment it is 154·0 to 225·0 (mean 194·6 ± 18·8) microns by 67·2 to 97·8 (mean 85·6 ± 6·9) microns; in the gravid segment it is 182·0 to 294·0 (mean 217·9 ±30·2) microns by 50·4 to 94·0 (mean 79·0 ± 13·5) microns.

Natural infestation

The material collected at Rustenburg consists either of immature specimens or of specimens in which the terminal segment(s) had been lost.

The *strobila* consists of four segments, the third being sexually mature and the last segment post-mature.

The *genital pore* (six specimens) in the mature segment is 44·4 to 61·2 per cent (mean 52·5 per cent), in the post-mature from 54·0 to 62·2 per cent (mean 58·4 per cent) of the length from the anterior margin. The number of *testes* (ten specimens) varies from 41 to 59 (mean 47·6 ± 5·5). Those anterior to the genital pore vary from 28 to 40 (mean 31·5 ± 3·9); and those posterior from 13 to 19 (mean 16·1 ± 2·1). The *cirrus sac* in the mature segment (three specimens) varies in length from 73·6 to 92·4 (mean 84·4) microns and in width from 41·4 to 56·0 (mean 46·2) microns. In the post-mature segment (four specimens) it is 92·4 to 128·8 (mean 108·2) microns by 56·0 to 59·8 (mean 58·8) microns.

Discussion

The specimens collected from the Cape hunting dog at Rustenburg correspond closely with the type specimens. Those from Ovine I/Cape hunting dog, however, differ in the number of testes, and in the size of the cirrus sac.

Four or more segments are described in three other species, viz. *E. felidis* (Ortlepp, 1937), *E. cameroni* (Ortlepp, 1934) and *E. granulosus* (Wright, 1962). *E. felidis* usually consists of four segments, but five may occur (Ortlepp, 1937). Were the subspecies *E. lycaontis* identical with *E. felidis* it would seem reasonable to expect that the cats infested with the experimental strain would have harboured at least a few specimens; they, however, were completely refractory. As attempts to infest silver foxes (*Vulpes chama*) were also unsuccessful it is unlikely that this material is identical with *E. cameroni* Ortlepp, 1934 from *Vulpes vulpes* in England.

In the experimental infestation appreciable numbers of worms were recovered from only the Cape hunting dogs; this subspecies appears to exhibit a marked degree of host specificity.

Diagnosis

Strobila usually five segments, but from four to seven may occur. Antepenultimate segment sexually mature. Genital pore just beyond midpoint in mature, more posterior in post-mature and gravid segments. Testes not less than 41, majority anterior to the genital pore.

Host: Intermediate: Sheep.

Definitive: *Lycaon pictus*.

Locality: Transvaal, South Africa.

Syn- and Homotype: Onderstepoort Helminthological Collection.

Echinococcus granulosus ortleppi Lopez-Neyra and Soler Planas, 1943. n.comb.

Syn: *E. ortleppi* Lopez-Neyra and Soler Planas, 1943.

The diagnosis of this subspecies is based on specimens identified as *E. granulosus* by Ortlepp (1934); Lopez-Neyra & Soler Planas (1943) consider it to be a new species, *E. ortleppi*. The helminths derived from Bovine 11/dog, jackal belong to this subspecies, as also specimens from three dogs with natural infestations.

Syntype

Only seven of the specimens identified as *E. granulosus* by Ortlepp (1934) could be re-examined.

The *strobila* varies from 2·99 to 4·11 (mean 3·42 ± 0·48) mm and consists of three to four, but usually three, segments. The penultimate segment is sexually mature. The ratio of the length of the mature to that of the gravid segment varies from 1:2·5 to 1:4·8 (mean 1:3·0). The gravid segment varies in length from 1·620 to 3·600 (mean 2·119) mm, and constitutes from 51·8 to 87·5 per cent (mean 61·1 per cent) of the total length.

The position of the *genital pore* in the mature segment is from 50·0 to 60·9 per cent (mean 55·0 per cent), in the gravid segment from 55·0 to 60·0 per cent (mean 57·2 per cent), of the length from the anterior margin. The *testes* number from 31 to 39 (mean 33·2 ± 3·5). The majority of the testes are situated anterior to the genital pore with no testes posterior to the vitellaria. The number anterior varies from 18 to 25 (mean 20·6 ± 3·0) and posterior from 11 to 14 (mean 12·6 ± 1·1) (Fig. 55). The *cirrus sac* in the mature segment varies from 101·2 to 119·6 (mean 112·0) microns in length and from 55·2 to 69·0 (mean 60·7) microns in width; in two gravid segments it is 115·0 microns long and 69·0 microns wide.

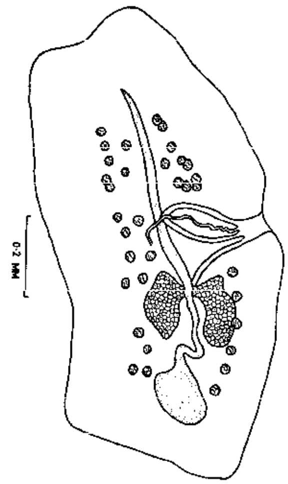

FIG. 55.—Sexually mature segment of *E. g. ortleppi* Lopez-Neyra and Soler Planas, 1943. n, comb. Syntype.

Homotype

Natural infestations: From three dogs with natural infestations 11, 14 and 20 worms respectively were examined. The *strobila* varies in length from 2·03 to 4·25 (mean 2·92 ± 0·2) mm. They consist of three segments, the second one being sexually mature. The ratio of the length of the mature segment to that of the gravid varies from 1: 1·7 to 1: 4·3 (mean 1: 2·8). The length of the gravid segment is from 0·864 to 2·808 (mean 1·703) mm, and constitutes from 42·6 to 66·1 per cent (mean 57·0 per cent) of the length of the strobila.

The *genital pore* in the mature segment is situated 43·8 to 61·1 per cent (mean 52·3 per cent) from the anterior margin; in the gravid segment it is 54·1 to 74·4, per cent (mean 60·9 per cent). The *testes* number from 28 to 42 (mean 34·9 ± 3·2), from 19 to 28 (mean 22·0 ± 2·0) anterior to and from 9 to 18 (mean 12·9 ± 2·1) posterior to the genital pore. The testes distribution resembles that of the syntypes, The *cirrus sac* in the mature segment is from 69·0 to 128·8 (mean 108·6 ± 16·7) microns long and from 33·6 to 78·2 (mean 58·7 ± 9·7) microns wide; in the gravid segment it is from 86·8 to 138·0 (mean 105·3 ± 17·0) microns by 41·4 to 69·0 (mean 55·3 ± 8·5) microns.

Experimental infestations: The *strobila* of the specimens resulting from the experimental infestations (Bovine II/dog, jackal) varies in length from 2·59 to 7·01 (mean 4·90 ± 0·7) mm. The strobila consists of two, three or four, usually three, segments, the penultimate being sexually mature. The ratio of the length of the mature to that of the gravid segment varies from 1: 1·0 to 1: 6·1 (1: 3·3). The gravid segment varies from 1·250 to 5·080 (mean 3·190) mm in length and constitutes from 39·4 to 91·4 per cent (mean 64·6 per cent) of the total length.

The position of the *genital pore* in the mature segment is from 40·0 to 67·6 per cent (mean 49·4 per cent), in the gravid segment from 46·9 to 68 per cent (mean 55·9 per cent), of their length from the anterior margin. The *testes* number from

25 to 47 (mean 32·2 ± 4·0); those anterior vary from 13 to 28 (mean 20·2 ± 2·7) and those posterior from 8 to 19 (mean 12·0 ± 2·3). The *cirrus sac* in the mature segment varies in length from 56·0 to 182·0 (mean 91·9 ± 20·9) microns; the width from 28·0 to 92·4 (mean 59·1 ± 11·1) microns; in the gravid segment it is 89·6 to 154·0 (mean 125·2 ± 14·4) microns by 56·0 to 81·2 (mean 65·9 ± 5·3) microns.

Discussion

E. g. ortleppi and *E. g. africanus* resemble one another in the number and the arrangement of the segments, but differ in the presence or absence of testes posterior to the vitellaria. This appears to be a valid criterion as only 0·5 per cent of the specimens derived from the experimental infestation did not conform. A further difference between these subspecies is that the dog and jackal appear to be equally susceptible to infestation with *E. g. ortleppi* but the dog appears to be less susceptible to *E. g. africanus* than is the jackal.

Diagnosis

Strobila two to four, usually three, segments; penultimate sexually mature, Testes 25 to 47; majority anterior to genital pore; none posterior to vitellaria.

Host: Intermediate: cattle.

Definitive: Canidae [domestic dog, *C.* (*T.*) *mesomelas*].

Locality: Transvaal, South Africa.

Syn- and Homotype: Onderstepoort Helminthological Collection.

Echinococcus granulosus felidis Ortlepp, 1937. n.comb.

Syn: *Echinococcus felidis* Ortlepp, 1937.

This subspecies is based on the type specimens of *E. felidis* Ortlepp, 1937 and additional specimens from four lions, collected in the Transvaal (Kruger National Park and Louis Trichardt) and in Southern Rhodesia (Kariba). The author is indebted to Dr. Roth, Veterinary Department, Southern Rhodesia for the Kariba material.

Syntype

The *strobila* in fifteen helminths varies in length from 3·42 to 5·33 (mean 4·21 ± 0·6) mm, consisting of four or five, but usually four, segments. The third segment is sexually mature in all the specimens. The ratio of the length of the mature to that of the gravid segment varies from 1: 1·6 to 1: 3·4 (mean 1: 1·9). The gravid segment is 1·008 to 2·196 (mean 1·836) mm long and constitutes from 41·1 to 48·8 per cent (mean 44·1 per cent) of the total length.

The *genital pore* in the mature segment is situated from 38·5 to 70·4 per cent (mean 56·2 per cent), in the post-mature segment from 53·5 to 64·1 per cent (mean 59·3 per cent), and in the gravid segment 61·5 to 72·2 per cent (mean 66·6 per cent) of the length from the anterior margin. The *testes* number 30 to 46 (mean 36·6 ± 4·2). They extend from posterior to the vitellaria to close to the anterior margin of the segment, the majority being anterior to the genital pore. There are from 19 to 29 (mean 22·9 ± 2·5) anterior and from 10 to 18 (mean 13·7 ± 2·3) posterior

to the genital pore (Fig. 56a). The *cirrus sac* in the mature segment is from 115·0 to 174·8 (mean 148·2 ± 15·5) microns long and from 55·2 to 92·0 (mean 77·3 + 13·3) microns wide; in the gravid segment it is 142·6 to 207·0 (mean 176·9 ± 21·7) microns by 64·4 to 96·6 (mean 83·2 ± 10·2) microns.

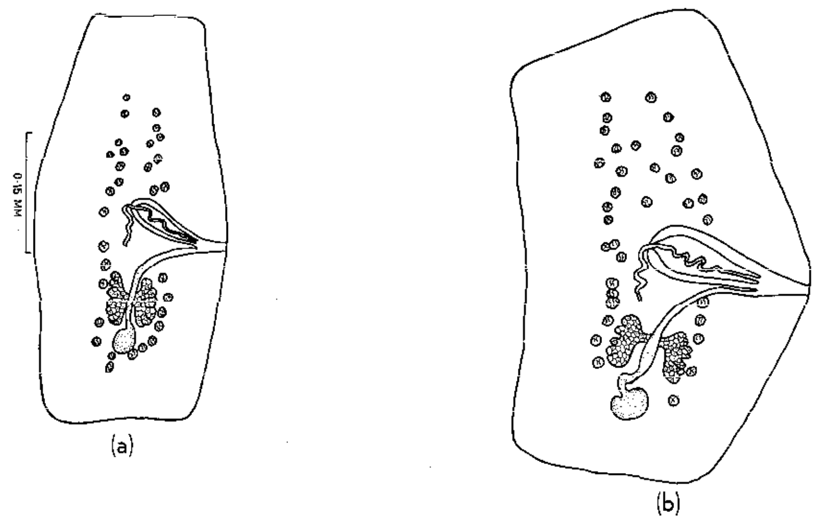

FIG. 56.—Sexually mature segment of *E.g. felidis* Ortlepp, 1937 n. comb.
a. Syntype
b. Specimen from Kariba

Homotype

Natural infestations: The *strobila* varies in length from 2·124 to 5·220 (mean 3·239 ± 0·3) mm. It consists of three segments in 18·5 per cent, of four in 47·0 per cent and of five in 34·5 per cent of 64 specimens. The penultimate segment was usually sexually mature but in 20·3 per cent of the worms the antepenultimate is sexually mature. The ratio of the length of the mature to that of the gravid segment varies from 1 : 1·1 to 1 : 3·0 (mean 1 : 1·7). The gravid segment varies from 0·684 to 1·980 (mean 1·381) mm in length and constitutes from 30·4 to 51·1 per cent (mean 40·4 per cent) of the total length.

The position of the *genital pore* in the mature segment varies from 38·0 to 63·2 per cent (mean 51·8 per cent) of its length from the anterior margin; in the post-mature segment this varies from 41·4 to 67·4 per cent (mean 56·3 per cent) and in the gravid segment from 45·4 to 65·9 per cent (mean 63·2 per cent). The *testes* number from 28 to 45 (mean 35·9 ± 3·5); the number anterior to the genital pore varies from 18 to 32 (mean 23·3 + 2·8) and posterior from 9 to 17 (mean 12·6 ± 1·9). The *cirrus sac* in the mature segment varies in length from 82·8 to 202·4 (mean 129·4 ± 24·0) microns, in width from 46·0 to 105·8 (mean 64·9 ± 9·9) microns; in the gravid segment it is 147·2 to 188·6 (mean 164·3) microns by 64·4 to 82·8 (mean 71·6 + 5·9) microns.

In those specimens in which the antepenultimate segment is sexually mature, the cirrus sac, in the post-mature segment, is 147·2 to 184·0 (mean 159·9 ± 13·7) microns by 56·0 to 78·2 (mean 71·7 ± 9·3) microns.

Specimens from two of the hosts, collected at Kariba and in the Kruger National Park, differ in that there are no testes posterior to the vitellaria (Fig. 56b).

Discussion

With the exception of the difference in testes distribution in two of the hosts the specimens from the five lions show very little variation. Although some specimens (20 per cent) resemble *E. g. lycaontis* in the position of the mature segment, *E. g. felidis* differs from it in having three to five instead of four to seven segments.

Diagnosis

Strobila three to five, usually four, segments. Penultimate or antepenultimate segment sexually mature. Genital pore just posterior to midpoint in mature, more posterior in post-mature and gravid segments. Testes 28 to 46 in number, majority anterior to genital pore, may or may not be present posterior to the vitellaria.

Host: Intermediate: Unknown.
Definitive: *Panthera leo.*

Locality: Transvaal, South Africa.

Syn- and Homotype: Onderstepoort Helminthological Collection.

Key to South African subspecies of Echinococcus granulosus (*Batsch,* 1786)

1.	Testes equally distributed, or majority posterior to the genital pore..	*granulosus*
	Testes mainly anterior to the genital pore................	2
2.	In felines; three to five, usually four, segments............	*felidis*
	In canines; two to seven segments......................	3
3.	Four to seven, usually three, segments; antepenultimate sexually mature..	*lycaontis*
	Two to four, usually five, segments; penultimate sexually mature	4
4.	Some testes present posterior to the vitellaria..............	*africanus*
	No testes posterior to the vitellaria.......................	*ortleppi*

5. *Extra-African material*

Echinococcus granulosus borealis Sweatman & Williams, 1963

Prof. T. W. M. Cameron, Canada and Dr. R. Rausch, Alaska, provided specimens from domestic dogs, the specimens from three of the dogs being from experimental infestations.

Experimental infestations

The *strobila* of 27 parasites varies in length from 2·952 to 5·720 mm (mean 4·081 $\pm$ 0·8 mm). The gravid specimens consist of three segments, the second being sexually mature. In 45 specimens the ratio of the length of the mature segment to that of the gravid is from 1:2·1 to 1:3·8 (mean 1:2·2). The gravid segment varies from 1·584 to 3·348 (mean 2·412) mm; and constitutes from 51·2 to 69·8 per cent (mean 56·5 per cent) of the total length.

The *genital pore* in the mature segment is from 35·7 to 60·0 per cent (mean 53·3 per cent) of its length from the anterior margin; in the gravid segment 51·9 to 71·2 per cent (mean 57·1 per cent). The *testes* in 48 specimens number from 32 to 51 (mean 39·1 ± 5·0); 16 to 30 (mean 21·6 ± 2·9) are anterior and 11 to 26 (mean 17·5 ± 3·0) posterior to the genital pore. The *cirrus sac* is round. In the mature segment it varies in length from 96·6 to 196·0 (mean 135·2 ± 22·3) microns and in width from 53·2 to 98·0 (mean 76·5 ± 11·7) microns; in the gravid segment it is 106·4 to 196·0 (mean 162·3 ± 17·7) microns by 56·0 to 103·6 (mean 83·8 ± 9·1) microns.

Natural infestation

These specimens had either lost their last segment or were immature. The *strobila* consists of two or three segments, the last one being sexually mature. One specimen, 2·700 mm long, appears to be complete; it consists of three segments, the second one being sexually mature.

The *genital pore* in the mature segment (ten specimens) is from 40·0 to 65·4 per cent (mean 50·5 per cent) of its length from the anterior margin; in the one gravid segment 59·5 per cent. The *testes* number (seven specimens) from 28 to 35 (mean 31·7 ± 3·2), from 16 to 20 (mean 18·0 ± 1·9) are anterior and from 12 to 15 (mean 13·7 ± 2·0) posterior to the genital pore. The *cirrus sac* in the mature segment (nine specimens) varies from 92·0 to 119·6 (mean 106·3 ± 9·3) microns by 55·2 to 78·2 (mean 64·4 ± 7·6) microns.

Discussion

The above two sets of specimens differ from the description given by Sweatman & Williams (1963) in that the cirrus sac is larger and the ratio of the length of the mature to that of the gravid segment is 1: 2·2 instead of 1: 3·0. The lower limit of the range of variation of the number of testes is 28 and not 36; however, the distribution of the testes relative to the genital pore is the same. In all other respects these worms agree with the description given by them.

Proposed revised diagnosis

Strobila three to five, usually three, segments. Penultimate segment sexually mature. Testes 28 to 55, majority anterior to genital pore. Cirrus sac round.

Host: Intermediate: Cervids, particularly moose (*Alces alces*).
Definitive: Canidae.

Type locality: Northern Ontario, Canada.

Plesiotype: USDA. Specimen No. 59724 (Sweatman & Williams, 1963).

Echinococcus granulosus canadensis Cameron, 1960.

Prof. T. W. M. Cameron kindly provided specimens from an experimental infestation of a dog with material of reindeer origin, and of a natural infestation of a wolf, *Canis lupus*, from Canada.

Experimental infestation

The specimens from reindeer/dog are not suitable for study. They consist of two segments only; the first is not yet sexually mature while the terminal one contains immature ova.

Natural infestation

The specimens from the wolf are incomplete, consisting of only two segments, the last being sexually mature. The *genital pore* in the mature segment (eight specimens) is 50·0 to 57·1 per cent (mean 53·0 per cent) of the length of the segment from the anterior margin. The number of *testes* (six specimens) varies from 28 to 36 (mean 31·6 ± 3·2) and they are equally distributed in the two halves of the segment. Those anterior to the genital pore number 13 to 18 (mean 15·8 ± 2·0) and those posterior 14 to 18 (mean 15·8 ± 1·5). The *cirrus sac* in the mature segment (eight specimens) varies from 114·8 to 168·0 (mean 139·1 ± 17·9) microns in length and from 56·0 to 92·4 (mean 80·3 ± 12·1) microns in width.

Discussion

The specimens from the wolf differ from the description given by Sweatman & Williams (1963) in that the complete strobila would apparently consist of three segments. According to Sweatman & Williams (1963) the strobila usually consists of two segments, but three may occur. Sweatman & Williams found that the majority of the testes are posterior to the genital pore, but in the specimens from the wolf the testes are equally divided in the two halves of the segment. It has already been pointed out, however, that this difference in testes distribution is also encountered in *E. g. granulosus* and is related to the degree of development of the genitalia. The genital pore is situated at or just posterior to the midpoint of both the mature and the gravid segment, while Sweatman & Williams found it to be anterior to the midpoint. The cirrus sac in the specimens from the wolf is longer than that reported by Sweatman & Williams. In Part I, however, it has been shown that the length of the cirrus sac is variable and that no significance can be attached to it.

Proposed revised diagnosis

Strobila usually two, sometimes three, segments. Penultimate sexually mature. Testes 21 to 40, either equally distributed anterior and posterior, or majority posterior to the genital pore.

Host: Intermediate: Reindeer (*Rangifer tarandus*).
Definitive: Canidae.

Type locality: Aklavik, N.W.T., Canada.

Plesiotype: USDA. Specimen No. 59725 (Sweatman & Williams, 1963).

Echinococcus granulosus newzealandensis nom. nov.

Syn: *E. g. granulosus* Sweatman & Williams (1963)

Specimens from New Zealand were made available by Dr. L. Whitten, New Zealand, and by Prof. T. W. N. Cameron, Canada, and specimens from a natural infestation of two dingos, *Canis dingo*, from Queensland, Australia by Dr. R. Rick, Australia.

New Zealand specimens

The *strobila* of 20 specimens vary in length from 2·520 to 4·320 (mean 3·398 ± 0·5) mm. The segments are three or four in number, the penultimate one being sexually mature. The ratio of the length of the mature to that of the gravid segment

varies from 1 : 1·5 to 1 : 3·2 (mean 1 : 1·9). The gravid segment is 0·936 to 2·160 (mean 1·728) mm long and constitutes from 43·5 to 55·7 per cent (mean 48·9 per cent) of the total length.

The *genital pore* in the mature segment is 43·8 to 61·5 per cent (mean 57·5 per cent) of its length from the anterior margin; in the gravid segment this varies from 53·2 to 66·0 per cent (mean 58·5 per cent). The *testes* number 34 to 52 (mean 43·0 ± 4·7); those anterior to the genital pore 21 to 33 (mean 25·0 ± 2·8) and those posterior 11 to 25 (mean 18·0 ± 3·9). The *cirrus sac* in the mature segment is from 112·0 to 184·0 (mean 147·7 ± 24·4) microns long and 59·8 to 92·0 (mean 76·7 ± 24·4) microns wide; in the gravid segment 112·0 to 207·0 (mean 174·1 ± 25·9) microns by 59·8 to 92·0 (mean 77·7 ± 8·7) microns.

Australian specimens

The *strobila* of nine complete specimens varies in length from 2·520 to 7·200 (mean 4·078 ± 1·7) mm. It consists of three or four segments, the penultimate one being sexually mature. The ratio of the length of the mature to that of the gravid segment varies from 1 : 1·1 to 1 : 2·0 (mean 1 : 1·6). The gravid segment varies in length from 1·008 to 2·556 (mean 1·646) mm and constitutes from 30·0 to 48·3 per cent (mean 41·5 per cent) of the length of the strobila.

The *genital pore* in the mature segment is from 47·1 to 64·9 per cent (mean 56·2 per cent) of its length from the anterior margin; in the gravid segment this varies from 56·9 to 59·2 per cent (mean 58·1 per cent). The *testes* (18 specimens) vary in number from 40 to 60 (mean 50·8 ± 6·3); from 25 to 41 (mean 32·7 ± 4·5) anterior and 14 to 22 (mean 18·1 ± 2·5) posterior to the genital pore. The *cirrus sac* in 13 mature segments varies in length from 112·0 to 190·4 (mean 137·4 ± 26·1) microns and in width from 42·0 to 78·4 (mean 67·4 ± 10·4) microns; in three gravid segments from 168·0 to 207·0 (mean 183·5) microns by 64·4 to 96·6 (mean 84·3) microns.

Discussion

The above specimens tally well with the description of "*E. granulosus granulosus*" Sweatman & Williams (1963). As already pointed out the Australasian material cannot be considered the nominate subspecies hence it is proposed that the name be changed to *Echinococcus granulosus newzealandensis*.

Proposed revised diagnosis

Strobila three to five, usually four, segments. Penultimate or antepenultimate segment sexually mature. Genital pore just posterior to midpoint in mature, more posterior in gravid segment. Testes 34 to 70 in number, majority anterior to genital pore. Seminal receptacle large and round.

Host: Intermediate: Primarily domestic sheep, bovids and domestic pigs.
Definitive: Dog, dingo.

Type locality: New Zealand.

Plesiotype: USDA. Specimen No. 59723 (Sweatman & Williams, 1963).

Echinococcus multilocularis sibiricensis Rausch & Schiller, 1954

Prof. T. W. M. Cameron and Dr. R. Rausch kindly provided specimens from six dogs; specimens from three dogs were from experimental infestations.

The *strobila* in 86 specimens varies in length from 1·080 to 3·096 (mean 1·887 ± 0·6) mm. The number of segments in 75 specimens varies from three to five; 28·0 per cent consists of three, 69·3 per cent of four and 2·7 per cent of five, segments. The penultimate or antepenultimate segment is sexually mature. In the 41 days old specimens the penultimate segment is sexually mature in 95·5 per cent, in 62 and 73 days old specimens the antepenultimate segment is sexually mature in 80·0 and 94·8 per cent respectively. The ratio of the length of the mature to that of the gravid segment varies from 1: 1·2 to 1: 3·8 (mean 1: 1·6). The gravid segment varies in length from 0·324 to 1·152 (mean 738·0) mm and constitutes 22·0 to 46·0 per cent (mean 34·0 per cent) of the total length.

The *genital pore* in the mature segment is from 20·0 to 42·8 per cent (mean 34·2 per cent) of its length from the anterior margin; in the post-mature segment this varies from 20·8 to 47·6 per cent (mean 33·3 per cent) and in the gravid from 25·0 to 45·5 per cent (mean 33·8 per cent). The *testes* number from 12 to 22 (mean 17·4 ± 2·4); from 0 to 6 (mean 3·4 ± 1·7) anterior and from 9 to 19 (mean 14·0 ± 2·1) posterior to the genital pore. The *cirrus sac* in the mature segment varies in length from 50·4 to 109·2 (mean 74·0 ± 15·6) microns and in width from 28·0 to 56·0 (mean 40·1 + 8·2) microns; in the post-mature segment from 58·8 to 92·0 (mean 77·8 ± 8·7) microns by 32·2 to 61·6 (mean 42·5 ± 8·8) microns; in the gravid segment from 72·8 to 112·0 (mean 88·9 ± 15·4) microns by 36·4 to 50·4 (mean 44·1 ± 1·6) microns.

Discussion

The specimens studied agree with the description given by Vogel (1957) in the number and arrangement of the segments, the position of the genital pore and the structure of the ovary and the gravid uterus. They have fewer testes, 12 to 22, mean 17·4, but the range does not differ significantly from that given by Vogel, 14 to 31, mean 22. In this investigation the testes distribution was determined relative to the genital pore and not relative to the cirrus sac, as was done by Vogel, which accounts for the discrepancy in the number of testes anterior to the genital pore and cirrus sac. In the present investigation 0 to 6 (mean 3·4) are anterior to the genital pore while Vogel found 0 to 5 (mean 2·3) anterior to the cirrus sac.

Echinococcus oligarthrus (Diesing, 1863) Cameron, 1926

Prof. T. W. M. Cameron and Dr. R. J. Ortlepp each made two specimens of this species available for study in the present investigation.

The *strobila* of three specimens varies in length from 1·80 to 2·48 (mean 2·06) mm. There are three segments, the second being sexually mature. The ratio of the length of the mature to that of the gravid segment varies from 1: 1·9 to 1: 2·4 (mean 1: 2·1). The gravid segment varies in length from 0·90 to 1·26 (mean 1·07) mm; it constitutes from 50·0 to 54·7 per cent (mean 51·8 per cent) of the strobila length.

The *genital pore* in the mature segment is from 33·3 to 38·9 per cent (mean 35·2 per cent) of its length from the anterior margin; in the gravid segment this is from 40·0 to 43·3 per cent (mean 42·3 per cent). The *testes* (four specimens) number from 21 to 33 (mean 26·5); from 7 to 16 (mean 9·5) are anterior and from 12 to 23 (mean 17·0) posterior to the genital pore. The *cirrus sac* in the mature segment varies in length from 55·2 to 70·0 (mean 62·6) microns and in width from 36·8 to 39·2 (mean 38·0) microns; in three gravid segments it is 50·6 to 72·8 (mean 62·6) microns by 46·0 to 47·6 (mean 47·1) microns.

Discussion

The four specimens described above vary in their testes distribution. Three specimens with a total of 21 to 30 (mean 24·3) testes have seven to eight (mean 7·3) anterior and 13 to 23 (mean 17·0) posterior to the genital pore. One specimen has 33 with 16 anterior and 17 posterior. Three of these specimens therefore show the same type of distribution as does *E. multilocularis*, but they have more anterior to the genital pore than has *E. multilocularis*.

According to Cameron (1926) the genital pore is just anterior to the midpoint of the segment. Rausch & Nelson (1963) also found it anterior to the midpoint, but did not specify its exact position. In the above specimens it corresponds with that of *E. multilocularis* where it is well anterior to the midpoint.

The testes number and distribution together with the position of the genital pore suggest a close relationship between *E. oligarthrus* and *E. multilocularis*. Further, there seems to be resemblance between the two in their host preferences. *E. oligarthrus* has been recovered from felines only, while *E. multilocularis* utilizes fox, the domestic dog and the domestic cat. Cameron (1926) considered *E. cruzi* Brumpt & Joyeux (1924) from *Dasyprocta agouti* in Brazil conspecific with *E. oligarthrus* (Diesing, 1863), but this has not been proved experimentally.

Discussion

Diagnostic criteria

The reliability of the number and arrangement of the segments, the distribution and number of the testes and host specificity, as criteria in the taxonomy of *E. granulosus* have possibly been over-estimated. These criteria will only be conclusively validated if they prove constant in subsequent generations of all the strains, as they have been shown in Porcine II. It is on the basis of the above criteria that *E. granulosus* specimens from South African carnivores are placed into five subspecies; until these criteria are invalidated the separation of subspecies based on them must be accepted.

The criterion most suspect is the absence of testes posterior to the vitellaria. The specimens derived from the experimental infestation (Bovine II) show but little variation in this respect. Natural infestations of *E. g. felidis*, however, show more variation. Should subsequent generations of *E. g. ortleppi* show a similar variation, it would then have to be considered conspecific with *E. g. africanus* which consistently shows testes posterior to the vitellaria.

E. g. granulosus new designation may be separated from the other four subspecies described in this paper in that in it the testes are either equally distributed in the two halves of the segment, or the majority are in the posterior half, whereas in the rest the majority of the testes are in the anterior half. These four subspecies may be differentiated from each other either on other morphological criteria and/or on their host specificity. Thus, although *E. g. ortleppi* and *E. g. africanus* differ morphologically only in the presence or absence of testes posterior to the vitellaria, they also differ in host preferences; the domestic dog and the blackbacked jackal being equally susceptible to *E. g. ortleppi* with the domestic dog the less susceptible to *E. g. africanus*. *E. g. lycaontis* may be diagnosed on the number and arrangement of the segments, but also on its marked specificity to the Cape hunting dog. *E. g. felidis* may be diagnosed on the number of the segments and its marked host specificity for the lion in which it is common, usually being present in great numbers.

Geographical distribution

Sweatman & Williams (1963) are of the opinion that *E. g. newzealandensis* (their *E. g. granulosus*) is more or less cosmopolitan in its distribution. This subspecies as yet has not been found in South Africa. The only subspecies which proved common to Southern Africa and another continent, is the (new) nominate subspecies *E. g. granulosus* from Europe.

In South Africa the cystic stage of *E. g. granulosus* novum designation has to date only been recovered from pigs and man. The neotypes from the type locality are derived from hydatid cysts from pigs but it is not known whether in Europe other domestic livestock may not act as intermediate hosts. Batsch's (1786) record of *Hydatigena granulosa* from sheep suggests that they may do so; experimental proof, however, is still wanting. The maintenance of the subspecies in South Africa (a direct introduction from Europe?) is probably due to the ease with which the cycle between pigs and domestic dogs can be completed. Its maintenance through other channels is problematical The parasites from the Blackbacked jackal resulting from experimental infestations with scolices of human origin (Human strain, Part I) appear to develop extremely rapidly; at 35 days these parasites, besides being larger, contained almost mature ova; they were more advanced in their development than those of the same origin and age from the domestic dog. Similarly they developed more rapidly than did *E. g. africanus* and *E. g. ortleppi* examined at the same age. It is thus apparent that the blackbacked jackal would be a suitable host for *E. g. granulosus*. Were it to become infested it could be surmised that a sylvatic as well as an urban cycle could be established in South Africa. However, this is but a remote possibility in that pig and/or man are unlikely prey for this small carnivore.

E. g. africanus has been recovered from the Transvaal and the Orange Free State. The Cape hunting dog and the blackbacked jackal appear to be more suitable hosts for this parasite than is the domestic dog. The Cape hunting dog undoubtedly plays some role in its dissemination in the Transvaal, but the blackbacked jackal probably plays the more important role in its total dissemination. The wider distribution of *E. g. africanus* may also be due to its ability to utilize both cattle and sheep as intermediate host, whereas *E. g. ortleppi* apparently only utilizes cattle. Under natural conditions the blackbacked jackal rarely has access to cattle viscera but as it preys on sheep it can play a major role as a disseminator in sheep-rearing areas.

E. g. ortleppi has been recovered from the Transvaal only. As the domestic dog and the blackbacked jackal appear to be equally susceptible to infestation, it seems reasonable to assume that this subspecies also occurs in other parts of the country. The apparent restriction may be more apparent than real since almost all of the dogs examined were from the immediate vicinity of Pretoria. Should *E. g. ortleppi* prove to be restricted to the Transvaal this may be the consequence of its host preferences. Its cystic stage was collected from the Pretoria Abattoir from cattle, originating from the Transvaal Bushveld. This area, together with the Northern Cape, forms the main beef-rearing area of the country. If cattle were the preferred intermediate hosts possibly more widespread collections would show a greater recovery from the beef-rearing, than from purely dairying areas.

E. g. felidis and *E. g. lycaontis* do not occur south of the Transvaal, as their normal hosts, i.e. lions and Cape hunting dogs respectively, are absent from these regions. The lion and the Cape hunting dog, however, occur in parts of South West Africa and the adjacent Northern Cape; it is therefore possible that these two subspecies may yet be found in these areas.

Indigenous carnivores as disseminators of hydatidosis

In view of the host specificity shown by some of the subspecies of *E. granulosus*, and of the variety of the indigenous carnivores in South Africa, the relatively large number of subspecies recovered during this investigation is not wholly unexpected. North America also has a varied carnivore fauna from which *E. multilocularis* as well as two subspecies of *E. granulosus* (i.e. *E. g. borealis* and *E. g. canadensis*) have been recovered.

The domestic dog undoubtedly is the most important source of infestation of domestic livestock in this country. It is susceptible to infestation with *E. g. granulosus*, *E. g. africanus* and *E. g. ortleppi*. It is less susceptible to infestation with *E. g. africanus* than is the blackbacked jackal, but nevertheless is one of its disseminators. It probably plays a more important role than does the blackbacked jackal in the dissemination of *E. g. granulosus*. It does not appear to be a vector of any significance of *E. g. lycaontis*.

The domestic cat does not appear to be important in the dissemination of any of the South African subspecies. This finding must, however, be confirmed experimentally, as a small number of *E. g. africanus* have become patent in it. Further, a few specimens of *E. g. ortleppi* were recovered from a cat 35 days after infestation, but none subsequently.

The blackbacked jackal [*C.* (*T.*) *mesomelas*] is common and widespread throughout South Africa. It was proved a suitable host for *E. granulosus sensus latus* by Gough (1908) and Viljoen (1937). The present investigation also shows it to be a suitable host for *E. g. granulosus*, *E. g. africanus* and *E. g. ortleppi*; it undoubtedly plays an important role in infesting domestic livestock with hydatidosis. Its role as a vector of *E. g. granulosus* in Southern Africa is difficult to assess as the cystic stage of this parasite has so far only been recovered from pigs (and man) and under normal circumstances, this animal would not have access to pig viscera. Likewise under natural conditions the blackbacked jackal would rarely gain access to cattle viscera, and therefore probably can play but a small role in the dissemination of *E. g. ortleppi*. As it preys on sheep it plays a major role in the dissemination of *E. g. africanus* in sheep-rearing areas.

The Cape hunting dog, *Lycaon pictus*, formerly had a wide-spread distribution, but is now almost entirely restricted to two National Parks and adjacent areas. In these areas, i.e. the Transvaal Bushveld, Northern Cape and South West Africa, it would play a major role in the dissemination of *E. g. africanus* and *E. g. lycaontis*. Since Cape hunting dogs are not readily available it was not possible to determine experimentally the suitability of this carnivore as a host for *E. g. ortleppi* and *E. g. granulosus*.

The lion, *Panthera leo*, like the Cape hunting dog, formerly had a wide distribution, but is now restricted to the same areas as the Cape hunting dog. As no lions were available it was not possible to test them with any of the experimental strains; it is therefore not known whether this animal is susceptible to infestation with any subspecies other than *E. g. felidis*. The cystic stage of this parasite is unknown, but wild herbivora probably are its intermediate host. Hydatid cysts have been recovered from the blue wildebeest (*Gorgon taurinus*) and off the zebra (*Equus burchelli*) in the Caprivi Strip, South West Africa (Verster, 1962); both the lion and the Cape hunting dog occur in this area. It is thus possible that cysts may represent the cystic stage of either *E. g. felidis* and/or *E. g. lycaontis*. Lions and Cape hunting dogs from this area have not yet been examined for the sexual stage.

Numerous hydatid cysts were present in the liver of a warthog (*Phacochoerus aethiopicus*) from Northern Rhodesia (Verster, 1962); these cysts may represent the cystic stage of either *E. g. felidis* or *E. g. lycaontis* as both the lion and the Cape hunting dog are indigenous to Northern Rhodesia and there is a close association between these animals.

The silver fox, *Vulpes chama*, occurs in most parts of South Africa, but, unlike the blackbacked jackal, is comparatively rare. It is possible to infest these animals experimentally with *E. g. africanus*, but only a few parasites become established and their development is retarded. Further, as this animal does not prey on sheep, but primarily feeds on small mammals, it can but play a negligible role in the dissemination of hydatidosis of domestic livestock.

Cameron & Webster (1959) recorded *Echinococcus* sp. from an unidentified hyaena in East Africa; Nelson & Rausch (1963) recovered " *E. granulosus* " in Kenya from three of 19 spotted hyaenas (*Crocuta crocuta*). As yet no *E. granulosus* subspecies have been recovered from hyaenas in South Africa.

Echinococcus spp. have not yet been recovered from the side-striped jackal, *Canis* (*Thos*) *adustus* (Nelson and Rausch, 1963). This animal is mainly tropical, hence in South Africa restricted to the lowveld of the Transvaal. It is unlikely that it is a vector of any importance, as it mainly preys on small mammals, and further, in South Africa does not occur in sheep-rearing areas.

The bat-eared fox, *Otocyon megalotis*, has not yet been found infested with these parasites, but as it preys mainly on small rodents and large insects, it is unlikely to be exposed to infestation by any of the presently known South African subspecies.

The aard wolf, *Proteles cristatus*, also is not likely to be incriminated as a vector as it feeds mainly on termites. An attempt to infest this animal with *Echinococcus* sp. proved unsuccessful whereas the same material fed to a dog proved to be viable (Verster, 1964).

Nelson & Rausch (1963) concluded that " the main cycle of transmission in Kenya is between dog and domestic livestock ", and that cycles involving wild carnivores and herbivores are relatively unimportant. These investigations have shown that in South Africa, however, wild carnivores are important vectors. The blackbacked jackal may play but a suborinate role to the dog in the dissemination of these parasites, yet it is an important source of infestation to domestic livestock. The Cape hunting dog with a restricted distribution, is of lesser importance. Should *E. g. felidis* prove capable of utilizing domestic livestock as intermediate hosts, then the lion still would not be an important vector as, like the Cape hunting dog, it has but a restricted distribution.

Indigenous herbivores as disseminators of echinococcosis

In South Africa domestic livestock are undoubtedly the most important disseminators of echinococcosis, their relative importance probably varying in the different regions. In restricted areas wild herbivores are probably important. As the size of the rostellar hooks cannot be used for specific identification, the various herbivores cannot be related to the subspecies of the parasite. For example, *E. g. ortleppi* has cystic hooks of the same size as has *E. g. granulosus* of porcine origin and the mean of these differs from that of *E. g. africanus* by only 3 microns.

At present it is impossible directly to assess the role of wild herbivores in the life-cycle of the subspecies of *E. granulosus*. The blue wildebeest, the zebra and the warthog are all incriminated by single records of cysts in South Africa (Verster, 1962). Nelson & Rausch (1963) found one blue wildebeest infested in Kenya.

The impala (*Aepyceros melampus*) constitutes 85 per cent of the prey of the Cape hunting dog (Bourliére, 1963) and 22·9 per cent of that of the lion (Brynaard & Pienaar, 1960). However, to date no hydatid cysts have been found in them in a very large sample of records (Pienaar, 1964). Between 550 and 600 impala are killed annually for game management purposes in the Kruger National Park, but no hydatid cysts have been found to date.

According to Brynaard & Pienaar (1960) the blue wildebeest is the most important prey of the lion, constituting 25 per cent of the kills made by them in the Kruger National Park. The zebra constitutes 13 per cent. Despite the fact that the records of hydatid cysts in these two herbivores are from as far afield as the Caprivi Strip, it seems reasonable to assume that the records are representative for South Africa as a whole and that hence one and/or the other is the source of infestation of *E. g. felidis* in the lion.

The only record of an intermediate host of *E.g. lycaontis* is the experimental infestation with cysts from sheep; however, it is possible that the cystic stage also occurs in wild herbivores. The feeding habits of the Cape hunting dog are not as well known as are those of the lion. However, like the lion, the Cape hunting dog *inter alia* preys on blue wildebeest, zebra and warthog.

The smaller antelopes such as steenbuck and duiker are preyed on by both the Cape hunting dog and the ubiquitous blackbacked jackal. These small herbivores, unlike the blue wildebeest and zebras, are not restricted to National Parks, Game Reserves and Game farms, but still occur randomly on many farms throughout Southern Africa. Should they prove suitable intermediate hosts, they would be important sources of infestation to carnivores.

The warthog, preyed upon by both the lion and the Cape hunting dog, although restricted to the Transvaal, to parts of the Northern Cape and South West Africa may prove to be an important source of infestation of these two wild carnivores.

The present state of our knowledge of the validity of the morphological criteria, of host specificity and of geographical distribution, either as seen in naturally acquired burdens, or in experimental infestations, opens up a wide field for further research. It is obvious that further work must be done on the validity of morphological criteria in subsequent generations, on the host preferences of the cystic as well as the adult stage of the different subspecies, on the serological differences, if any, between the subspecies and on the geographical distribution of the subspecies.

SUMMARY

1. The nominate subspecies of *E. granulosus* (Batsch, 1786) is redesignated from the type locality, Europe.
2. Five subspecies of *E. granulosus* are described from South African carnivores: *E. g. granulosus*, *E. g. africanus*, *E. g. felidis*, *E. g. lycaontis* and *E. g. ortleppi*.
3. *E. g. granulosus* has so far only been recovered from the Transvaal; *E. g. ortleppi* appears to be restricted to the Transvaal; *E. g. africanus* occurs in the Orange Free State and the Transvaal; *E. g. lycaontis* and *E. g. felidis* like their definitive hosts are restricted to the Transvaal.

4. The domestic dog appears to be the most important source of infestation to domestic livestock.

5. Wild carnivores are important disseminators in various parts of the country; the blackbacked jackal is probably as important as is the domestic dog in sheep-rearing areas; the lion and the Cape hunting dog are of importance in restricted areas only; while the importance of the silver fox is negligible.

6. Domestic livestock are the most important source of infestation to carnivores. The role of wild herbivores as disseminators is not known, but they are probably of importance only in restricted areas.

Acknowledgements

I would like to thank the research workers and institutions that gave me such generous assistance. In particular I would like to acknowledge the following:—

Comparative material was placed at my disposal by:—

Prof. T. W. M. Cameron, Canada; Dr. R. L. Rausch, Alaska; Dr. R. F. Riek, Australia; Dr. H. H. Roth, Southern Rhodesia; Prof. H. Vogel, Germany; Dr. L. Whitten, New Zealand.

Infestive material was made available by:—

Dr. C. G. Crocker, Pretoria (Human strain) and the authorities of the Johannesburg and Pretoria Municipal Abattoirs.

Carnivores for these experiments were made available by:—

The Director, National Zoological Gardens, Pretoria, and the Director of Nature Conservation, Transvaal.

Information regarding the distribution and habits of wild carnivores from:—

Dr. N. J. van der Merwe, National Parks Board.

Advice regarding the procedure in taxonomy by:—

Drs. G. van Sonn, and L. Vári of the Transvaal Museum.

Translation of articles by:—

Dr. Rayski and Dr. Gertrud Theiler.

Advice regarding the statistical analysis by:—

Messrs. C. M. Havenga, J. P. van Dyk and J. S. du Plessis of the Department of Agriculture Technical Services.

The encouragement of my promoters, Dr. Gertrud Theiler and the late Dr. R. J. Ortlepp.

The able technical assistance and overtime put in by:—

Miss Marie Collins, Mrs. M. Prinsloo and Mr. Johann Louw.

The typing of the manuscript, partly outside office hours, by:—

Miss Corrie van Rooyen.

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TABLE 1.—*Experimental design*

Strain	Bovine		Ovine		Porcine			Human
Age of infestation in days	I	II	I	II	I	II 1st Generation	II 2nd Generation	
35		Dog *C.* (*T.*) *mesom.* Cat		Dog *C.* (*T.*) *mesom.* Cat				Dog *C.* (*T.*) *mesom.*
48	*L. pictus* *L. pictus* *C. dingo* Dog Dog *V. chama* *V. chama* Cat* Cat*		*L. pictus* *L. pictus* *L. pictus* *C. dingo* Dog Dog *V. chama* *V. chama* Cat* Cat*		Dog Dog	Dog	Dog *C.* (*T.*) *mesom.*	
60					Dog			
76		Dog *C.* (*T.*) *mesom.* Cat		Dog *C.* (*T.*) *mesom.* Cat		Dog *C.* (*T.*) *mesom.*		Dog *C.* (*T*) *mesom.*
95		Dog *C.* (*T.*) *mesom.* Cat		Dog *C.*(*T.*)*mesom.*† Cat		Dog	Dog *C.* (*T.*) *mesom.*	
109					Dog			
118		Dog *C.* (*T.*) *mesom.* Cat		Dog *C.* (*T.*) *mesom.*		Dog		
135		Dog *C.* (*T.*) *mesom.*			Dog	Dog		

Lycaon pictus: Cape hunting dog
Canis dingo: Dingo of Australia
Vulpes chama: Silver fox
Canis (*Thos*) *mesomelas:* Blackbacked jackal

* Half the number of scolices given the other animals.
† Accidentally overdosed

TABLE 3.—*Size of cystic hooks* (in microns)

(*a*) *Large hooks*

Strain	No.	Total Length, BE		Dorsal Blade Length, CE		Ventral Blade Length, DE		Handle Length, BC	
		Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.
Bovine II............	100	27·1–32·6	29·4±1·2	21·5–29·0	25·7±1·3	12·1–16·8	14·2±0·9	1·8–6·2	3·7±0·8
Ovine II.............	100	21·5–39·3	26·3±1·5	18·6–27·4	23·3±1·3	9·8–15·1	13·2±1·1	1·3–6·3	3·1±1·0
Porcine I............	50	27·3–32·1	29·6±1·1	22·6–28·8	25·4±1·5	12·7–15·7	14·3±0·7	2·1–7·1	4·2±1·0
Porcine II, 1st Gen....	50	27·0–31·6	29·3±1·3	19·2–26·8	24·0±1·5	12·0–15·9	14·3±0·8	4·2–7·6	5·3±0·8
Porcine II, 2nd Gen...	50	25·1–33·2	29·8±1·3	18·6–28·3	24·0±1·7	12·5–16·4	14·4±0·9	3·4–7·7	5·8±1·1
Human...............	50	25·4–29·3	27·4±1·0	21·2–25·5	23·3±1·2	11·8–15·0	13·3±0·8	2·7–6·6	4·1±0·8

(*b*) *Small hooks*

Strain	No.	Total Length, BE		Dorsal Blade Length, CE		Ventral Blade Length, DE		Handle Length, BC	
		Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.
Bovine II............	50	22·5–28·3	25·4±1·5	16·9–23·2	19·6±1·6	8·4–11·9	10·2±0·8	3·5–7·4	5·8±1·1
Ovine II.............	47	19·4–26·5	22·8±1·4	13·7–21·8	18·6±1·8	7·6–11·9	9·5±1·0	2·0–9·1	4·2±1·6
Porcine I............	25	16·9–27·6	24·5±2·3	13·9–23·2	18·9±2·3	7·8–12·6	10·4±1·0	1·8–9·3	5·6±1·5
Porcine II. 1st Gen....	25	22·5–26·9	25·5±1·1	15·0–20·4	18·0±1·2	9·6–12·2	10·8±0·7	5·5–9·5	7·5±1·1
Porcine II, 2nd Gen...	25	18·3–28·2	26·1±1·9	15·5–20·9	18·4±1·5	9·1–11·9	11·0±0·6	2·3–12·0	7·7±1·9
Human...............	20	19·6–25·7	23·2±1·5	15·3–21·0	17·8±1·5	8·7–10·8	9·9±0·6	3·4–7·1	5·5±1·1

TABLE 4.—*Total length of large hooks* (in microns)

Strain	Age	Host	No.	B to E		A to F	
				Range	Mean ± S.D.	Range	Mean ± S.D.
Bovine I	48	*L. pictus*, 1	50	34·2–45·2	39·6±2·4	34·9–46·9	41·2±2·4
		L. pictus, 2	50	37·2–46·3	39·7±2·1	38·8–47·4	41·1±2·1
		C. dingo	50	34·1–40·1	36·4±1·1	35·0–39·4	37·6±0·9
		Dog	50	32·1–38·9	36·0±1·8	34·2–40·6	37·6±1·5
Bovine II	35	Dog	50	33·5–41·5	37·2±1·8	35·0–42·7	39·4±1·7
		C. (*T.*) *mesomelas*	50	32·1–40·2	36·9±2·0	35·7–42·2	38·9±1·7
	76	Dog	50	33·9–44·1	38·8±2·4	37·5–47·0	42·1±2·4
		C. (*T.*) *mesomelas*	50	37·3–46·3	40·2±1·9	40·2–49·4	43·7±2·2
	118	Dog	50	36·6–44·3	39·6±1·7	39·4–47·7	43·0±1·9
		C. (*T.*) *mesomelas*	50	36·2–42·9	39·9±1·8	38·1–46·5	42·3±2·2
	135	Dog	50	36·4–43·7	40·7±2·2	39·9–46·6	43·5±2·1
		C. (*T.*) *mesomelas*	50	34·3–42·8	39·9±1·7	40·7–47·4	44·0±1·8
Ovine I	48	*L. pictus*, 1	50	33·4–41·1	37·2±2·0	34·1–42·4	38·8±1·7
		L. pictus, 2	50	31·0–42·8	37·0±2·4	34·6–44·2	39·2±2·3
Ovine II	35	Dog	50	29·3–34·7	32·2±1·4	33·1–39·9	35·2±1·5
		C. (*T.*) *mesomelas*	50	29·6–35·3	32·8±1·7	31·0–38·5	35·6±1·6
	76	Dog	50	30·7–38·5	34·4±1·9	33·2–40·8	37·3±1·9
		C. (*T.*) *mesomelas*	50	31·9–37·9	35·0±1·7	35·3–41·4	38·5±1·5
	95	Dog	50	30·3–38·5	34·2±1·9	34·2–42·0	38·2±1·9
		C. (*T.*) *mesomelas*	50	28·2–41·0	35·0±2·5	32·1–42·1	38·5±3·2
	118	*C.* (*T.*) *mesomelas*	50	31·2–39·6	35·7±1·7	34·8–42·7	39·1±1·8
Porcine I	48	Dog	50	34·5–40·3	37·8±1·4	36·0–42·8	39·9±1·3
	60	Dog	50	32·5–40·6	36·5±2·0	33·7–43·7	38·5±2·3
	109	Dog	50	32·5–40·1	36·3±1·5	35·4–42·4	39·0±1·4
	135	Dog	50	30·4–39·0	35·9±1·8	33·1–42·2	38·8±1·6
Porcine II 1st Generation	48	Dog	50	32·1–38·9	35·7±1·5	35·0–41·4	38·7±1·5
	76	Dog	50	30·4–39·2	35·3±1·5	33·3–41·0	38·7±1·6
		C. (*T.*) *mesomelas*	50	32·5–39·2	36·1±1·6	34·4–42·2	39·0±1·9
	95	Dog	50	34·2–39·6	36·7±1·4	34·0–42·6	38·9±1·6
	118	Dog	50	31·4–39·5	35·9±2·2	34·1–42·9	38·7±2·0
	135	Dog	50	34·1–39·0	37·1±1·1	37·8–42·0	40·0±1·0
Porcine II 2nd Generation	48	Dog	50	37·4–43·4	40·4±1·6	38·4–46·2	42·1±1·4
		C. (*T.*) *mesomelas*	36	34·9–41·3	37·4±1·8	36·0–42·4	39·2±1·9
	95	Dog	50	37·4–44·0	40·7±1·9	40·3–45·8	42·7±1·0
		C. (*T.*) *mesomelas*	19	35·3–40·2	37·8±1·4	37·0–42·0	39·5±0·9
Human	35	*C.* (*T.*) *mesomelas*	50	30·0–39·2	35·1±2·3	31·8–40·5	35·6±1·8
	76	Dog	37	30·9–38·0	34·5±1·9	32·3–39·6	36·1±1·9
		C. (*T.*) *mesomelas*	50	35·1–42·9	38·5±2·2	37·4–44·9	40·4±2·1

TABLE 5.—*Dorsal and ventral blade length of large hooks* (in microns)

Strain	Age	Host	No.	Dorsal Blade Length (CE)		Ventral Blade Length (DE)		Handle Length (BC)	
				Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.
Bovine I	48	*L. pictus*, 1	50	23·1–29·6	26·1±1·3	12·8–16·7	14·6±0·9	8·0–16·3	13·5±1·9
		L. pictus, 2	50	22·7–29·8	26·0±1·3	12·1–16·2	14·5±0·9	10·6–17·2	13·8±1·7
		C. dingo	50	22·9–28·8	25·7±1·2	12·9–15·6	14·4±0·5	8·5–13·1	10·7±1·1
		Dog	50	23·3–28·2	25·6±1·0	11·7–15·3	14·0±0·8	6·6–12·9	10·5±1·5
Bovine II	35	Dog	50	22·4–29·6	26·3±1·5	13·0–16·6	14·8±0·8	7·3–13·1	10·9±1·5
		C. (T.) mesomelas	50	22·1–28·9	26·2±2·1	12·8–16·0	14·7±0·8	7·4–13·7	10·8±1·7
	76	Dog	50	23·2–29·1	26·6±1·5	12·8–16·6	14·7±0·8	8·1–16·7	12·3±2·0
		C. (T.) mesomelas	50	23·2–29·4	26·2±1·3	13·1–16·2	14·9±0·7	11·2–18·6	14·1±1·6
	118	Dog	50	24·4–31·4	26·6±1·8	12·6–16·5	14·8±0·7	10·2–15·8	13·0±1·2
		C. (T.) mesomelas	50	23·4–28·2	26·1±1·0	13·2–16·1	14·7±0·7	10·3–16·6	13·8±1·5
	135	Dog	50	23·3–28·9	26·5±1·4	12·7–15·9	14·6±0·7	10·4–16·6	14·2±1·5
		C. (T.) mesomelas	50	22·1–28·3	25·9±1·3	12·6–16·7	14·7±0·7	11·2–16·9	13·9±1·2
Ovine I	48	*L. pictus*, 1	50	21·5–28·7	24·8±1·7	12·4–15·8	14·3±0·9	6·9–15·5	12·3±1·7
		L. pictus, 2	50	20·4–29·5	24·2±1·8	11·5–15·8	13·7±1·0	9·2–17·4	12·8±1·6
Ovine II	35	Dog	50	20·4–25·7	23·4±1·5	11·7–14·4	13·4±0·6	6·4–11·9	8·8±1·1
		C. (T.) mesomelas	50	20·6–28·9	24·3±1·9	12·3–15·4	13·7±0·8	6·2–12·6	8·5±1·6
	76	Dog	50	20·8–26·9	23·2±1·4	11·8–15·1	13·5±0·7	7·7–13·3	10·5±1·6
		C. (T.) mesomelas	50	21·3–28·6	24·1±1·7	11·2–16·2	13·6±1·0	5·8–12·7	10·1±1·4
	95	Dog	50	19·6–26·9	23·9±1·6	12·0–14·6	13·8±1·0	7·9–14·0	10·4±1·4
		C. (T.) mesomelas	50	19·4–26·6	24·9±1·8	11·5–15·7	13·7±1·0	7·6–15·3	11·0±1·8
	118	*C. (T.) mesomelas*	50	22·5–26·8	24·7±0·8	11·7–15·1	13·7±0·8	8·3–14·0	11·1±1·4
Porcine I	48	Dog	50	20·9–30·6	25·7±1·5	13·0–16·2	14·9±0·6	8·6–14·4	12·1±1·5
	60	Dog	50	23·6–28·6	25·6±1·2	12·6–16·2	14·8±0·8	7·3–13·7	10·9±1·7
	109	Dog	50	22·3–27·8	25·5±1·3	13·9–16·5	15·0±0·6	7·4–15·6	10·9±1·5
	135	Dog	50	20·9–28·1	24·9±1·6	12·2–16·2	14·8±0·9	7·6–13·4	10·9±1·1
Porcine II 1st Generation	48	Dog	50	22·7–28·0	25·4±1·5	12·9–16·2	14·7±0·9	7·3–13·3	10·4±1·4
	76	Dog	50	21·0–28·0	24·6±1·7	12·4–15·1	14·2±0·8	8·6–13·5	10·7±1·3
		C. (T.) mesomelas	50	22·9–27·3	24·9±1·2	13·5–16·1	14·7±0·7	8·3–14·4	11·2±1·2
	95	Dog	50	22·7–27·5	24·8±1·1	13·3–16·0	14·8±0·8	9·8–13·8	11·9±1·1
	118	Dog	50	19·7–28·2	24·5±1·9	12·4–16·0	14·5±0·9	8·9–15·3	11·4±1·6
	135	Dog	50	22·4–27·6	25·2±1·0	12·8–16·2	14·7±0·8	9·7–13·6	11·8±0·9
Porcine II 2nd Generation	48	Dog	50	23·5–28·7	26·1±1·2	14·0–16·9	15·3±0·7	11·6–17·8	14·3±1·5
		C. (T.) mesomelas	36	24·0–28·0	25·6±1·0	14·4–16·9	15·4±0·6	9·1–14·3	11·7±1·1
	95	Dog	50	23·2–29·6	26·0±1·3	12·9–16·2	14·9±0·7	11·8–17·4	14·5±1·2
		C. (T.) mesomelas	19	23·0–28·9	25·9±1·5	13·4–16·5	15·0±0·9	10·5–14·0	11·9±1·0
Human	35	*C. (T.) mesomelas*	50	21·2–26·1	23·8±1·3	11·8–15·4	13·4±0·7	7·8–14·8	11·3±2·0
	76	Dog	37	21·5–27·9	24·5±1·4	12·0–15·4	13·7±0·9	7·6–13·5	10·1±1·3
		C. (T.) mesomesla	50	22·7–27·1	24·8±1·2	12·1–14·7	14·7±0·6	10·4–17·4	13·7±1·9

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TABLE 6.—*Total length of small hooks* (in microns)

Strain	Age	Host	No.	Length, BE		Length, AF	
				Range	Mean ± S.D.	Range	Mean ± S.D.
Bovine I	48	*L. pictus*, 1	19	21·8–37·7	30·8±3·6	22·8–39·1	32·4±3·8
		L. pictus, 2	15	22·8–33·5	29·1±2·7	23·8–34·3	30·6±3·0
		C. dingo	14	24·7–31·8	27·8±2·4	26·4–32·7	29·0±2·3
		Dog	13	23·8–30·3	27·3±2·2	24·7–32·2	28·7±2·5
Bovine II	35	Dog	17	23·7–36·3	30·3±3·2	25·4–34·8	30·6±2·4
		C. (T.) mesomelas	13	23·9–31·5	28·3±2·6	34·7–27·7	31·7±2·8
	76	Dog	16	26·8–37·6	31·3±2·8	29·3–41·1	34·0±3·3
		C. (T.) mesomelas	20	23·7–37·2	28·8±3·8	22·5–36·6	31·0±3·6
	118	Dog	15	22·2–34·8	30·0±4·5	23·6–36·6	31·1±4·2
		C. (T.) mesomelas	13	25·5–35·7	30·9±3·7	24·8–38·8	33·5±4·5
	135	Dog	20	20·3–37·3	29·5±4·7	25·9–36·8	32·7±3·2
		C. (T.) mesomelas	13	27·1–33·8	30·7±2·5	27·1–38·8	33·0±3·8
Ovine I	48	*L. pictus*, 1	15	22·9–35·3	30·0±3·7	26·5–35·7	31·8±3·1
		L. pictus, 2	13	23·4–31·2	28·4±3·1	25·2–34·0	30·3±3·5
Ovine II	35	Dog	14	22·9–27·9	25·5±1·6	24·2–32·7	28·9±1·9
		C. (T.) mesomelas	18	24·5–30·6	27·6±1·5	26·0–32·1	29·9±1·7
	76	Dog	12	22·3–31·8	26·9±2·7	24·3–35·3	30·6±3·6
		C. (T.) mesomelas	10	21·9–30·7	28·0±2·8	23·6–34·3	30·3±3·7
	95	Dog	13	22·5–34·0	26·1±3·3	25·0–36·4	30·3±3·3
		C. (T.) mesomelas	13	26·1–33·9	29·8±3·8	25·2–37·9	32·4±3·6
	118	Dog	11	24·1–30·1	27·5±2·6	26·6–34·5	31·6±2·6
Porcine I	48	Dog	15	25·7–35·9	29·9±2·9	26·2–32·6	30·6±1·9
	60	Dog	9	24·7–32·2	28·4±2·6	26·3–32·2	28·8±2·0
	109	Dog	8	23·3–29·6	26·4±1·9	23·4–33·2	29·1±3·6
	135	Dog	10	22·0–30·3	27·8±3·2	25·7–34·7	29·9±2·9
Porcine II 1st Generation	48	Dog	9	27·1–34·7	29·7±3·2	27·6–35·8	31·4±3·2
	76	Dog	10	22·9–29·2	26·1±2·2	26·7–32·4	30·0±2·2
		C. (T.) mesomelas	11	26·9–32·1	29·5±1·8	27·1–35·4	30·5±3·1
	95	Dog	10	25·9–31·4	28·4±1·7	28·6–34·6	32·6±2·0
	118	Dog	9	23·8–31·9	27·5±3·0	25·4–36·2	30·1±4·3
	135	Dog	12	24·1–34·2	29·2±3·3	28·3–35·9	32·2±2·3
Porcine II 2nd Generation	48	Dog	7	21·9–35·4	31·4±4·4	23·6–36·4	33·6±4·5
		C. (T.) mesomelas	9	28·3–31·0	30·5±1·6	30·0–35·4	32·4±1·8
	76	Dog	8	29·6–38·8	34·5±3·2	33·0–39·1	36·4±1·9
		C. (T.) mesomelas	5	27·1–33·5	31·3±2·6	29·3–36·3	33·9±2·9
Human	35	*C. (T.) mesomelas*	16	23·1–30·9	27·0±2·5	25·0–32·0	28·2±2·4
	76	Dog	14	22·9–31·0	25·7±2·5	22·9–33·5	27·4±3·0
		C. (T.) mesomelas	18	22·2–32·8	29·0±1·0	25·6–34·4	30·5±3·2

TABLE 7.—*Dorsal and ventral blade and handle lengths of small hooks* (in microns)

Strain	Age	Host	No.	Dorsal Blade Length (CE)		Ventral Blade Length (DE)		Handle Length (BC)	
				Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.
Bovine I	48	*L. pictus*, 1	19	15·4–23·9	18·8±2·0	9·5–12·3	10·9±0·8	4·1–16·8	12·1±3·4
		L. pictus, 2	15	16·9–21·8	18·8±1·6	9·8–11·5	10·6±0·6	5·0–15·5	10·3±2·9
		C. dingo	14	16·6–22·6	19·0±1·9	9·8–13·4	11·0±0·8	6·2–11·7	8·7±1·9
		Dog	13	16·0–20·6	18·8±1·2	9·3–11·3	10·5±0·7	5·0–11·9	8·5±2·5
Bovine II	35	Dog	17	15·2–25·4	19·8±2·3	9·1–13·7	10·7±1·1	8·4–14·0	10·6±1·6
		C. (T.) mesomelas	13	18·1–20·2	19·1±0·9	9·4–11·7	10·8±0·7	5·5–11·7	9·1±2·4
	76	Dog	16	15·9–21·0	18·7±1·4	8·8–11·5	10·7±0·7	8·3–16·0	12·6±2·8
		C. (T.) mesomelas	20	14·5–22·4	18·8±1·9	9·4–11·9	10·6±0·7	5·8–15·8	10·0±2·7
	118	Dog	15	15·1–25·2	19·3±2·9	8·8–12·0	10·4±0·9	6·5–14·5	10·7±2·6
		C. (T.) mesomelas	13	15·4–22·2	18·7±1·8	9·2–12·2	10·8±0·9	5·8–16·7	12·1±3·1
	135	Dog	20	12·1–20·7	17·7±2·1	9·3–11·8	10·6±0·6	5·0–16·7	11·7±3·4
		C. (T.) mesomelas	13	15·7–20·8	18·4±1·7	10·4–11·6	10·9±0·5	9·4–16·3	12·2±2·2
Ovine I	48	*L. pictus*, 1	15	14·1–21·1	17·8±2·2	8·6–11·6	10·4±1·0	5·5–15·6	12·1±3·2
		L. pictus, 2	13	14·0–17·9	16·3±1·3	8·4–10·8	9·8±1·0	7·1–16·5	12·1±2·6
Ovine II	35	Dog	14	13·7–19·5	16·7±1·8	8·1–10·5	9·3±0·7	5·6–11·7	8·8±1·1
		C. (T.) mesomelas	18	15·9–22·1	18·3±1·7	8·7–11·0	9·6±0·6	7·4–11·7	9·3±1·2
	76	Dog	12	14·4–22·4	17·3±2·9	8·2–10·8	9·4±0·9	6·8–12·1	9·6±1·8
		C. (T.) mesomelas	10	17·2–22·0	19·5±1·6	7·9–11·4	9·9±1·0	3·6–11·2	8·3±2·2
	95	Dog	13	15·4–24·7	18·1±2·6	9·1–13·0	10·0±1·1	6·8–13·0	8·9±1·9
		C. (T.) mesomelas	13	14·7–22·5	20·3±2·5	7·6–11·0	10·0±1·1	5·6–12·8	9·5±2·3
	118	*C. (T.) mesomelas*	11	14·4–22·5	17·8±2·6	7·6–12·9	9·7±1·6	7·6–13·3	9·8±1·7
Porcine I	48	Dog	15	17·2–23·5	19·7±2·1	10·1–13·3	11·6±0·9	7·8–13·7	10·2±1·6
	60	Dog	9	16·9–19·0	17·9±0·8	10·4–11·4	10·9±0·4	7·7–15·1	10·5±2·6
	109	Dog	8	14·9–19·2	17·3±1·3	9·9–12·5	10·9±0·8	6·6–12·0	8·9±1·7
	135	Dog	10	12·5–19·8	17·2±2·2	9·5–11·5	10·6±0·7	7·9–13·3	10·7±2·0
Porcine II 1st Generation	48	Dog	9	16·3–22·0	19·3±2·0	10·0–13·9	11·5±1·3	7·5–13·7	10·5±2·1
	76	Dog	10	15·3–19·7	18·0±1·2	9·5–11·6	11·0±0·2	6·2–10·4	8·0±1·8
		C. (T.) mesomelas	11	16·4–21·5	18·3±1·5	9·4–12·2	10·9±0·9	8·5–14·4	11·3±1·6
	95	Dog	10	15·5–20·7	18·2±1·4	9·6–11·8	11·0±0·7	6·9–13·9	10·2±2·2
	118	Dog	9	16·0–20·5	18·1±1·4	10·1–12·0	11·1±0·6	6·4–13·4	9·4±2·0
	135	Dog	12	15·8–20·3	17·9±1·1	9·2–11·9	10·7±0·8	6·9–15·9	11·4±2·9
Porcine II 2nd Generation	48	Dog	7	17·7–21·1	19·7±1·2	11·0–12·3	11·8±0·5	12·3–15·3	13·1±1·6
		C. (T.) mesomelas	9	17·3–21·3	19·0±1·2	10·8–12·3	11·6±0·6	9·2–13·1	11·6±1·3
	76	Dog	8	17·6–22·9	19·6±1·7	10·4–13·3	11·6±1·0	12·0–17·9	15·0±2·0
		C. (T.) mesomelas	5	19·3–20·2	19·7±0·1	10·9–12·7	11·9±0·7	7·4–13·4	11·5±2·3
Human	35	*C. (T.) mesomelas*	16	14·6–18·4	16·7±1·0	9·0–11·1	10·0±0·7	6·2–14·4	10·0±2·5
	76	Dog	14	16·5–23·2	18·6±1·9	9·7–10·6	10·1±0·4	3·7–10·5	7·2±1·9
		C. (T.) mesomelas	18	15·3–21·8	17·5±1·8	9·1–11·7	10·2±0·7	5·7–16·2	11·6±2·8

TABLE 8.—*Summary of total length of hooks* (in microns)

(*a*) *Large hook*

Strain	No.	BE		AF	
		Range	Mean±S.D.	Range	Mean±S.D.
Bovine I	200	32·1—46·3	37·9±2·6	34·2—47·4	39·4±2·5
Bovine II	400	32·1—46·3	39·2±2·3	35·0—49·4	42·1±2·7
Ovine I	100	31·0—42·8	37·1±2·2	34·1—44·2	39·0±2·0
Ovine II	350	28·2—41·0	34·2±2·2	31·0—42·7	37·5±2·4
Porcine I	200	30·4—40·6	36·6±1·8	33·1—43·7	39·1±1·8
Porcine II	300	30·4—39·6	36·1±1·8	33·3—42·9	39·0±1·7
2nd Generation	155	34·9—43·4	39·5±2·1	36·0—46·2	41·3±2·0
Human	137	30·0—42·9	36·2±2·3	31·8—44·9	37·8±2·8

(*b*) *Small hook*

Strain	No.	BE		AF	
		Range	Mean±S.D.	Range	Mean±S.D.
Bovine I	61	21·8—37·7	30·0±3·1	22·8—39·1	30·4±3·3
Bovine II	127	20·3—37·6	29·9±3·7	22·5—38·8	32·1±3·6
Ovine I	28	22·9—35·3	29·3±3·5	25·2—35·7	31·1±3·4
Ovine II	91	22·3—34·0	27·3±2·9	23·6—37·9	30·5±3·9
Porcine I	42	22·0—35·9	28·4±3·0	23·4—34·7	29·8±2·6
Porcine II	61	22·9—34·7	28·4±2·8	25·4—36·2	31·2±3·0
2nd Generation	29	21·9—38·8	32·0±3·4	23·6—39·1	34·0±3·1
Human	48	22·2—32·8	27·4±3·0	22·9—34·4	28·8±3·1

TABLE 9.—*Summary of dorsal and ventral blade and handle length* (in microns)

(a) Large hook

Strain	No.	Dorsal Blade Length		Ventral Blade Length		Handle Length	
		Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.
Bovine I	200	22·7–29·8	25·8±1·2	11·7–16·7	14·4±0·8	6·6–17·2	12·1±2·2
Bovine II	400	22·1–31·4	26·3±1·4	12·6–16·7	12·6±0·7	7·3–18·6	12·9±1·9
Ovine I	100	20·4–29·5	24·5±1·8	11·5–15·8	14·0±1·0	6·9–17·4	12·6±1·7
Ovine II	350	19·4–28·9	24·2±1·6	11·2–16·2	13·6±0·9	5·8–15·3	10·1±1·7
Porcine I	200	20·9–30·6	25·4±1·4	12·2–16·5	14·9±0·7	7·3–15·6	11·2±1·5
Porcine II	300	19·7–28·2	24·9±2·3	12·4–16·2	14·6±0·8	7·3–15·3	11·2±1·4
2nd Generation	155	23·0–29·6	26·0±1·3	12·9–16·9	15·2±0·7	9·1–17·8	13·5±1·8
Human	137	21·2–27·9	24·3±1·5	11·8–15·4	13·6±0·7	7·6–10·4	11·8±2·3

(b) Small hook

Strain	No.	Dorsal Blade Length		Ventral Blade Length		Handle Length	
		Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.
Bovine I	61	15·4–23·9	18·8±1·6	9·3–13·4	10·8±0·8	4·1–16·8	10·1±3·1
Bovine II	127	12·1–25·4	18·8±2·0	8·8–13·7	10·7±0·8	5·0–16·7	11·1±2·8
Ovine I	28	14·0–21·1	17·1±2·0	8·4–11·6	10·1±1·0	5·5–16·5	12·1±2·9
Ovine II	91	13·7–24·7	18·3±2·5	7·6–13·0	9·7±1·0	3·6–13·3	9·2±1·8
Porcine I	42	12·5–23·5	18·3±2·1	9·5–13·3	11·1±0·8	6·6–15·1	10·2±2·0
Porcine II	61	15·3–22·0	18·3±1·4	9·2–13·9	11·0±0·8	6·2–15·9	10·2±2·4
2nd Generation	29	17·3–22·9	19·5±1·3	10·4–13·3	11·7±0·7	7·4–17·9	12·9±2·3
Human	48	14·6–23·2	17·5±1·7	9·0–11·7	10·1±0·6	3·7–14·4	9·8±3·0

TABLE 10.—*Size of accessory hooks situated posteriorly to the small hooks* (in microns)

Strain	Age in days	Host	No.	Total Length		Ventral Blade Length	
				Range	Mean	Range	Mean
Bovine I................	48	Dog..........................	2	16·9—17·6	16·6	9·5	9·5
Bovine II..............	35	Hydatid cyst..................	1	—	14·5	—	5·1
		Dog..........................	1	—	18·7	—	9·6
		C. (T.) mesomelas.............	2	16·8—17·2	17·0	7·6—8·0	7·8
Ovine I................	48	*L. pictus*, 2....................	1	—	21·3	—	11·5
Porcine I..............		Hydatid cyst..................	4	15·0—19·3	16·6	6·8— 9·0	8·0
	48	Dog..........................	3	16·4—20·0	14·8	8·0— 9·1	8·4
	60	Dog..........................	5	16·5—20·1	18·8	7·4— 9·8	8·8
	109	Dog..........................	1	—	21·4	—	9·8
	135	Dog..........................	2	18·0—20·3	19·2	7·7— 8·6	8·2
Porcine II............. 1st Generation..........		Hydatid cyst..................	4	15·6—19·5	17·6	7·9—10·3	8·7
	76	Dog..........................	1	—	21·0	—	9·4
		C. (T.) mesomelas.............	2	19·0—19·9	19·5	8·9— 9·7	9·3
	95	Dog..........................	1	—	15·6	—	7·8
	135	Dog..........................	3	17·7—19·3	18·3	8·2—10·3	9·3
Porcine II............. 2nd Generation.........	48	Dog..........................	2	16·9—20·7	18·8	7·4—10·4	8·9
	95	*C. (T.) mesomelas*.............	2	18·2—20·2	19·2	9·0— 9·3	9·2
Human.................		Hydatid cyst..................	12	13·5—18·6	17·2	6·9— 8·8	8·0
	35	*C. (T.) mesomelas*.............	9	14·2—20·8	17·4	7·2— 9·8	8·5
	76	*C. (T.) mesomelas*.............	6	18·6—23·5	20·6	9·4—10·1	9·9

TABLE 11.—*Number of segments per specimen (expressed as a percentage of the number examined)*

Strain	Age	Host	No.	All specimens examined			No.	Gravid specimens only		
				2	3	4		2	3	4
Bovine I	48	*L. pictus*, 1	48	8·3	83·4	8·3	19	—	89·5	10·5
		L. pictus, 2	38	—	86·8	13·2	18	—	94·4	5·6
		C. dingo	57	28·1	71·9	—	3	—	66·7	33·3
		Dog	49	49·0	51·0	—	14	28·6	71·4	—
		V. chama	8	37·5	62·5	—	1	—	100·0	—
		Total	200	23·5	71·5	5·0	55	7·3	85·4	7·3
Bovine II	35	Dog	1	—	100·0	—	—	—	—	—
		C. (T.) mesomelas	32	9·4	90·6	—	—	—	—	—
	76	Dog	24	—	79·2	20·8	11	—	72·7	27·3
		C. (T.) mesomelas	32	3·1	96·9	—	20	—	100·0	—
	95	Dog	6	—	100·0	—	1	—	100·0	—
		C. (T.) mesomelas	30	3·3	90·0	6·7	16	—	87·5	12·5
	118	Dog	23	4·3	95·7	—	10	—	100·0	—
		C. (T.) mesomelas	18	—	61·1	38·9	7	—	71·4	28·6
	135	Dog	30	—	90·0	10·0	22	—	90·9	9·1
		C. (T.) mesomelas	27	3·7	92·6	3·7	22	4·5	95·5	—
		Total	223	3·1	88·8	8·1	129	0·8	92·2	7·0
Ovine II	35	Dog	29	51·7	48·3	—	—	—	—	—
		C. (T.) mesomelas	38	21·1	65·8	13·1	—	—	—	—
	76	*C. (T.) mesomelas*	15	13·3	86·7	—	2	—	100·0	—
	95	*C. (T.) mesomelas*	33	—	45·5	54·5	27	—	55·6	44·4
		Total	115	21·7	58·3	20·0	29	—	58·6	41·4
Porcine I	48	Dog	24	—	100·0	—	12	—	100·0	—
	60	Dog	24	8·3	91·7	—	11	—	100·0	—
	109	Dog	32	3·1	81·3	15·6	15	—	80·0	20·0
	135	Dog	24	62·5	37·5	—	3	—	100·0	—
		Total	104	17·3	78·0	4·8	41	—	92·7	7·3
Porcine II 1st Generation	48	Dog	22	22·7	77·3	—	17	17·7	82·3	—
	76	Dog	23	21·7	78·3	—	4	—	100·0	—
		C. (T.) mesomelas	22	40·9	54·6	4·5	10	30·0	70·0	—
	95	Dog	21	52·4	47·6	—	4	25·0	75·0	—
	118	Dog	22	9·1	90·9	—	16	6·3	93·7	—
	135	Dog	20	95·0	5·0	—	—	—	—	
		Total	130	39·2	70·0	0·8	51	15·4	84·6	—
Porcine II 2nd Generation	48	Dog	23	17·4	82·6	—	10	—	100·0	—
	95	Dog	27	11·1	88·9	—	1	—	100·0	—
		Total	50	14·0	86·0	—	11	—	100·0	—
Human	35	Dog	1	100·0	—	—	—	—	—	—
		C. (T.) mesomelas	14	—	85·7	14·3	—	—	—	—
	76	Dog	19	10·5	80·5	—	4	—	100·0	—
		C. (T.) mesomelas	26	—	53·9	46·1	13	—	23·1	76·9
		Total	60	5·0	71·7	23·3	27	—	55·6	44·4

TABLE 12.—*Position of the sexually mature segment (expressed as a percentage of the number examined)*

Strain	Age	Host	No.	All Specimens				No.	Specimens with Ova			
				No mature segment	3rd last	2nd last	Last		No mature segment	3rd last	2nd last	Last
Bovine I	48	*L. pictus*, 1	47	—	—	100·0	—	17	—	—	100·0	—
		L. pictus, 2	37	8·1	5·4	86·5	—	22	13·6	9·1	77·3	—
		C. dingo	61	—	—	78·7	21·3	4	—	—	100·0	—
		Dog	45	—	2·2	97·8	—	13	—	—	100·0	—
		V. chama	8	—	—	65·2	37·5	1	—	—	100·0	—
		Total	198	1·5	1·5	88·9	8·1	57	5·3	3·5	91·2	—
Bovine II	35	Dog	1	—	—	100·0	—	—	—	—	—	—
		C. (T.) mesomelas	32	—	—	100·0	—	—	—	—	—	—
	76	Dog	24	—	—	100·0	—	11	—	—	100·0	—
		C. (T.) mesomelas	32	—	—	100·0	—	22	—	—	100·0	—
	95	Dog	6	—	—	100·0	—	1	—	—	100·0	—
		C. (T.) mesomelas	30	—	—	100·0	—	16	—	—	100·0	—
	118	Dog	22	—	—	100·0	—	10	—	—	100·0	—
		C. (T.) mesomelas	18	—	—	100·0	—	7	—	—	100·0	—
	135	Dog	30	—	—	100·0	—	22	—	—	100·0	—
		C. (T.) mesomelas	29	—	—	100·0	—	23	—	—	100·0	—
		Total	224	—	—	100·0	—	112	—	—	100·0	—
Ovine I	48	*L. pictus*	29	—	100·0	—	—	19	—	100·0	—	—
Ovine II	35	Dog	30	—	—	—	100·0	—	—	—	—	—
		C. (T.) mesomelas	36	—	—	55·6	44·4	—	—	—	—	—
	76	*C. (T.) mesomelas*	15	—	—	93·3	6·7	2	—	—	100·0	—
	95	*C. (T.) mesomelas*	33	—	—	100·0	—	27	—	—	100·0	—
		Total	114	—	—	58·8	41·2	29	—	—	100·0	—
Porcine I	48	Dog	22	—	—	100·0	—	12	—	—	100·0	—
	60	Dog	24	—	—	100·0	—	11	—	—	100·0	—
	109	Dog	30	—	—	100·0	—	15	—	—	100·0	—
	135	Dog	23	4·3	—	95·7	—	3	33·3	—	66·6	—
		Total	99	1·0	—	99·0	—	41	2·4	—	97·6	—
Porcine II 1st Generation	48	Dog	22	—	—	100·0	—	17	—	—	100·0	—
	76	Dog	23	—	—	100·0	—	4	—	—	100·0	—
		C. (T.) mesomelas	22	—	—	100·0	—	10	—	—	100·0	—
	95	Dog	21	—	—	100·0	—	4	—	—	100·0	—
	118	Dog	22	4·5	—	95·5	—	16	6·3	—	93·7	—
	135	Dog	20	—	—	75·0	25·0	—	—	—	—	—
		Total	130	0·8	—	95·4	3·8	51	2·0	—	98·0	—
Porcine II 2nd Generation	48	Dog	23	—	—	100·0	—	10	—	—	100·0	—
	95	Dog	27	11·1	—	85·2	3·7	1	—	—	100·0	—
		Total	50	6·0	—	92·0	2·0	11	—	—	100·0	—
Human	35	*C. (T.) mesomelas*	14	—	—	100·0	—	—	—	—	—	—
	76	Dog	19	—	—	100·0	—	4	—	—	100·0	—
		C. (T.) mesomelas	26	—	—	100·0	—	13	—	—	100·0	—
		Total	59	—	—	100·0	—	17	—	—	100·0	—

TABLE 13.—*Total length of worms with ova in the uterus (in mm)*

Strain	Age in Days	Host	Two Segments			Three Segments			Four Segments		
			No.	Range	Mean±S.D.	No.	Range	Mean±S.D.	No.	Range	Mean±S.D.
Bovine I	48	*L. pictus*, 1	—	—	—	15	2·93–4·84	3·94±0·56	2	3·73–4·00	3·87
		L. pictus, 2	—	—	—	18	2·51–3·77	3·04±0·36	4	2·71–4·12	3·31
		C. dingo	—	—	—	2	2·21–3·20	2·71	1	—	2·86
		Dog	4	1·83–3·62	2·52	10	1·98–3·20	2·43±0·45	—	—	—
		V. chama	—	—	—	1	—	2·90	—	—	—
		Total	4	1·83–3·62	2·52	46	1·98–4·84	3·18±0·73	7	2·71–4·12	3·40±0·56
Bovine II	76	Dog	—	—	—	8	3·66–5·41	4·58±0·67	3	4·12–6·86	5·46
		C. (T.) mesomelas	—	—	—	23	4·12–7·01	5·54±0·86	—	—	—
	95	Dog	—	—	—	1	—	4·88	—	—	—
		C. (T.) mesomelas	—	—	—	14	3·96–6·02	4·83±0·18	2	3·15–4·69	3·92
	118	Dog	—	—	—	10	2·86–4·80	3·98±0·78	—	—	—
		C. (T.) mesomelas	—	—	—	5	3·70–4·31	3·96	2	3·81–5·05	4·43
	135	Dog	—	—	—	20	4·12–6·48	5·14±0·74	2	4·26–6·06	5·16
		C. (T.) mesomelas	1	—	4·03	21	3·51–5·37	4·53±0·53	1	—	6·67
		Total	1	—	4·03	102	2·86–7·01	4·89±0·70	10	3·15–6·86	5·01±1·24
Ovine II	76	*C. (T.) mesomelas*	—	—	—	2	3·16–3·70	3·43	—	—	—
	95	*C. (T.) mesomelas*	—	—	—	12	3·39–5·45	4·44±0·70	15	3·04–6·13	4·75±0·86
		Total	—	—	—	14	3·16–5·45	4·30±0·75	15	3·04–6·13	4·75±0·86
Porcine I	48	Dog	—	—	—	12	3·44–4·65	3·82±0·34	—	—	—
	60	Dog	—	—	—	11	2·26–3·74	3·20±0·49	—	—	—
	109	Dog	—	—	—	12	2·15–3·15	2·65±0·41	3	3·48–3·89	3·63
	135	Dog	—	—	—	3	2·04–2·78	2·44	—	—	—
		Total	—	—	—	38	2·04–4·65	3·16±0·63	3	3·48–3·89	3·63
Porcine II 1st Generation	48	Dog	3	2·63–3·63	3·33	14	2·85–3·77	3·34±0·32	—	—	—
	76	Dog	—	—	—	4	2·78–3·52	3·18	—	—	—
		C. (T.) mesomelas	3	2·89–3·63	3·21	7	2·85–3·48	3·21±0·28	—	—	—
	95	Dog	1	—	2·63	3	3·48–3·66	3·56	—	—	—
	118	Dog	1	—	2·89	15	2·96–3·52	3·20±0·22	—	—	—
		Total	8	2·63–3·63	3·14±0·42	43	2·78–3·77	3·27±0·88	—	—	—
Porcine II 2nd Generation	48	Dog	—	—	—	10	3·20–4·50	3·74±0·27	—	—	—
	95	Dog	—	—	—	1	—	3·64	—	—	—
		Total	—	—	—	11	3·20–4·50	3·73±0·34	—	—	—
Human	76	Dog	—	—	—	4	4·00–4·75	4·45	—	—	—
		C. (T.) mesomelas	—	—	—	3	3·31–4·44	3·90	10	3·74–6·41	5·64±0·85
		Total	—	—	—	7	3·31–4·75	4·22±0·50	10	3·74–6·41	5·64±0·85

TABLE 14.—*Total length of all worms examined (in mm)*

Strain	Age in days	Host	Two segments			Three segments			Four segments		
			No.	Range	Mean±S.D.	No.	Range	Mean±S.D.	No.	Range	Mean±S.D.
Bovine I	48	*L. pictus*, 1	—	—	—	31	2·06–3·77	2·83±0·44	5	3·05–4·00	3·59
		L. pictus, 2	4	2·13–3·09	2·64	40	2·06–4·84	3·33±0·75	4	2·71–4·16	3·31
		C. dingo	16	1·64–2·40	1·95±0·22	41	1·29–3·24	2·42±0·51	1	2·86	2·86
		Dog	24	0·99–3·62	2·13±0·54	25	1·37–3·58	2·19±0·53	—	—	—
		V. chama	3	1·72–2·10	1·93	5	1·85–2·90	2·36	—	—	—
		Total	47	0·99–3·62	2·11±0·48	142	1·29–4·84	2·73±0·70	10	2·71–4·16	3·37±0·47
Bovine II	35	Dog	—	—	—	1	3·43	3·43	—	—	—
		C. (T.) mesomelas	3	2·59–3·58	3·07	29	3·12–4·80	4·00±0·41	—	—	—
	75	Dog	—	—	—	19	2·86–5·41	3·87±0·78	5	3·12–6·86	4·77
		C. (T.) mesomelas	1	4·95	4·95	31	4·08–7·01	5·33±0·84	—	—	—
	95	Dog	—	—	—	6	2·67–4·89	3·69	—	—	—
		C. (T.) mesomelas	1	3·43	3·43	27	2·71–6·02	4·28±0·76	2	3·15–4·69	3·92
	118	Dog	—	—	—	21	2·29–4·84	3·45±0·77	—	—	—
		C. (T.) mesomelas	—	—	—	11	2·63–4·34	3·64±0·55	7	3·39–5·05	3·86
	135	Dog	—	—	—	27	3·20–6·48	4·80±0·90	3	3·74–6·06	4·69
		C. (T.) mesomelas	1	4·03	4·03	25	2·78–5·37	4·42±0·60	1	6·67	6·67
		Total	6	2·59–4·95	3·61±0·82	197	2·63–7·01	4·31±0·93	18	3·12–6·86	4·41±1·15
Ovine II	35	Dog	15	1·60–2·52	2·03±0·26	14	1·56–2·48	2·11±0·30	—	—	—
		C. (T.) mesomelas	8	2·02–2·78	2·44	25	2·24–3·43	2·77±0·32	5	3·05–3·96	3·25
	75	*C. (T.) mesomelas*	2	2·32–2·40	2·36	13	2·78–4·27	3·35±0·47	—	—	—
	95	*C. (T.) mesomelas*	—	—	—	15	3·39–5·45	5·06±0·64	18	3·04–6·13	5·65±0·83
		Total	25	1·60–2·78	2·18±0·99	67	1·56–5·45	3·11±0·90	23	3·04–6·13	4·33±0·95
Porcine I	48	Dog	—	—	—	22	3·15–4·65	3·65±0·36	—	—	—
	60	Dog	2	3·03–3·18	3·11	22	2·15–3·74	3·05±0·44	—	—	—
	109	Dog	1	2·44	2·44	26	1·81–3·15	2·42±0·34	5	2·44–3·89	3·27
	135	Dog	15	1·74–3·11	2·46±0·47	9	2·04–2·92	2·58	—	—	—
		Total	18	1·74–3·18	2·53±0·44	79	1·81–4·65	2·96±0·62	5	2·44–3·89	3·27
Porcine II 1st Generation	48	Dog	5	2·74–3·63	3·21	17	2·85–3·77	3·28±0·33	—	—	—
	75	Dog	5	2·59–3·18	2·95	18	2·66–3·52	2·98±0·19	—	—	—
		C. (T.) mesomelas	9	2·33–3·63	3·05	12	2·85–3·52	3·19±0·24	1	3·37	3·37
	95	Dog	11	2·29–3·33	2·83±0·32	10	2·41–3·89	2·98±0·46	—	—	—
	118	Dog	2	2·89	2·89	20	2·78–3·52	3·13±0·24	—	—	—
	135	Dog	19	1·22–1·92	1·65±0·20	1	2·07	2·07	—	—	—
		Total	51	1·22–3·63	2·48±0·71	78	2·07–3·89	3·11±0·58	1	3·37	3·37
Porcine II 2nd Generation	48	Dog	4	2·63–3·42	2·88	19	2·41–4·50	3·52±0·43	—	—	—
	95	Dog	3	1·94–2·45	2·20	24	1·84–3·64	2·34±0·43	—	—	—
		Total	7	1·94–3·42	2·59±0·47	43	1·84–4·58	2·86±0·73	—	—	—
Human	36	*C. (T.) mesomelas*	—	—	—	12	3·28–6·08	4·47±0·71	2	4·43–5·58	5·01
	76	Dog	2	3·31–3·89	3·60	17	2·92–4·75	3·75±0·56	—	—	—
		C. (T.) mesomelas	—	—	—	14	2·63–5·69	3·41±0·92	12	3·64–6·41	5·35±1·0
		Total	2	3·31–3·89	3·60	43	2·63–6·08	3·84±0·83	14	3·64–6·41	5·30±0·98

TABLE 15.—*Length of the terminal segment*

Strain	Age	Host	No.	Length (in microns) Range	Length (in microns) Mean	Ratio to Total Length of Strobila (%) Range	Ratio to Total Length of Strobila (%) Mean
Bovine I	43	*L. pictus*, 1	17	1,333·5–2,933·7	2,229·2	45·0–71·3	56·8
		L. pictus, 2	22	1,104·9–2,247·9	1,615·8	43·3–64·4	53·0
		C. dingo	3	1,295·4–1,828·8	1,562·1	57·1–58·6	56·7
		Dog	14	1,219·2–2,476·5	1,614·8	58·2–72·4	65·7
		V. chama	1	—	1,562·1	—	54·0
		Total	57	1,104·9–2,933·7	1,794·1	43·3–72·4	57·6
Bovine II	76	Dog	11	1,676·4–5,076·7	2,926·8	39·4–81·7	60·2
		C. (T.) mesomelas	22	2,857·5–4,953·0	3,747·0	57·1–85·7	68·2
	95	Dog	1	—	2,857·5	—	58·6
		C. (T.) mesomelas	16	1,247·9–4,076·7	2,883·1	39·6–67·7	60·4
	118	Dog	10	1,333·5–3,048·0	2,206·0	40·2–63·9	55·5
		C. (T.) mesomelas	7	1,409·7–2,819·4	2,337·6	55·8–63·9	59·9
	135	Dog	22	2,476·5–4,572·0	3,666·3	61·1–91·4	69·8
		C. (T.) mesomelas	23	2,095·5–4,229·1	3,057·8	56·8–87·0	66·6
		Total	112	1,247·9–5,076·7	3,185·5	39·4–91·4	64·6
Ovine I	43	*L. pictus*	18	1,333·5–2,667·0	2,054·5	22·3–45·2	36·4
Ovine II	76	*C. (T.) mesomelas*	2	1,790·7–1,981·2	1,886·0	53·6–56·6	55·1
	95	*C. (T.) mesomelas*	27	1,562·1–3,657·6	2,315·3	42·3–60·2	50·2
		Total	29	1,562·1–3,657·6	2,285·7	42·3–60·2	50·6
Porcine I	43	Dog	12	1,776·0–2,405·0	2,019·6	50·9–55·2	52·9
	60	Dog	11	1,146·0–2,035·0	1,893·7	53·2–58·9	56·3
	109	Dog	15	851·0–1,850·0	1,326·4	35·2–54·1	43·8
	135	Dog	3	962·0–1,517·0	1,344·3	42·7–60·5	50·2
		Total	41	851·0–2,405·0	1,682·8	35·2–60·5	50·3
Porcine II 1st Generation	48	Dog	17	1,702·0–2,553·0	2,198·0	54·8–71·4	65·7
	76	Dog	4	1,702·0–2,035·0	1,887·0	52·6–64·0	60·5
		C. (T.) mesomelas	10	1,443·0–1,961·0	1,702·0	48·8–59·6	53·1
	95	Dog	4	1,517·0–2,405·0	2,035·0	55·3–65·7	60·9
	118	Dog	16	1,628·0–2,251·0	2,018·8	55·0–78·2	63·6
		Total	51	1,443·0–2,553·0	2,007·4	48·8–78·2	61·9
Porcine II 2nd Generation	48	Dog	10	1,800·0–2,376·0	2,174·4	54·5–60·0	58·0
	95	Dog	1	—	2,340·0	—	64·2
		Total	11	1,800·0–2,376·0	2,189·4	54·5–64·2	58·6
Human	76	Dog	4	2,340·0–3,096·0	2,772·0	58·6–65·2	62·3
		C. (T.) mesomelas	13	1,476·0–3,600·2	2,880·1	39·4–65·5	54·0
		Total	17	1,476·0–3,600·2	2,854·6	39·4–65·5	55·9

TABLE 16.—*Width of second last and last segment* (*in microns*)

Strain	Age	Host	No.	Second last segment		Last segment	
				Range	Mean	Range	Mean
Bovine I	48	*L. pictus*, 1	17	228·6—401·7	283·5	304·8—571·5	402·5
		L. pictus, 2	22	247·2—844·7	385·1	350·2—800·1	564·2
		C. dingo	3	195·7—266·7	219·7	350·2—495·4	383·4
		Dog	14	173·9—370·8	311·6	257·5—609·6	434·5
		V. chama	1	—	247·2	—	533·4
		Total	57	173·9—844·7	327·0	257·5—800·1	473·0
Bovine II	75	Dog	11	228·6—457·2	364·2	457·2—762·0	580·2
		C. (T.) mesomelas	22	190·5—609·6	338·9	419·1—609·6	478·9
	95	Dog	1	—	381·0	—	571·5
		C. (T.) mesomelas	16	278·1—685·8	482·6	432·6—723·9	503·3
	118	Dog	10	381·0—495·3	392·4	342·9—647·7	487·7
		C. (T.) mesomelas	7	304·8—495·3	404·2	533·4—838·2	623·0
	135	Dog	22	266·7—495·3	366·4	495·6—762·0	599·2
		C. (T.) mesomelas	23	226·7—533·4	330·7	419·1—685·8	514·2
		Total	112	190·5—685·8	374·9	342·9—838·2	541·3
Ovine I	48	*L. pictus*	18	381·1—723·9	536·0	495·3—838·2	650·3
Ovine II	75	*C. (T.) mesomelas*	2	342·9—381·0	323·9	457·2—533·4	495·3
	95	*C. (T.) mesomelas*	27	228·6—457·2	354·2	419·1—800·1	562·0
		Total	29	228·6—457·2	352·1	419·1—800·1	557·4
Porcine I	48	Dog	12	296·0—370·0	322·6	481·0—629·0	551·9
	60	Dog	11	259·0—518·0	380·1	444·0—814·0	679·5
	109	Dog	15	222·0—333·0	282·8	333·0—629·0	530·3
	135	Dog	3	296·0—370·0	325·0	484·1—555·0	519·0
		Total	41	222·0—518·0	323·6	333·0—814·0	575·8
Porcine II 1st Generation	48	Dog	17	222·0—444·0	347·5	370·0—703·0	539·8
	76	Dog	4	259·0—407·0	342·5	444·0—666·0	555·0
		C. (T.) mesomelas	10	257·5—518·0	229·6	407·0—555·0	573·5
	95	Dog	4	259·0—401·7	331·7	473·0—592·0	516·2
	118	Dog	16	148·0—370·0	320·0	370·0—666·0	550·4
		Total	51	148·0—518·0	314·2	370·0—703·0	549·1
Porcine II 2nd Generation	48	Dog	10	360·0—468·0	432·0	576·0—720·0	662·4
	95	Dog	1	—	504·0	—	792·0
		Total	11	360·0—504·0	438·6	576·0—792·0	674·2
Human	75	Dog	4	324·0—360·0	342·0	468·0—504·0	495·0
		C. (T.) mesomelas	13	324·0—504·0	419·2	504·0—792·0	625·9
		Total	17	324·0—504·0	401·1	468·0—792·0	595·7

TABLE 17.—*Ratio of length mature: gravid segment*

Strain	Age	Host	No.	Range	Mean
Bovine I	48	*L. pictus*, 1	20	1:1·8–1:3·9	1:2·6
		L. pictus, 2	21	1:1·6–1:3·3	1:2·5
		C. dingo	3	1:2·5–1:3·3	1:3·0
		Dog	12	1:2·2–1:4·5	1:3·5
		V. chama	1	1:2·5	1:2·5
		Total	57	1:1·6–1:4·5	1:2·7
Bovine II	76	Dog	13	1:1·2–1:4·1	1:2·7
		C. (T.) mesomelas	22	1:2·4–1:6·1	1:3·6
	95	Dog	1	1:2·6	1:2·6
		C. (T.) mesomelas	16	1:1·3–1:3·7	1:2·9
	118	Dog	10	1:1·4–1:3·6	1:2·5
		C. (T.) mesomelas	7	1:1·0–1:3·7	1:2·5
	135	Dog	22	1:2·7–1:6·1	1:4·0
		C. (T.) mesomelas	21	1:2·6–1:5·0	1:3·5
		Total	112	1:1·0–1:6·1	1:3·3
Ovine I	48	*L. pictus*	20	1:1·6–1:3·3	1:2·1
Ovine II	75	*C. (T.) mesomelas*	2	1:2·9	1:2·9
	95	*C. (T.) mesomelas*	27	1:1·5–1:3·1	1:2·0
		Total	29	1:1·5–1:3·1	1:2·1
Porcine I	48	Dog	12	1:2·0–1:2·3	1:2·2
	60	Dog	10	1:1·9–1:2·5	1:2·3
	109	Dog	16	1:1·1–1:2·4	1:1·6
	135	Dog	3	1:1·5–1:3·7	1:2·4
		Total	41	1:1·1–1:3·7	1:2·0
Porcine II 1st Generation	48	Dog	17	1:2·4–1:5·0	1:3·6
	76	Dog	4	1:2·1–1:3·7	1:3·0
		C. (T.) mesomelas	11	1:2·0–1:3·1	1:2·4
	95	Dog	4	1:2·1–1:3·9	1:3·1
	118	Dog	15	1:2·4–1:7·5	1:3·5
		Total	51	1:2·0–1:7·5	1:3·2
Porcine II 2nd Generation	48	Dog	1	1:2·1–1:2·9	1:2·5
	95	Dog	1	1:3·7	—
		Total	2	1:2·1–1:3·7	1:2·7
Human	35	*C. (T.) mesomelas*	12	1:1·4–1:3·2	1:1·9
	76	Dog	4	1:2·9–1:3·6	1:3·3
		C. (T.) mesomelas	12	1:1·4–1:3·2	1:2·4
		Total	28	1:1·4–1:3·6	1:2·3

TABLE 18.—*Size of scolex, rostellum and suckers (in microns)*

Strain	Age	Host	No.	Scolex		No.	Rostellum		No.	Suckers	
				Range	Mean±S.D.		Range	Mean±S.D.		Range	Mean±S.D.
Bovine I..........	48	*L. pictus*, 1............	37	150·0—260·0	208·5±43·0	36	79·9—154·5	109·0±14·4	37	61·6—133·9	107·3±19·4
		L. pictus, 2............	39	180·0—288·0	231·2±48·0	41	82·4—183·3	104·7±17·5	39	82·4—136·3	108·6±13·7
		C. dingo..............	45	175·0—240·0	202·4±22·2	37	56·4—131·6	99·6±16·8	45	70·5—117·5	94·1±10·2
		Dog..................	44	144·0—250·0	194·4±16·7	47	75·2—103·4	88·6± 9·5	44	72·8—112·8	89·6±10·4
		V. chama.............	12	170·0—310·0	222·5±42·7	8	94·0—131·6	106·3±13·8	8	84·6—133·9	109·0±14·2
		Total.........	177	144·0—288·0	209·4±37·9	169	56·4—183·3	100·1±16·4	173	61·6—136·3	99·7±15·8
Bovine II.........	35	Dog..................	1	—	247·2	1	—	113·3	1	—	103·0
		C. (T.) mesomelas.	32	206·0—381·0	262·3±38·9	32	108·1—154·5	123·2±11·8	31	103·0—145·7	122·4±12·4
	76	Dog..................	24	226·6—319·3	269·5±28·3	24	113·3—154·5	132·6± 9·8	24	103·0—154·5	129·6±12·1
		C. (T.) mesomelas.	29	247·2—319·3	285·9±24·7	31	123·6—155·1	137·4±10·6	32	103·0—154·5	134·5±13·6
	95	Dog..................	5	236·9—319·3	292·5±35·4	5	123·6—144·2	133·9±10·3	5	103·0—123·6	117·4± 9·2
		C. (T.) mesomelas.	27	216·3—381·1	298·7±33·8	28	133·9—175·1	153·0±14·2	29	113·3—175·1	135·5±12·9
	118	Dog..................	21	226·6—278·1	260·0±18·4	21	113·3—144·2	127·0± 7·5	23	103·0—154·5	126·7±11·8
		C. (T.) mesomelas.	18	257·5—370·8	291·8±28·5	18	103·0—175·1	143·1±15·8	18	113·3—154·5	135·0± 9·9
	135	Dog..................	30	278·1—391·4	324·8±30·8	30	123·6—164·8	140·8± 9·9	29	113·3—164·8	140·3±10·1
		C. (T.) mesomelas.	27	226·6—360·5	306·7±36·6	27	123·6—154·5	137·3± 9·0	27	113·3—154·5	138·9±12·3
		Total.........	214	206·0—391·4	288·2±37·6	217	103·0—175·1	136·5±15·7	219	103·0—175·1	127·5±38·1
Ovine I...........	48	*L. pictus*..............	26	117·5—339·9	236·6±42·3	24	89·3—126·9	111·3±27·6	28	94·0—133·9	116·1±12·4
Ovine II..........	35	Dog..................	23	228·6—298·7	256·0±18·4	26	94·0—144·2	121·5±12·2	23	98·7—126·9	133·4± 7·8
		C. (T.) mesomelas.	33	216·0—290·0	243·9±24·4	28	98·7—144·2	120·8±12·0	33	94·0—133·9	112·0± 9·9
	75	*C. (T.) mesomelas*.	7	185·4—249·1	225·3±29·6	11	113·3—185·4	137·8±22·8	8	103·4—133·9	118·6±13·3
	95	*C. (T.) mesomelas*.	32	141·0—267·8	222·8±30·3	33	103·4—150·4	128·9±11·6	32	89·3—123·6	108·5±10·4
		Total.........	95	141·0—298·7	236·0±44·2	98	94·0—185·4	125·6±14·4	96	89·3—133·9	111·7±10·2
Porcine I.........	48	Dog..................	18	236·9—288·4	255·2±16·8	20	92·7—123·6	109·5± 7·4	19	84·6—113·3	96·7± 8·1
	60	Dog..................	22	185·4—329·6	303·4±30·8	21	92·7—123·6	116·0±10·2	21	94·0—133·9	110·2± 9·2
	109	Dog..................	31	195·7—288·4	224·6±21·3	30	82·4—133·9	100·0±14·6	31	82·4—113·3	97·9±10·8
	135	Dog..................	24	206·0—288·4	260·1±20·9	24	103·0—164·8	138·4±20·3	22	92·7—133·9	104·4±10·7
		Total.........	95	185·4—329·6	254·9±45·2	95	82·4—164·8	115·2±20·5	93	82·4—133·9	101·9±11·1
Porcine II........ 1st Generation....	48	Dog..................	22	206·0—398·7	276·6±33·4	22	92·7—133·9	119·9±13·3	22	92·7—133·9	111·7±14·1
	76	Dog..................	23	216·3—298·7	278·6±37·6	23	123·6—144·2	130·3± 9·1	23	103·0—144·2	120·5±11·4
		C. (T.) mesomelas.	22	226·6—360·5	297·3±37·1	22	103·0—144·2	122·7±11·0	22	92·7—144·2	116·6±11·6
	95	Dog..................	21	236·9—339·9	299·7±26·0	21	123·6—164·8	138·8±12·0	21	123·6—154·5	135·9±11·1
	118	Dog..................	22	226·6—391·4	286·1±30·0	22	123·6—154·5	133·9± 8·4	22	103·0—144·2	128·3± 9·9
	135	Dog..................	20	329·6—422·3	370·1±29·4	18	123·6—144·2	133·9± 8·7	16	103·0—144·2	121·7±10·1
		Total.........	130	206·0—422·3	300·2±45·6	128	92·7—164·8	129·7±12·4	126	92·7—154·5	122·4±13·8
Porcine II........ 2nd Generation...	48	Dog..................	22	280·0—350·0	311·8±17·4	21	130·0—150·0	139·5± 8·7	22	100·0—140·0	119·1±11·1
	95	Dog..................	27	250·0—330·0	301·9±20·0	27	100·0—150·0	130·0±13·0	27	100·0—130·0	111·9±10·8
		Total.........	49	250·0—350·0	306·3±19·9	48	100·0—150·0	134·2±12·2	49	100·0—140·0	115·1±11·4
Human...........	35	*C. (T.) mesomelas*.	13	190·0—310·0	276·2±35·0	13	110·0—130·0	123·1± 7·5	13	90·0—120·0	101·5± 9·9
	76	Dog..................	18	200·0—270·0	238·9±19·4	19	80·0—120·0	96·1±10·6	26	90·0—130·0	105·8±10·3
		C. (T.) mesomelas.	24	210·0—270·0	240·0±16·9	26	80·0—110·0	89·5± 7·2	18	90·0—110·0	101·1± 7·6
		Total.........	55	190·0—310·0	248·2±27·6	58	80·0—130·0	99·2±15·7	57	90·0—130·0	103·4± 9·5

TABLE 19.—*Distance of the genital pore from the anterior margin of the segment (%) (all the specimens examined)*

Strain	Age	Host	No.	Mature		No.	Gravid	
				Range	Mean		Range	Mean
Bovine I	48	*L. pictus*, 1	32	43·9–61·5	53·2	31	43·5–64·5	54·5
		L. pictus, 2	38	43·2–59·2	49·2	35	41·0–61·8	52·9
		C. dingo	45	41·2–55·5	49·0	43	50·0–75·8	59·2
		Dog	25	37·5–53·6	47·4	32	35·6–62·5	50·2
		V. chama	8	36·4–53·7	48·6	6	50·0–65·6	58·1
		Total	148	36·4–61·5	49·6	147	35·6–75·8	54·5
Bovine II	35	Dog	6	42·9–55·6	49·5	5	45·0–57·1	50·6
		C. (T.) mesomelas	30	37·5–61·5	48·4	31	46·5–64·6	52·2
	75	Dog	27	41·7–64·9	52·9	23	48·9–72·2	58·3
		C. (T.) mesomelas	31	39·1–59·3	48·3	29	46·9–72·5	56·8
	95	Dog	6	46·2–54·6	50·0	5	50·0–64·9	56·5
		C. (T.) mesomelas	29	41·2–59·4	48·3	28	45·5–57·7	51·0
	118	Dog	24	40·0–67·6	52·8	10	51·4–66·7	57·7
		C. (T.) mesomelas	18	43·8–56·3	49·4	17	52·4–65·6	59·3
	135	Dog	30	41·7–52·6	46·7	30	48·7–68·8	56·4
		C. (T.) mesomelas	27	41·2–60·9	50·4	27	47·3–61·5	54·6
		Total	226	37·5–67·6	50·0	205	45·0–72·5	55·1
Ovine II	35	Dog	29	45·3–64·0	54·3	—	—	—
		C. (T.) mesomelas	38	41·7–75·0	54·3	23	48·7–73·3	59·9
	75	*C. (T.) mesomelas*	12	47·8–60·0	53·1	13	33·3–59·6	51·3
	95	*C. (T.) mesomelas*	31	48·0–73·1	96·0	30	47·1–66·2	57·0
		Total	110	41·7–75·0	54·6	66	33·3–73·3	56·9
Porcine I	48	Dog	22	47·8–66·7	51·1	23	54·4–80·9	58·3
	60	Dog	24	43·8–59·1	49·1	24	53·3–63·6	57·6
	109	Dog	32	41·7–62·5	52·6	26	45·7–70·4	58·0
	135	Dog	15	43·8–66·7	53·2	23	54·6–68·0	60·0
		Total	93	41·7–66·7	51·4	96	45·7–80·9	58·5
Porcine II 1st Generation	48	Dog	20	41·2–58·3	49·3	17	48·9–67·4	56·9
	76	Dog	23	42·9–66·7	50·8	22	42·6–80·6	55·7
		C. (T.) mesomelas	21	42·9–61·1	51·9	19	48·7–63·4	56·2
	95	Dog	21	40·0–57·1	47·6	20	46·2–61·5	52·2
	118	Dog	21	41·2–55·6	47·6	21	50·9–61·5	56·2
	135	Dog	11	44·4–63·6	52·9	15	47·6–60·0	54·5
		Total	117	40·0–66·7	49·7	114	42·6–80·6	55·3
Porcine II 2nd Generation	48	Dog	23	41·2–57·1	47·9	15	45·0–58·5	52·6
	95	Dog	25	42·9–57·1	50·7	17	43·8–58·8	50·9
		Total	48	41·2–57·1	49·4	32	43·8–58·8	51·7
Human	35	*C. (T.) mesomelas*	14	44·6–56·4	52·5	14	55·4–69·4	60·8
	76	Dog	18	42·3–54·6	49·5	18	46·7–59·5	53·2
		C. (T.) mesomelas	26	43·8–57·7	51·8	25	48·7–64·0	55·8
		Total	58	43·2–57·7	51·2	57	46·7–69·4	56·2

TABLE 20.—*Distance of genital pore from the anterior margin of the segment (%) specimens with mature ova only*

Strain	Age	Host	No.	Mature		No.	Gravid	
				Range	Mean		Range	Mean
Bovine I	48	*L. pictus*, 1	13	43·2–53·9	48·6	11	41·0–57·4	52·5
		L. pictus, 2	20	38·6–61·5	53·1	18	43·5–63·0	54·2
		C. dingo	3	44·4–50·0	47·9	1	—	68·8
		Dog	12	43·6–53·1	47·0	12	38·5–62·5	51·9
		V. chama	1	—	36·4	1	—	61·0
		Total	49	38·6–61·5	49·8	43	38·5–63·0	53·6
Bovine II	76	Dog	23	40·0–59·3	48·2	23	46·9–65·4	56·4
		C. (T.) mesomelas	11	46·4–64·9	55·5	8	50·0–65·2	60·5
	95	Dog	1	—	50·0	—	—	—
		C. (T.) mesomelas	16	42·3–59·4	48·4	15	47·5–57·7	52·9
	118	Dog	11	40·0–67·6	53·5	5	51·4–66·7	60·7
		C. (T.) mesomelas	7	48·6–52·6	50·4	6	55·4–65·6	61·2
	135	Dog	21	41·2–52·6	46·8	21	51·8–68·8	57·9
		C. (T.) mesomelas	23	41·2–60·9	50·8	23	47·7–61·5	55·2
		Total	113	40·0–67·6	49·4	101	46·9–68·8	55·9
Ovine II	76	*C. (T.) mesomelas*	2	50·0–56·3	53·2	2	51·9–59·6	55·5
	95	*C. (T.) mesomelas*	25	48·2–64·5	56·5	25	47·1–66·2	56·5
		Total	27	48·2–64·5	56·2	27	47·1–66·2	56·9
Porcine I	48	Dog	12	47·8–66·7	51·1	12	56·3–80·9	60·5
	60	Dog	11	43·8–54·2	49·5	11	54·7–63·6	58·9
	109	Dog	16	44·8–60·0	52·7	14	45·7–70·4	60·1
	135	Dog	2	47·6–63·6	55·6	3	57·7–59·5	58·9
		Total	41	43·8–66·7	51·5	40	45·7–80·9	59·8
Porcine II 1st Generation	48	Dog	15	41·2–58·3	49·4	12	54·6–67·4	58·1
	76	Dog	4	42·9–66·7	51·2	4	52·7–80·6	60·0
		C. (T.) mesomelas	10	47·1–61·1	52·0	9	48·7–63·4	56·0
	95	Dog	4	42·9–56·3	48·4	4	51·2–61·5	55·3
	116	Dog	14	43·8–55·6	48·0	14	50·0–61·4	56·2
		Total	47	41·2–66·7	49·6	43	48·7–80·6	57·0
Porcine II 2nd Generation	48	Dog	10	45·0–53·9	49·4	5	48·5–57·8	54·8
	95	Dog	1	—	52·9	1	—	53·9
		Total	11	45·0–53·9	49·7	6	48·5–57·8	54·6
Human	76	Dog	4	47·8–54·6	50·6	4	53·9–57·1	55·8
		C. (T.) mesomelas	13	50·0–57·1	53·7	13	50·6–64·0	56·3
		Total	17	47·8–57·1	53·0	17	50·6–64·0	56·2

TABLE 21.—*Number and distribution of testes*

Strain	Age in days	Host	No.	Total		Anterior		Posterior	
				Range	Mean±S.D.	Range	Mean±S.D.	Range	Mean±S.D.
Bovine I	48	*L. pictus*, 1	31	31–49	38·8±4·8	16–30	21·8±3·3	12–22	17·0±2·4
		L. pictus, 2	24	30–49	37·1±4·6	15–30	20·4±3·3	10–22	16·7±2·9
		C. dingo	19	26–39	31·0±3·4	15–23	18·2±2·5	10–19	12·8±2·0
		Dog	29	25–39	30·2±3·6	14–24	17·4±2·6	8–16	12·8±2·1
		V. chama	5	25–34	30·2±3·3	14–19	17·2±1·9	11–15	13·0±3·2
		Total	108	25 49	34·3±5·6	14–30	19·4±3·4	8–22	14·9±3·1
Bovine II	35	Dog	4	31–33	31·8	18–20	19·0	11–14	12·8
		C. (T.) mesomelas	22	25–39	29·6±3·3	13–24	18·8±2·5	8–15	10·8±1·9
	76	Dog	23	25–47	33·0±5·6	16–27	19·7±2·4	9–19	13·0±2·9
		C. (T.) mesomelas	25	25–38	31·5±3·4	15–28	20·2±2·7	8–15	11·4±2·0
	95	Dog	10	27–40	34·0±4·6	17–24	20·4±2·4	9–17	13·6±2·5
		C. (T.) mesomelas	24	27–39	31·6±2·8	16–28	20·7±2·3	8–15	10·9±1·8
	118	Dog	20	27–35	30·8±2·4	17–26	19·9±2·2	8–15	11·0±1·9
		C. (T.) mesomelas	16	29–45	36·6±4·1	19–27	22·5±2·3	8–19	14·1±2·6
	135	Dog	25	28–41	32·0±3·0	17–28	20·5±2·9	9–17	11·8±1·8
		C. (T.) mesomelas	26	26–41	32·8±4·1	16–31	20·3±3·4	9–16	12·5±1·6
		Total	195	25–47	32·2±4·0	13–28	20·2±2·7	8–19	12·0±2·3
Ovine I	48	*L. pictus*	25	58–80	68·4±7·1	34–53	41·5±5·1	21–34	26·9±4·1
Ovine II	35	Dog	26	29–49	39·7±4·8	17–34	25·5±3·8	10–21	14·2±2·4
		C. (T.) mesomelas	36	32–54	43·3±2·8	21–33	27·6±3·3	10–25	15·6±3·2
	76	*C. (T.) mesomelas*	5	37–53	43·4±6·2	25–34	28·2±3·4	12–19	15·2±3·1
	95	*C. (T.) mesomelas*	30	39–54	45·1±4·0	22–37	28·7±3·5	11–21	16·4±2·6
		Total	97	29–54	42·9±4·3	17–37	27·4±3·7	10–25	15·5±2·9
Porcine I	48	Dog	10	28–38	31·2±3·6	13–19	15·5±2·0	14–19	15·7±1·6
	60	Dog	9	35–41	37·4±1·8	13–19	16·7±1·7	18–23	20·8±1·6
	109	Dog	21	30–42	36·1±3·9	13–24	19·0±2·8	14–23	17·1±2·2
	135	Dog	1	—	32·0	—	16·0	—	16·0
		Total	41	28–42	35·1±4·1	13–24	17·6±2·8	14–23	17·5±2·6
Porcine II 1st Generation	48	Dog	8	30–36	33·0±2·2	12–18	15·8±2·4	16–18	17·3±0·7
	76	Dog	20	35–47	40·4±3·3	18–24	20·0±1·6	14–24	20·5±2·4
		C. (T.) mesomelas	18	37–50	41·3±3·1	18–23	20·7±1·6	19–27	20·6±2·0
	95	Dog	8	36–49	44·8±4·7	14–25	21·0±1·2	21–27	23·8±1·8
	118	Dog	13	36–47	40·7±3·4	13–24	19·3±2·3	17–25	21·4±2·6
	135	Dog	2	37–41	39·0	19–21	20·0	16–22	19·0
		Total	69	30–50	40·3±4·4	12–25	19·7±2·6	14–27	20·6±2·7
Porcine II 2nd Generation	48	Dog	19	35–49	41·9±4·0	15–25	19·6±2·5	18–27	22·3±2·4
	95	Dog	19	38–50	44·3±3·3	19–27	22·3±2·1	18–25	22·0±2·2
		Total	38	35–50	43·1±3·8	15–27	20·9±2·7	18–27	22·2±2·3
Human	35	Dog	4	34–39	37·0	19–23	21·3	12–19	25·7
		C. (T.) mesomelas	10	44–51	47·4±1·8	20–25	22·5±1·3	22–28	24·9±1·8
	76	Dog	14	44–55	48·7±1·1	20–29	23·6±2·6	22–30	25·1±2·2
		C. (T.) mesomelas	20	41–51	46·6±2·7	20–27	22·4±1·7	21–30	24·2±2·4
		Total	48	34–55	45·6±4·1	19–29	22·7±2·0	12–30	22·9±3·3

TABLE 22.—*Size of cirrus sac (in microns)*

Strain	Age in days	Host	Mature Segment					Gravid Segment				
			No.	Length		Width		No.	Length		Width	
				Range	Mean ± S.D.	Range	Mean ± S.D.		Range	Mean ± S.D.	Range	Mean ± S.D.
Bovine I........	48	*L. pictus*, 1.......	21	75·6–106·4	86·1 ± 8·8	36·4–75·2	49·4 ± 9·3	9	82·8–105·8	93·0 ± 8·5	50·6–64·4	55·2 ± 5·1
		L. pictus, 2.......	20	72·8–114·8	93·7 ± 13·6	33·6–64·4	51·8 ± 7·6	10	82·8–124·2	104·1 ± 13·7	50·6–61·6	56·9 ± 3·8
		C. dingo..........	13	64·4–98·0	85·9 ± 11·6	33·6–56·0	46·7 ± 7·1	12	95·2–112·0	104·5 ± 5·6	50·4–84·6	58·4 ± 8·9
		Dog.............	4	70·0–75·6	72·1	42·0–56·0	46·2	7	78·4–103·6	86·4 ± 8·6	39·2–53·2	48·8 ± 4·8
		V. chama.........	1	100·8	100·8	56·0	56·0	2	117·6–131·6	124·6	56·0–61·6	58·8
		Total......	59	64·4–114·8	87·9 ± 12·2	33·6–75·2	49·5 ± 8·1	40	78·4–131·6	99·7 ± 12·9	39·2–84·6	55·7 ± 6·8
Bovine II.......	35	Dog.............	2	58·8–70·0	64·4	33·6–56·0	44·8	5	109·2–123·6	114·3 ± 7·9	58·8–70·0	63·8 ± 4·2
		C. (T.) mesomelas.	16	56·0–112·0	81·9 ± 14·6	42·0–70·0	57·9 ± 8·7	23	112·0–154·0	133·3 ± 11·2	56·0–72·8	66·2 ± 4·3
	75	Dog.............	23	70·0–142·8	101·5 ± 19·1	42·0–70·0	60·0 ± 9·3	14	98·0–134·4	117·6 ± 10·4	56·0–70·0	64·2 ± 5·3
		C. (T.) mesomelas.	15	75·6–112·0	88·9 ± 12·3	50·4–70·0	61·8 ± 6·7	19	117·6–168·0	135·7 ± 16·4	56·0–75·6	68·7 ± 5·8
	95	Dog.............	5	86·8–182·0	129·9 ± 46·0	44·8–81·2	71·1 ± 20·3	0	—	—	—	—
		C. (T.) mesomelas.	22	78·4–134·4	102·2 ± 17·6	42·0–75·6	62·5 ± 9·2	18	89·6–140·0	120·0 ± 14·9	56·0–78·4	66·6 ± 4·9
	118	Dog.............	17	84·0–134·4	105·3 ± 14·5	44·8–92·4	60·6 ± 10·2	3	95·2–112·0	101·7	56·0–58·8	57·9
		C. (T.) mesomelas.	17	84·0–126·0	106·4 ± 14·6	28·0–70·0	56·2 ± 14·2	14	112·0–151·2	126·2 ± 12·6	56·0–67·2	64·0 ± 3·3
	135	Dog.............	22	75·6–140·0	104·9 ± 21·7	36·4–78·4	60·5 ± 11·5	23	106·4–140·0	125·5 ± 10·1	56·0–81·2	68·2 ± 6·0
		C. (T.) mesomelas.	24	64·4–123·2	86·2 ± 16·2	33·6–70·0	52·9 ± 9·1	17	89·6–145·6	120·2 ± 13·7	56·0–72·8	63·4 ± 4·9
		Total......	163	56·0–182·0	91·9 ± 20·9	28·0–92·4	59·1 ± 11·1	136	89·6–154·0	125·2 ± 14·4	56·0–81·2	65·9 ± 5·3
Ovine II........	35	Dog.............	14	126·0–210·0	166·9 ± 22·1	56·0–100·8	79·3 ± 12·0	0	—	—	—	—
		C. (T.) mesomelas.	15	136·3–220·9	182·4 ± 24·5	67·2–98·0	83·9 ± 8·2	13	182·0–215·6	192·8 ± 12·3	84·6–108·1	91·6 ± 6·6
	75	*C. (T.) mesomelas*.	0	—	—	—	—	9	159·8–224·0	176·6 ± 19·3	75·6–98·0	85·0 ± 6·7
	95	*C. (T.) mesomelas*.	22	140·0–210·0	160·8 ± 18·1	61·6–95·2	77·1 ± 9·0	11	154·0–210·0	176·7 ± 15·1	64·4–95·2	78·7 ± 9·9
		Total......	51	126·0–220·9	168·8 ± 23·3	56·0–100·8	79·7 ± 9·9	33	154·0–224·0	183·0 ± 16·9	64·4–108·1	85·5 ± 9·5
Porcine I.......	48	Dog.............	11	72·8–114·8	96·7 ± 12·4	56·0–95·2	67·7 ± 10·5	6	103·6–131·6	120·4 ± 10·8	70·0–75·6	70·9 ± 2·3
	60	Dog.............	12	84·0–151·2	108·0 ± 19·4	56·0–84·0	69·8 ± 7·7	19	120·4–156·8	134·1 ± 10·9	70·0–84·0	75·6 ± 3·7
	109	Dog.............	13	70·0–109·2	84·9 ± 13·5	44·8–67·2	54·3 ± 9·3	7	103·4–136·3	115·4 ± 11·6	58·8–70·5	65·9 ± 4·6
	135	Dog.............	1	128·8	128·8	78·4	78·4	12	103·6–140·0	120·6 ± 9·6	56·0–70·0	65·1 ± 5·1
		Total......	37	70·0–151·2	97·1 ± 18·4	44·8–95·2	64·0 ± 11·5	44	103·4–156·8	125·6 ± 12·9	56·0–84·0	70·6 ± 6·3
Porcine II...... 1st Generation	48	Dog.............	15	84·0–140·0	113·5 ± 15·7	47·6–72·8	64·4 ± 7·4	5	120·4–168·0	135·0 ± 19·2	56·0–67·4	62·2 ± 4·4
	76	Dog.............	19	70·0–120·4	101·6 ± 14·7	42·0–75·6	60·1 ± 10·7	7	117·6–140·0	132·4 ± 8·7	56·0–98·0	70·8 ± 14·2
		C. (T.) mesomelas.	15	84·0–131·6	107·2 ± 16·1	39·2–70·0	59·0 ± 8·9	9	106·4–140·0	124·1 ± 10·5	56·0–75·6	63·8 ± 5·6
	95	Dog.............	10	84·0–134·4	111·4 ± 15·9	53·2–64·4	59·8 ± 5·1	6	126·0–178·6	143·6 ± 18·0	70·0–84·0	74·7 ± 7·2
	118	Dog.............	14	70·0–112·0	101·4 ± 11·1	42·0–70·0	58·2 ± 7·5	13	103·6–168·0	132·7 ± 14·4	56·0–86·8	65·9 ± 8·6
	135	Dog.............	5	123·2–168·0	139·4 ± 17·4	64·4–72·8	68·3 ± 3·2	12	109·2–140·0	127·9 ± 9·5	58·8–78·4	67·0 ± 6·1
		Total......	78	70·0–168·0	108·6 ± 17·3	39·2–75·6	60·7 ± 2·7	52	103·6–178·6	131·5 ± 13·7	56·0–98·0	67·1 ± 8·7
Porcine II...... 2nd Generation.	48	Dog.............	15	103·6–140·0	118·9 ± 13·4	44·8–72·8	62·4 ± 7·4	4	138·0–147·2	141·3 ± 4·0	67·2–78·2	71·1 ± 4·5
	95	Dog.............	12	112·0–154·0	132·8 ± 12·1	56·6–98·0	69·5 ± 11·1	13	117·6–182·0	138·4 ± 17·7	56·0–70·0	64·3 ± 4·9
		Total......	27	103·6–154·0	125·1 ± 13·9	44·8–98·0	65·5 ± 9·7	17	117·6–182·0	138·4 ± 17·7	56·0–78·2	65·9 ± 5·6
Human.........	35	*C. (T.) mesomelas*.	10	114·8–169·2	129·7 ± 14·9	56·0–89·6	73·9 ± 13·5	10	117·6–187·6	148·1 ± 23·0	50·4–75·6	61·6 ± 8·5
	76	Dog.............	13	84·0–134·4	108·5 ± 14·4	56·0–84·0	68·7 ± 7·9	3	137·2–142·8	140·0	50·4–81·2	69·1
		C. (T.) mesomelas.	12	84·0–126·0	103·8 ± 13·9	44·8–67·2	58·6 ± 6·1	0	—	—	—	—
		Total......	35	84·0–169·2	113·0 ± 17·7	44·8–89·6	66·7 ± 9·7	13	117·6–187·6	146·3 ± 20·3	50·4–81·2	63·3 ± 10·5

TABLE 23.—*Size of ova and oncosphere hooks*

Strain	Age	Host	No.	Ova				No.	Oncosphere hooks	
				Smallest diameter		Greatest diameter				
				Range	Mean	Range	Mean		Range	Mean
Bovine I	48	*L. pictus*, 1	7	27·8–29·4	28·7	35·8–51·9	37·9	2	10·7–11·6	11·2
		L. pictus, 2	20	28·9–35·9	30·9	33·3–40·4	37·2	14	10·3–13·3	11·1
		Dog, 2	4	28·9–35·9	32·0	37·7–43·0	40·5	—	—	—
		Total	31	27·8–35·9	30·5±2·2	33·3–43·0	37·8±2·2	16	10·3–13·3	11·1±0·8
Bovine II	76	Dog	12	28·2–33·3	30·2	33·5–40·8	37·9	12	9·2–12·5	10·6
		C. (T.) mesomelas	2	28·6–28·9	28·8	38·6–39·4	39·0	—	—	—
	118	Dog	4	28·5–30·9	27·9	36·0–38·2	36·9	6	10·0–11·5	10·8
		C. (T.) mesomelas	16	26·0–33·2	30·8	32·8–40·6	38·2	12	10·3–13·0	11·1
	135	Dog	18	28·0–35·9	30·8	30·9–41·3	36·9	14	8·6–13·1	11·5
		C. (T.) mesomelas	14	29·1–33·2	31·2	35·1–40·4	38·2	10	9·9–11·8	10·9
		Total	66	26·0–35·9	30·7±1·8	30·9–41·3	37·7±2·1	54	8·6–13·1	11·0±1·0
Ovine I	48	*L. pictus*	8	30·9–33·8	32·0	35·6–38·7	37·3	3	10·1–10·6	10·4
		L. pictus	10	35·1–41·2	37·2	39·0–44·5	42·2	29	8·5–13·5	11·1
		Total	18	30·9–41·2	34·9±3·1	35·6–44·5	40·0±2·9	32	8·5–13·5	11·1±1·4
Ovine II	76	Dog	12	30·5–34·8	33·1	33·8–40·8	38·4	17	9·5–14·0	11·7
		C. (T.) mesomelas	8	28·8–35·4	32·5	36·3–41·9	39·4	—	—	—
	95	Dog	8	30·4–34·8	32·6	35·1–43·9	39·3	8	10·1–12·9	12·2
		C. (T.) mesomelas	12	29·5–34·3	31·6	35·5–39·3	37·7	16	9·4–13·8	11·8
	118	*C. (T.) mesomelas*	9	31·9–34·3	32·9	37·3–39·9	38·3	9	11·0–14·2	12·4
		Total	49	28·8–35·4	32·5±1·6	33·8–43·9	38·5±1·6	50	9·4–14·2	11·9±1·1
Porcine I	48	Dog	8	29·6–39·8	32·9	34·1–43·2	37·3	8	9·6–11·5	10·8
	60	Dog	6	29·9–35·1	33·1	33·5–38·0	36·0	6	10·1–11·0	10·6
	109	Dog	2	32·0–32·6	32·3	34·7–36·4	35·6	—	—	—
	135	Dog	8	31·6–35·4	32·9	34·7–37·7	36·3	8	9·3–12·7	10·7
		Total	24	29·6–39·8	32·9±2·4	33·5–43·2	36·5±2·1	22	9·3–12·7	10·7±1·0
Porcine II 1st Generation	48	Dog	12	30·6–34·6	32·5	33·4–38·6	35·9	8	9·8–12·3	11·0
	76	Dog	12	29·3–34·5	31·3	31·7–42·1	34·7	12	9·6–13·2	11·4
		C. (T.) mesomelas	12	28·7–37·1	32·8	33·3–39·1	35·8	10	10·3–12·6	11·4
	95	Dog	8	29·5–34·3	31·7	32·8–37·2	35·4	6	9·2–11·5	10·2
	118	Dog	16	29·8–33·5	31·8	31·6–40·2	35·0	10	10·8–12·4	11·4
		Total	60	28·7–37·1	32·0±1·6	31·6–42·1	35·3±0·7	46	9·2–13·2	11·6±1·3
Porcine II 2nd Generation	95	Dog	4	30·6–33·8	32·4	33·2–35·8	35·0	—	—	—
		C. (T.) mesomelas	10	28·9–31·9	30·2	31·9–35·4	33·9	8	10·1–13·1	11·2
		Total	14	28·9–33·8	30·8±1·5	31·9–35·8	34·2±1·3	8	10·1–13·1	11·2±1·1
Human	35	*C. (T.) mesomelas*	4	32·5–33·5	33·1	34·5–39·9	36·5	6	9·9–13·3	11·4
	76	*C. (T.) mesomelas*	14	28·9–33·4	30·8	33·9–37·4	35·8	4	9·2–10·5	10·0
		Total	18	28·9–33·5	31·3±1·5	33·9–39·9	36·0±1·5	10	9·2–13·3	10·8±1·2

TABLE 24.—*Variation in size of the three pairs of oncosphere hooks*

Strain	Age	Host	No.	Short		Medium		Long	
				Range	Mean	Range	Mean	Range	Mean
Bovine I..........	48	*L. pictus*, 2............	1	—	10·8	—	11·3	—	11·4
Bovine II.........	118	*C. (T.) mesomelas*......	1	—	10·3	—	10·7	—	13·0
	135	Dog..................	1	—	10·0	—	10·7	—	12·6
Ovine I...........	48	*L. pictus*..............	7	8·5—10·8	9·6	9·4—12·2	10·7	10·5—13·5	12·4
Ovine II..........	75	Dog..................	1	—	9·5	—	9·5	—	9·8
	95	*C. (T.) mesomelas*......	1	—	9·4	—	10·7	—	12·9
Porcine I.........	49	Dog..................	1	—	9·5	—	10·6	—	11·3

TABLE 25.—*Number of worms recovered at post-mortem*

Age of infestation in days	Host	Origin of Infestive Material: Bovine I	Bovine II	Ovine I	Ovine II	Porcine I	Porcine II Generation 1st	Porcine II Generation 2nd	Human
35	Dog	—	530	—	640	—	—	—	242
	C. (*T.*) *mesomelas*	—	9,300	—	10,000	—	—	—	352
	Cat	—	2	—	2	—	—	—	—
48	*L. pictus*	—	—	6	—	—	—	—	—
	L. pictus	14,200	—	7,061	—	—	—	—	—
	L. pictus	23,005	—	14,672	—	—	—	—	—
	C. dingo	4,580	—	12	—	—	—	—	—
	Dog	580	—	2	—	0	4,829	571	—
	Dog	3,384	—	250	—	1,292	—	—	—
	V. chama	10	—	0	—	—	—	—	—
	V. chama	120	—	0	—	—	—	—	—
	*Cat	63	—	0	—	—	—	—	—
	*Cat	6	—	0	—	—	—	—	—
	C. (*T.*) *mesomelas*	—	—	—	—	—	—	181	—
60	Dog	—	—	—	—	48,471	—	—	—
75	Dog	—	1,770	—	2,190	—	3,120	—	250
	C. (*T.*) *mesomelas*	—	8,040	—	6,670	—	5,634	—	976
	Cat	—	0	—	0	—	—	—	—
95	Dog	—	324	—	2,200	—	1,845	315	—
	C. (*T.*) *mesomelas*	—	3,140	—	48,660†	—	—	1,432	—
	Cat	—	0	—	0	—	—	—	—
109	Dog	—	—	—	—	15,970	—	—	—
118	Dog	—	3,152	—	152	—	4,735	—	—
	C. (*T.*) *mesomelas*	—	635	—	3,792	—	—	—	—
	Cat	—	0	—	—	—	—	—	—
135	Dog	—	16,226	—	—	18,540	578	—	—
	C. (*T.*) *mesomelas*	—	7,866	—	—	—	—	—	—

* One half the number of scolices administered to the other carnivores
† Accidentally overdosed

TABLE 26.—*Percentage of patent worms*

Age of infestation in days	Host	Bovine		Ovine		Porcine			Human
		I	II	I	II	I	II		
							Generation		
							1st	2nd	
48	*L. pictus*	88·6	—	61·7	—	—	—	—	—
	L. pictus	50·0	—	65·6	—	—	—	—	—
	C. dingo	13·3	—	—	—	—	—	—	—
	Dog	29·4	—	0	—	54·6	66·7	43·5	—
	V. chama	12·5	—	—	—	—	—	—	—
	C. (*T.*) *mesomelas*	—	—	—	—	—	—	0	—
60	Dog	—	—	—	—	45·8	—	—	—
75	Dog	—	51·9	—	48·3	—	17·4	—	19·0
	C. (*T.*) *mesomelas*	—	60·1	—	16·7	—	47·8	—	83·3
95	Dog	—	51·1	—	22·6	—	23·3	3·7	—
	C. (*T.*) *mesomelas*	—	48·5	—	66·7	—	—	73·3	—
109	Dog	—	—	—	—	53·1	—	—	—
118	Dog	—	43·5	—	—	—	73·9	—	—
	C. (*T.*) *mesomelas*	—	70·0	—	23·3	—	—	—	—
135	Dog	—	95·8	—	—	12·5	16·7	—	—
	C. (*T.*) *mesomelas*	—	75·0	—	—	—	—	—	—