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STUDIES ON THE TAXONOMY OF STRONGYLOIDES

(NEMATODA; STRONGYLOIDIDAE)

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for the Degree of Doctor of Philosophy
in the Graduate School of Tropical Veterinary Science
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March 1986

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institute of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

Richard Speare

March, 1986

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ABSTRACT

The taxonomy of *Strongyloides* has been critically assessed, firstly from the viewpoint of nomenclature, and subsequently from the aspect of morphology with emphasis placed on the practical problems of differentiating species.

On the higher taxon level, the classification of the genus was discussed and placement in the Rhabdiasoidea favoured, although it was acknowledged that this was a compromise based on lack of knowledge of the Rhabdiasidae. The argument was presented that the valid name of the genus is *Strongiloides*, not *Strongyloides*, but that adoption of the former name would lead to instability without benefit. One hundred and three names used for species were located in the literature. Fifty three were considered valid, 18 invalid and 32 unavailable. Of this latter group, 22 were *lapsi calamorum*, 5 were *nomina nuda*, two had unacceptable spelling, and three lacked a differential diagnosis. The only species names which were considered invalid and are in common use were *S.ransomi* and *S.planiceps*, junior synonyms of *S.suis* and *S.cati* respectively.

The genus was defined by description of the eighteen life cycle stages. This was based on Little (1966a,b) and some additions and corrections made to his basically sound definition of *Strongyloides*. The proposal was made that the parasitic female lacks cephalic papillae. Some changes in the limits of dimensions of the parasitic female were made, and it was emphasized that the maximum width relative to length, the distance of the vulva from the mouth relative to length, and the intramucosal location of the parasite are significant generic characters. The existence of perivulval nerve endings in the parasitic female was noted. The definition of the free living adults was essentially unchanged from that of Little, with the exception that the midventral preanal papilla of the free living male differs from the six paired caudal papillae. The existence of a papilla on the midpoint of the anterior cloacal lip was confirmed.

Artifactual changes in all adult stages were described. The

most common were degeneration due to death of worms or their host and those caused by the immune response of the host. The significance of artifactual changes in the taxonomy of *Strongyloides* was addressed, with particular reference to unusual features described in the literature for various species of *Strongyloides*.

The criteria used to differentiate species in the genus were critically assessed. Those of most use were the stomal shape in the en face view and the ovary type of the parasitic famale, the distribution of caudal papillae in the free living male and features of gubernaculum and spicules, the post vulval constriction and posterior rotation of the vulva in the free-living female, and the stage of the parasite found in freshly voided faeces. Minor criteria were the shape of the tail in the parasitic female, the higher taxon classification of the host, and the occurrence of autoinfective larvae.

Practical problems arising in the identification of unknown specimens were discussed. A significant problem not solved by this thesis is that 41 of the 53 valid species have not been adequately described. Consequently, an unusual approach to identification of unknown specimens was developed. This involved the use of a comprehensive host-*Strongyloides* list to demarcate a series of selection groups comprised of different species. The unknown specimen is compared with the first selection group, and points of similarity noted. Comparison then proceeds through the selection groups whose base broadens progressively. In this way, poorly described species are not omitted from the differential diagnosis. An attempt was made to apply these principles to the *Strongyloides* sp infecting man in Papua Nuigini. Available information indicated it was most consistent with *S.fuelleborni*.

The nett effect of this thesis is a nomenclatural spring cleaning of the species in the genus, a precise definition of the genus with a clearer demarcation of generic characters, clarification of the significance of artifacts on the morphology useful for taxonomy, delimitation of those characters of use in differentiating species, and proposal of a practical scheme for identifying unknown specimens.

KEY TO ABBREVIATIONS USED IN FIGURES AND TABLES.

A	= anus.
AAP	= anterior anal papilla
AD1	= anterior adanal papilla
AD2	= posterior adanal papilla
ARO	= anterior reflection of ovary
ARO-O	= distance between anterior reflection of ovary and posterior end of oesophogus
ART	= anterior reproductive tract
AU	= anterior uterus
B	= oesophageal bulb
BC	= buccal capsule
C1	= anterior part of oesophogeal corpus
C2	= posterior part of oesophogeal corpus
D	= deirid, cervical papilla
DLP	= dorsolateral perivulval papilla
E	= eggs
EP	= excretory pore
G	= gubernaculum
GP	= genital primordium
I	= intestine
Is	= oesophogeal isthmus
J	= junction of testis and vas
L	= length
LP	= lateral papilla
M-V	= distance between anterior end of female and vulva
NR	= nerve ring
O	= posterior end of oesophogus
OES	= oesophogus
OM	= ovum
OV	= ovary
Ovd	= oviduct
P	= phasmid
PO	= preanal organ
PRO	= posterior reflection of ovary
PRO-A	= distance between posterior reflection of ovary and anus
PRT	= posterior reproductive tract

PU = posterior uterus
PVP = perivulval papillae
S = spicule
SDPo = subdorsal postanal papilla
SVP = subventral preanal papilla
SVPo = subventral postanal papilla
Te = testis
T = tail
V = vulva
U = uterus.

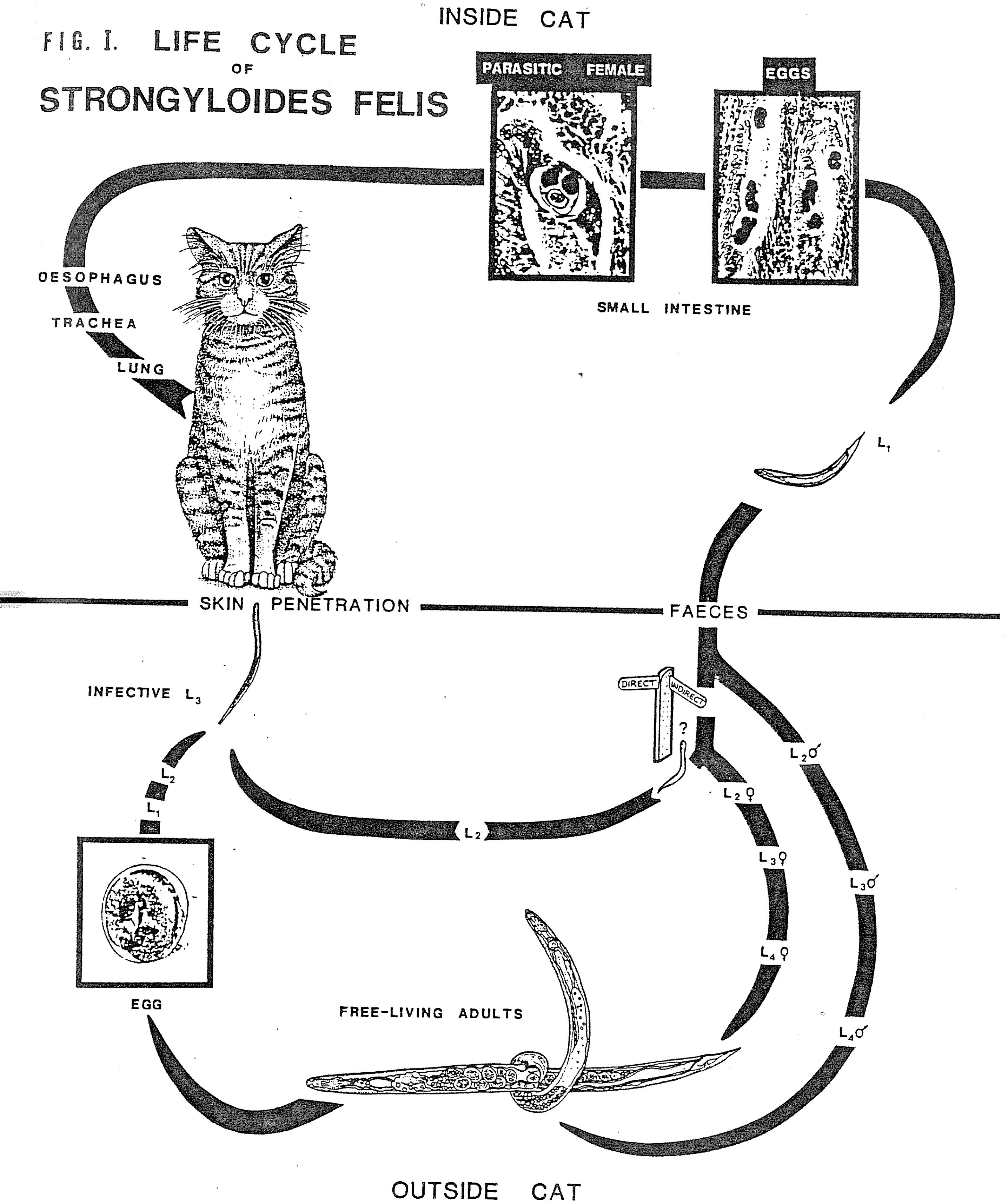
GENERAL INTRODUCTION

The differentiation of species in the genus *Strongyloides* has been a problem since discovery of the type species, *S.stercoralis*, in 1876. Members of the genus in many cases show an alternation of parasitic and free living generations with markedly different morphologies (Fig.I). A controversy occurred initially over whether the free-living stages of *S.stercoralis* and the parasitic form found shortly after represented one species or two. This was resolved by the early 1880's. The problem was then to find criteria by which separate species of *Strongyloides* could be distinguished. This has proved a difficult task.

Many of the difficulties are related to the size of the nematodes. Both the parasitic and free-living stages are small. Owing to their small size *Strongyloides* are fragile, are difficult to find, post-mortem autolysis is rapid, and they are physically difficult to manipulate. The oil immersion lens is required for examination of many features. Their small size also means that differences in the shape of various body parts, or in the positions of papillae, are often expressed in distances less than 10μm. The difference between a stoma that is oval in *en face* view and one that is dumb-bell shaped may be a medial deviation of 1μ of the lateral margins. Consequently, uncertainty can arise in the mind of the observer over whether the differences seen are real, artifactual or even imagined.

A second set of problems is related to the biology of the genus. The parasitic generation consists of females only. There is no parasitic male, a stage which in nematode taxonomy usually forms the cornerstone of species diagnosis. This lack is compensated for by the existence of free-living males and females, although culture of faeces is necessary to obtain them, and they do not always occur, let alone develop. The parasitic female is parthenogenetic (Zaffagnini, 1973; Triantaphyllou and Moncol, 1977). Dioecious reproduction gives a species genetic polymorphism while the variation possible in a species reproducing parthenogenetically is

FIG. I. LIFE CYCLE OF STRONGYLOIDES FELIS



much less. In the latter situation females faithfully reproduce themselves with progeny showing little change from the parent generation. Parthenogenesis may account for the remarkable uniformity of morphology in the genus. Differences between species of *Strongyloides* are rarely determined by the presence or absence of a character but usually are expressed in terms of degree. Uniformity is so great that superficially many species of *Strongyloides* look the same, adding to the taxonomic problems.

The taxonomy of *Strongyloides* is not in its infancy. Useful criteria have been established (Little, 1966a). They enable reasonably closely related species to be differentiated, but in practice have been rarely applied by parasitologists. A major problem is that so few species in the genus have been examined using the newer taxonomic criteria. Only 11 species have been fully described. One of the aims of this study, therefore, is to critically examine as many described species as possible to provide a basis with which comparisons can be made.

Perusal of the literature reveals that several processes are liable to cause artifactual changes in the morphology of *Strongyloides*. These will be examined.

Morphology was chosen as the main taxonomic tool to be used in this study. Several reasons prompted this. Firstly, Little (1966a) had shown species could be differentiated using criteria visible under the light microscope. Light microscopy is a technique which is universally available and relatively easily applied. For a technique to be useful in the practical sense it must have the latter characteristics. Biological studies such as host ranges of particular species of *Strongyloides* (Fleming et al, 1979; Melvin and Chandler, 1950) and ability of free-living stages of different strains to cross (Augustine, 1940) were cumbersome and added little to the understanding of the taxonomy of the genus. Two species examined immunologically showed many shared antigens (Grove and Blair, 1981), and although the species could be easily separated morphologically, differentiation by immunological techniques would not have been possible. Protein electrophoresis has not been used for *Strongyloides*, but minimum amounts of material for a full examination would require large numbers of worms owing to their small size. The technique could be of possible use in theoretical studies only.

Morphological criteria allow limited numbers of specimens whose identity is unknown to be compared with published descriptions and deposited specimens. Once species have been fully described, the next step is to use more sophisticated techniques to test the taxons delimited by the morphological criteria. We are not yet at this stage.

The aims of this study are:

(1) To examine the classification of the genus and the validity of the generic name (Chapter 1).

(2) To redefine the genus (Chapter 2).

(3) To list names of *Strongyloides* found in the literature and to critically examine these from the nomenclatural viewpoint (Chapter 3).

(4) To describe techniques which can be used in examining *Strongyloides* (Chapter 4).

(5) To describe the morphology of artifactual changes (Chapter 5).

(6) To critically examine the criteria used to differentiate between species (Chapter 6).

(7) To illustrate how these criteria can be applied in a particular case (Chapter 7).

CHAPTER 1

CLASSIFICATION OF *STRONGYLOIDES*.

1.1 HIGHER TAXON LEVEL.

The classification of *Strongyloides* shown in Table 1:1 was proposed by Little (1966a).

TABLE 1:1. Classification of *Strongyloides* and related genera.

Class:	Nematoda		
Order:	Rhabdita		
Superfamily:	Rhabdiasoidea Railliet, 1916		
Family:	Strongyloididae Chitwood and McIntosh, 1934		
Genus:	*Strongyloides*	*Parastrongyloides*	*Leipernema*
	Grassi, 1879	Morgan, 1928	Singh, 1976

The relationship of *Strongyoides* to certain free-living rhabditoids was recognised when the type species, *S.stercoralis* , was discovered (Bavay, 1876). The superfamily Rhabditoidea was subsequently proposed to accommodate this group. *Strongyloides* was not placed in a separate family until Chitwood and McIntosh (1934) proposed the family Strongyloididae. Prior to this Travassos (1930a) had placed *Strongyloides* in the family Rhabdiasidae and had proposed a new subfamily, the Strongyloidinae for *Strongyloides* and Parastrongyloides. Travassos had followed Railliet (1916) in dividing the Rhabditoidea into the Rhabdiasidea and the Rhabditoidea. Chitwood and McIntosh (1934), Chitwood and Chitwood (1950) and Anderson and Bain (1982) placed the Strongyloididae in the superfamily Rhabditoidea and ignored the Rhabdiasoidea.

Little (1966a) in a redefinition of the genus *Strongyloides* considered the Strongyloididae and the Rhabdiasidae to be sufficiently different to warrant their placement in the superfamily Rhabdiasoidea. Hyman (1951) had separated Rhabdiasoidea and Rhabditoidea, but had raised both to the rank of order. Yamaguti (1961) created a new order, Rhabdiasidea, for the rhabdiasoids. The most recent review of the higher taxon classification (Anderson and Bain, 1982) ignores Little's classification and uses that of Chitwood and McIntosh (1934), placing Strongyloididae in the Rhabditoidea. None of these workers, however, gave precise reasons why their particular classification should be adopted.

If Little's classification is accepted, the families remaining in the superfamily Rhabditoidea are Rhabditidae and Cephalobidae, free-living saprophagous forms rarely associated with vertebrates, Cylindrocorporidae, including free-living and saprophagous species and three species of *Longibucca* Chitwood, 1933 found in the gastrointestinal tract of a snake and two species of bat, and the Angiostomatidae, parasites of salamanders and terrestrial gastropods (Anderson and Bain, 1982). The Rhabdiasoidea contains only two families, Strongyloididae and Rhabdiasidae, all members of which are parasites of terrestrial vertebrates. These families may not be closely related. Ballantyne (1971) in an unpublished comparative study of the Rhabdiasidae and the Strongyloididae with some data on free-living rhabditoids found that the families Rhabdiasidae and Strongyloididae did not appear to be very closely related although they both had the same number of head papillae and exhibited alternation of parasitic and free-living generations. He concluded that the classification into two families in the Rhabdiasoidea was the most appropriate pending further study since it drew attention to the occurrance of free-living and parasitic generations and was convenient.

The limited number of chromosomal studies on *Strongyloides* have shown that compared with the other members of the Rhabditida, a reduction in chromosal number has occurred (Triantaphyllou, 1983). *S.ratti* has n = 3 (Bolla and Roberts, 1968); while *S.ransomi* and *S.papillosus* has n = 2, where an X chromosome appears to have fused with an autosome (Triantaphyllou and Moncol, 1977). Most free-living rhabditoids have a haploid chromosome number of six, as do members of *Rhabdias*, the type genus of the Rhabdiasoidea. *Strongyloides* represents an advanced state of karyotypic evolution among the Rhabditida (Triantaphyllou, 1983). Strongyloididae, therefore, does not rest comfortably with the Rhabdiasidae in the Rhabdiasoidea. The Rhabdiasoidea contain no exclusively free-living members, the parasitic form is found only in the gut or lungs of terrestrial vertebrates and they exhibit alternation of generations. Such a classification is a compromise based on superficial data, but more accurately reflects relationships between the families than placement of all in the Rhabditoidea. The preliminary evidence cited suggests that the Strongyloididae are at least sufficiently different to warrant placement in their own superfamily, but more comprehensive comparative studies are required, particularly of the other members of the Rhabdiasoidea, before such a change is justified.

1.2 GENERIC LEVEL.

Strongyloididae contains three genera, *Strongyloides*, *Parastrongyloides* and *Leipernema*. The free-living generation in all are small rhabditoid nematodes, while the parasitic generation is a small, slender stage. The genera can be distinguished using the parasitic stage (Little, 1966a; Anderson and Bain, 1982). *Strongyloides* possesses only a parasitic female with a shallow buccal capsule (Little, 1966a), *Parastrongyloides* is dioecious with a globular buccal capsule (Morgan, 1928), and *Leipernema* lacks a parasitic male and the anterior ends of the oesophagus of the parasitic female protrudes through the stoma (Singh, 1976) (see Fig.1:1).

Fig.1:1. Lateral view of heads of parasitic females from the Strongyloididae. A. *Strongyloides stercoralis* ex small intestine of dog; B. *Parastrongyloides sp.nov.* ex small intestine of echidna, *Tachyglossus aculeatus*; C. *Leipernema leiperi* ex small intestine of pangolin, *Manus pentadactylus* (from Singh, 1976 p270 Fig.2).

1.3 NAME OF THE GENUS.

Strongyloides papillosus (Wedl, 1856) is the oldest species in the genus although originally placed in *Trichosoma*. The second oldest is the type species, *S.stercoralis* (Bavay, 1876), described originally as *Anguillula stercoralis* from the free-living generation in human faeces (Bavay, 1876). Initially the occurrence of both free-living and parasitic generations was not realised and in 1877 the parasitic female was found and described as *Anguillula intestinalis* (Bavay, 1877a). Suspicion that these were two forms of the same parasite soon arose (Bavay, 1877b). Conclusive proof was not provided until five years later (Grassi, 1882). *A.intestinalis* is, therefore, the junior synonym of *A.stercoralis*. Since the correct identity of *S.papillosus* was not recognised until 1911 when

Ransom placed it in *Strongyloides*, *S.stercoralis* was established as the type species.

The generic name was unstable until the early 1900's. Various names used for both the genus and the type species are listed in Table 1:2.

TABLE 1:2. Names used for *Strongyloides* and *S.stercoralis*.

GENUS

Valid name:	*Strongiloides* Grassi, 1879
Rejected names:	*Trichosoma* Wedl, 1856
	Rhabditis Bavay, 1876
	Anguillula Bavay, 1876
	Leptodera Cobbold, 1879
	Pseudorhabditis Perroncito, 1881
	Rhabdonema Leuckart, 1882
	Strongyloides Anon, 1879

TYPE SPECIES

Valid name:

Strongiloides stercoralis (Bavay, 1876) Grassi, 1879

Rejected names:

Anguillula stercoralis Bavay, 1876
Rhabditis stercoralis Bavay, 1876
Anguillula intestinalis Bavay, 1877
Leptodera stercoralis (Bavay, 1876) Cobbold, 1879
Leptodera intestinalis (Bavay, 1877) Cobbold, 1879
Strongiloides intestinalis (Bavay, 1877) Grassi, 1879
Pseudorhabditis stercoralis (Bavay, 1876) Perroncito, 1881
Rhabdonema strongyloides Leuckart, 1882
Rhabdonema intestinale (Bavay, 1877) Blanchard, 1885
Rhabditis intestinalis Oerley, 1886
Strongyloides intestinalis (Bavay, 1876) Anon, 1879
Strongyloides stercoralis (Bavay, 1876) Stiles & Hassall, 1902

Hall (1916) and Yorke and Maplestone (1926) listed *Stercoralis* Tanaka, 1910 as a generic synonym. They failed to provide a reference and I have been unable to locate a paper by Tanaka in that year.

When Bavay (1876) placed his species in the pre-existing genus *Anguillula*, he also included *Rhabditis* as a generic synonym. Cobbold (1879) placed the parasite in *Leptodera*, another synonym of *Rhabditis*; Perroncito (1881) proposed the new generic name of *Pseudo*-rhabditis and Leuckart (1882) proposed *Rhabdonema*. The name currently used for the genus is *Strongyloides* and is attributed to Grassi (Thayer, 1902). Grassi (1879a), however, writing in Italian in Recondiconti Dell Instituto Lombardo, Di Scienze e Lettere, Milano : 2 ; xii (p233) used *Strongiloides*. Italian has no "y".

It is apparent from the text that Grassi was making a comparison with *Nematodirus filicollis*; a synonym at the time was *Strongylus filicollis* Molin, 1861 :

> "Da questi studj e da altri comparativi, specialmente collo *Strongilo filicolle* della pecora col quale il nostro verme ha molta somiglianza, io sono venuto nella opinione che la cosidetta anguillula intestinale debba considerarsi come un genere molto affine allo strongilo, da denominarsi *Strongiloides*; ma sovra questo punto tornero in una prossima lettura in cui, se gli indizj di recenti sperimenti non mi ingannano, riferiro intera la storia dello sviluppo del-l'anguillula intestinale."

(see also Fig.1:2)

Fig.1:2. English translation of Grassi's Italian (1879a p233).

"From these studies and from other comparisons, especially with *Strongilo filicolle* in sheep with which our worm has much in common, I am led to believe that the so called intestinal anguillula is to be considered as a genus with close affinity to the strongyles, to be called *Strongiloides*; but I shall come back to this point in a future reading in which, if the indications of recent experiments do not decieve me, I shall relate the entire history of the development of the intestinal anguillula."

The generic name *Strongylus* was proposed by Muller in 1780 and was spelt with a "y". One could argue, therefore, that had "y" been available to Grassi, he would have used the spelling "*Strongyloides*", not "*Strongiloides*". *Strongiloides*, however, satisfies all provisions of Articles 10 to 20 of the International Code of Zoological Nomenclature, 1985. Emendation is possible only under Article 32 "Original Spelling" and only under c(ii):

"(ii) there is in the original publication itself, without recourse to any external source of information, clear evidence of an inadvertent error, such as a *lapsus calami* or a copyist's or printer's error (incorrect transliteration or latinisation and use of an inappropriate connecting vowel are not to be considered inadvertent errors);"

To assess whether Grassi's use of *Strongiloides* was inadvertent Grassi's subsequent publications were viewed (Grassi, 1879b; 1882a&b; 1883a,b,&c; 1885; Grassi and Parona, 1879; Grassi and Calandruccio, 1884 ; Grassi and Segre, 1887). Grassi did not use *Strongiloides* again. *Strongyloides*, however, was used in the same year in an abstracting journal (Medicina Contemparanea, Milano 3: 495-497). The anonomous author reviewed Grassi's 1879 paper and used the name *Strongyloides intestinalis*. *Strongyloides* is therefore a *lapsus calami* by this reviewer and consequently unavailable. The next author to use *Strongyloides* appears to be

Leuckart (1882), but the same ruling will apply to his and all subsequent uses. Grassi used *Anguillula* or *Rhabdonema* in all subsequent publications. Examination of Grassi's publications for the use of "y" revealed use for "Bavay" (Grassi 1882; Grassi and Calandruccio, 1884 p492) and for "*Rhabdonema strongyloides*" (Grassi, 1883b p261; Grassi and Calandruccio, 1884 pp492,494). Grassi therefore had the option of using "y" had he so desired. The use of "i" in *Strongiloides* was not inadvertent ; it was a result of the limitations of the language used and Grassi's choice to use a strictly latinised form. The correct name of the genus is therefore *Strongiloides* Grassi, 1879.

Hall (1916 p6) listed *Strongiloides* as a synonym of *Strongyloides*, but indicated the latter name was the valid name for the taxon. He gave as authorities *Strongiloides* Grassi, 1879a and *Strongyloides* Grassi, 1879b, and used *Strongyloides* as the valid name without comment. This was an error, since *Strongiloides* has priority. No other author has listed *Strongiloides*.

Adoption of *Strongiloides* as the valid name of the genus, although correct, would disrupt nomenclatural stability as a whole. Mindful of the accusation of "taxonomic nit-picker", I decided to consult the International Commission on Zoological Nomenclature. My attention was drawn to Opinion 66 of 1915, by which *Strongyloides* was placed on the Official list (Fig.1:3). Although this act does not give the name precedence over any other (Article 78), it clearly indicates that at that time *Strongyloides* was considered to be the most appropriate name for the genus. The same opinion holds true today. A change of name would be disruptive without benefit. *Strongyloides* should be retained.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

In replying to this letter, please quote the following reference number:

ZN(G)34

ICZN

c/o BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD,
LONDON, SW7 5BD
TEL. 01-589 6323, Ext. 387

3 February 1986

Dr. Richard Speare,
Graduate School of Tropical Medicine,
James Cook University,
Townsville Q 4811,
Australia.

Dear Dr. Speare,

Thank you for your letter of January 22.

The name Strongyloides was placed on the Official List by Opinion 66 of 1915. Under the Code (Article 78) this act does not of itself give the name precedence over any other, but it does clearly indicate that at that time specialists carefully considered it, and concluded it to be the appropriate name, as I believe has always been true.

I see that Grassi in 1879 used both Strongiloides and Strongyloides; presumably it is implicit in your letter that the former was earlier, and has priority. Nevertheless, the fact that the latter spelling has been on the Official List for over 70 years should not be ignored except for very good reasons, and I feel that to pursue the proposed case would probably be a rather unrewarding use of time.

We do of course very much appreciate your interest. If you do wish to present cases to the Commission we can send you a copy of the guide-lines to authors, and any recent number of the Bulletin of Zoological Nomenclature will provide models.

Yours sincerely,

~~Dr. P. K.~~ Tubbs

FIG.1:3. Letter from the International Commission on Zoological Nomenclature re validity of generic name.

1.4 SUMMARY.

The classification of the genus has been discussed and that proposed by Little (1966a) considered to be the most suitable compromise, with the comment that further comparative work may show relationships between the Strongyloididae and the Rhabdiasidae to be not as close as implied by inclusion in the same superfamily.

The most controversial point to emerge from the historical review, however, is that the generic name as it now stands is in all probability incorrect. "*Strongiloides*" is the correct spelling. Adoption of this name would have the effect of changing all valid names in the genus. This would not serve stability of nomenclature in the genus. Opinion 66 of 1915 of the International Commission on Zoological Nomenclature placed *Strongyloides* on the Official list of Names. This opinion should be followed today.

CHAPTER 2

DEFINITION OF THE GENUS

2.1 INTRODUCTION.

"define" :

1. to explain the nature or essential qualities of;

2. to determine or fix the boundaries or extent of.

(Random House Dictionary of the English Language)

These two meanings are highly germaine to taxonomy and the definition of taxa. They encompass both vital aspects of a "good" definition; firstly, the description of those essential qualities which make the taxon what it is, and secondly, the setting of limits to enable a particular taxon to be recognised as distinct from others. On the generic level, the definition should include only those traits found in all members of the genus. It should not include those characters used to separate particular species within the genus.

Members of *Strongyloides* show a uniformity of morphology which simplifies the description of the generic characters and the fixing of generic boundaries. At first, the genus was poorly defined, and some species were included which did not belong (viz., *S.bovis* and *S.viviparus*). The first formal generic definition appears to be that of Brumpt (1913). This was expanded by Yorke and Maplestone (1926) and modified by Yamaguti (1961). Little (1966a) redefined the genus by giving comprehensive descriptions of 12 of the 18 life cycle stages. Emphasis was placed on the parasitic female, the free-living adults, and the infective larva, with descriptions of the first, second, third and fourth stage larvae of the indirect cycle, first and second stage larvae of the direct cycle and eggs both of the parasitic and free-living generations.

Prior to this redefinition, a number of characteristics had not been regarded as generic features, and had been used to separate species in the genus. Little's redefinition had great value in stating that certain features were generic. The most important of these was that the free-living males of all species had a solitary mid-line papilla and six pairs of caudal papillae, and that within certain limits these papillae were found in predictable locations. Other important points were that the spicules and gubernaculum of all males had a similar general morphology, the parasitic female had no lips and a constant number of cephalic papillae, and that the free-living females and larval stages varied little in morphology between species. Little's descriptions were comprehensive, precise and clearly stated.

The definition of *Strongyloides* that follows is based on Little (1966a). It is intended to serve both as a definition of the genus and as an introduction to important aspects of its morphology. In this thesis Little's definition has been modified in two ways; firstly, generic features omitted by Little have been included, and secondly, errors have been corrected. If Little's description has been considered to be complete and correct, it has been reproduced unchanged and no comment made.

The specimens upon which the study is based are listed in Appendix I, and the techniques used are given in Chapter 4. The specific names used are those deemed to be valid in Chapter 3. Invalid synonyms used by the authors cited are given in parenthesis after the valid name.

Table 2:1 contains dimensions for the parasitic females of those species of *Strongyloides* ruled to be valid in Chapter 3. These dimensions are taken solely from the literature, either from the original description or, if this was inadequate, the most complete set of data available was used.

Unavailable values are shown as "–", and calculated values as "*". Many of the earlier authors failed to give means and gave ranges only. In this case, "mean" was estimated as the mid-point of the range; i.e., minimum + maximum ÷ 2 = "mean". Some authors (Schwartz and Alicata, 1930; Basir, 1950) listed the dimensions of a series of individual worms; consequently, means and standard deviations could be accurately calculated. These values are marked with "●". Proportions, e.g., oesophageal length / body length, were calculated by dividing means. These are marked with "*". Where measurements of a series of worms were given, the proportions were calculated for each individual worm, and mean and standard deviation calculated for the series. This is indicated by "●".

TABLE 2:1. Dimensions of parasitic females of valid species of Strongyloides : from literature.

ID NO	SPECIES	LENGTH	MAX. WIDTH	OESOPHAGUS	M-V	TAIL	WIDTH /L %	OES /L %	M-V /L %	TAIL /L %	REFERENCE
1	*S.agoutii*	5170±724.2 (3940-6450)	44±6.3 (30-59)	1210±135.9 (975-1450)	3420* (2665-4150)*	91±9.9 (75-109)	0.85*	23.4* (20-25)	66.2* (64-68)*	1.76* (1.7-1.9)*	Griffiths,1940
2	*S.akbari*	1408.5* (1273-1544)	32.5 (31-34)	650	887.4*	31	2.31*	42.1	63.0	2.0	Mirza & Narayan,1935
3	*S.amphibiophilus*	1850 (30-32)	31* (510-525)	517.5	1230 (58-64)	61*	1.68*	28*	66.5	3.3*	Perez Vigueras,1942
4	*S.ardeae*	1890 (1500-2100)	35 (30-40)	650 (480-780)	1280 (920-1500)	35 (30-50)	1.85*	34.4*	67.7*	1.85*	Little,1966b
5	*S.avium*	2200	42.5* (40-45)	700	1400	55	1.93*	31.88*	63.6*	2.5*	Cram,1929
6	*S.bufonis*	1650* (1500-1800)	30* (23-37)	440* (370-510)	–	65* (60-70)	1.82*	33.3	–	3.9*	Rao & Singh, 1968
7	*S.carinii*	1500* (1300-1700)	40	600* (500-700)	1100* (1000-1200)	60	2.67*	40*	75	4.0*	Pereira,1935
8	*S.cati*	2800 (2370-3330)	40.2*	707*	1825.6*	37.9*	1.44*	25.2*	65.2	1.35*	Rogers,1939
9	*S.cebus*	4070 (2800-5000)	59 (50-80)	930 (740-1300)	2540 (1800-2900)	71 (60-95)	1.45*	22.9*	62.4*	1.74*	Little,1966a
10	*S.chapini*	4583.3±870.2* (3800-5520)	27.8±1.2* (26-28)	–	–	–	0.6*	–	–	–	Sandground, 1925
11	*S.cruzi*	2425* (1630-3220)	65* (40-90)	578.5* (525-632)	1542.5* (1295-1790)	77.5 (72-81)	2.68*	17.9*	63.6*	3.2*	Rodrigues,1968
12	*S.cubaensis*	2300* (2200-2400)	48	550* (540-560)	1350* (1300-1400)	73* (70-76)	2.09*	23.9*	66.6*	3.17*	Perez Vigueras,1942
13	*S.darevskyi*	1500* (1400-1600)	34.5* (33-36)	530* (460-600)	–	51.5* (48-55)	2.30*	35.3*	–	3.43*	Shapilo,1976
14	*S.dasypodis*	2010 (1600-2300)	36 (30-40)	780 (630-870)	1360 (1000-1600)	41 (33-52)	1.79*	38.8*	67.7*	2.04*	Little,1966b
15	*S.elephantis*	3090±310* (2680-3670)	35.6±3.5* (29-39)	750 (680-830)	2255.7*	49.6±2.5* (46-54)	1.15*	24.3*	73±1.7*	1.61±0.16*	Greve,1969
16	*S.erschowi*	6500 (5500-7500)	87.5*	1052.5* (937-1168)	–	–	1.35*	16.2*	–	–	Popova,1928
17	*S.eryxi*	3180* (2670-3690)	40	975* (880-1070)	2140* (1750-2530)	76.5* (63-90)	1.26*	33.3*	66.7*	2.41*	Mirza & Narayan,1935
18	*S.felis*	2760* (2600-2920)	42* (39-45)	690*	1857.5*	70.4* (63-104)	1.52*	25	67.3* (66.6-68)	2.55*	Chandler,1925b (2.3-2.8)
19	*S.fuelleborni*	3470 (2900-4200)	51 (43-55)	800 (710-980)	2210 (1700-2700)	56 (45-70)	1.47*	23.1*	63.7*	1.61*	Little,1966a
20	*S.gulae*	2170 (1800-2400)	34 (30-40)	850 (710-1000)	1510 (1200-1700)	77 (60-95)	1.57*	39.2*	69.6*	3.55*	Little,1966b
21	*S.herodiae*	2585* (2370-2800)	34* (32-36)	595* (530-660)	–	50.5* (48-53)	1.32*	23	–	2.05*	Boyd,1966
22	*S.lutrae*	1860 (1600-2500)	29 (25-37)	750 (650-870)	1250 (1100-1400)	40 (30-62)	1.56*	40.33*	67.2*	2.15*	Little,1966b
23	*S.martis*	2961* (2856-3066)	48* (43-53)	727* (682-772)	–	61* (57-65)	1.62*	24.6*	–	2.06*	Petrov,1940
24	*S.minimum*	1452.5* (1125-1780)	38.5* (37-40)	531* (512-550)	–	50	2.65*	36.6*	–	3.44*	Travassos,1930

ID NO	SPECIES	LENGTH	MAX. WIDTH	OESOPHAGUS	M-V	TAIL	WIDTH /L %	OES /L %	M-V /L %	TAIL /L %	REFERENCE
25	*S.mustelorum*	3300	60	900	1900	-	1.82*	27.3*	57.6*	-	Cameron & Parnell,1933
26	*S.myopotami*	4120 (3100-5200)	37 (30-42)	1090 (80-1300)	2850 (2200-3600)	57 (40-75)	0.90*	26.5*	69.2*	1.38*	Little,1966a
27	*S.nasua*	2240* (2080-2400)	50* (48-52)	880*	1608* (1472-1744)	-	2.23*	39.3*	71.8*	-	Darling, 1911
28	*S.ophidae*	3150* (2700-3600)	40	1090* (1050-1130)	2101*	85* (70-100)	1.27*	33.3	66.7	2.7*	Pereira,1929
29	*S.oswaldi*	3000	60	480	1800	-	2.0*	16*	60*	-	Travassos,1930
30	*S.papillosus*	5312±371● (4780-5850)	57.5● (50-65)	839±83● (720-950)	3233±263● (2860-3540)	64.5±7.1● (54-78)	1.08*	15.8±0.6● (15-17)●	60.9±2.4● (58-67)●	1.22±0.13● (1.1-1.4)●	Basir,1950
31	*S.pavonis*	3410 (2730-4190)	50.4 (43-60)	805 (725-915)	2090 (1685-2495)	62.3 (51-75)	1.48*	23.6*	61.1 (59-65)	1.83*	Sakamoto & Yamashito,1970
32	*S.pereirai*	1740* (1560-1920)	44* (40-48)	470* (400-540)	1160.6*	68* (64-72)	2.53*	27.0*	66.7*	3.90*	Travassos,1930
33	*S.petrovi*										
34	*S.physali*	1650 (1400-2100)	38 (33-45)	550 (470-670)	1150 (1000-1400)	56 (50-65)	2.30*	33.3*	69.7*	3.39*	Little,1966b
35	*S.procyonis*	2590 (1800-2900)	31 (28-37)	700 (640-760)	1710 (1200-1900)	53 (50-64)	1.2[1]	26.9*	66.0*	2.05*	Little,1966
36	*S.putorii*	2200* (2090-2310)	38.5* (33-44)	169.5* (166-173)	1358* (1261-1455)*	41	1.75*	7.7*	61.7*	1.86*	Morosov,1939
37	*S.quiscali*	1825* (1630-2020)	43* (42-44)	520* (500-540)	1135* (1000-1270)	42.5* (41-44)	2.36*	28.5*	62.2*	2.3*	Barus,1968
38	*S.ratti*	2370 (2100-3100)	34 (30-38)	740 (730-760)	1600 (1400-1900)	55 (45-65)	1.43*	31.2*	67.5*	2.32*	Little,1966
39	*S.ratti* v. ondatrae	4000	33	1000	2500*	57.5* (55-60)	0.82*	25*	62.5*	1.44*	Chandler,1941
40	*S.robustus*	6100 (4500-6800)	67.5* (60-75)	1140 (860-1260)	3560*	75* (70-80)	0.61*	18.3* (17.7-19.0)	61.0*	1.22* (65-57)	Chandler,1942
41	*S.rostombekowi*	2740	60	1000	1815*	140	2.19*	36.5*	66.2*	5.1*	Gamzemlidse, 1941
42	*S.serpentis*	3170 (2400-3700)	40 (30-50)	1280 (890-1500)	2180 (1700-2500)	75 (50-100)	1.26*	40.3*	68.8*	2.37*	Little,1966b
43	*S.sigmodontis*	4300* (3900-4700)	31	885* (870-900)	2700* (2600-2800)	53	0.72* (19-22)	20.5*	63.5* (63-64)	1.23*	Melvin & Chandler,1950
44	*S.spiralis*	1568.2±167.5 (1200-2025)	31.8+2.0 (28-37)	601.2±55.6 (391-740)	1126.9±126.7 (860-1400)	54.6±6.0 (40-74)	2.03*	38.3*	71.9*	3.48*	Grabda-Kazubska 1978
45	*S.stercoralis*	2420 (2100-2700)	37 (30-40)	570 (480-670)	1670 (1400-1800)	54 (40-70)	1.5[1]	23.8	69*	2.23*	Little,1966a&b
46	*S.stercoralis* v. vulpi	2200	32.5	575	1500	40	1.48*	26.1*	68.2*	1.82*	Mirza & Narayan,1935
47	*S.suis*	3942.2±443.1● (3330-4490)	61±2.8● (54-62)	783±91.4● (605-883)	2527±419.3● (1922-2968)	70.9±9.5● (67-83)	1.55*	19.2● (18-24)●	64.2● (61-74)●	1.81● (1.4-2.2)●	Schwartz & Alicata,1930
48	*S.thylacis*	3040 (2250-3820)	40* (30-50)	875* (780-970)	1980 (1450-2400)	-	1.32*	28.8*	65.1	-	Mackerras,1959
49	*S.tumefaciens*	5000	109	875* (750-1000)	3400	110* (106-114)	2.18*	17.5*	68.0	2.2	Price & Dikmans,1941
50	*S.turkmenica*	1905* (1740-2070)	39* (33-45)	467.5* (381-554)	1070*	45.5* (42-49)	2.05*	24.5*	56.2*	2.39*	Kurtieva,1953

ID NO	SPECIES	LENGTH	MAX. WIDTH	OESOPHAGUS	M-V	TAIL	WIDTH /L %	OES /L %	M-V /L %	TAIL /L %	REFERENCE
51	*S.venezuelensis*	2590	38	680	1740	44	1.47*	26.3*	67.2*	1.7*	Little,1966a
		(2000-3200)	(33-41)	(650-780)	(1400-2200)	(38-58)					
52	*S.vulpis*										
53	*S.westeri*	8500*	875*	1350*	5669.5*	125*	1.03*	15.5*	66.7	1.47*	Ihle,1917
		(8000-9000)	(80-95)	(1200-1500)		(120-130)					

[I] These values were inadvertently transposed in Little (1966b; Table V). Correct values have been substituted.
* = calculated from original values as explained in text;
● = calculated from full series of original measurements as explained in text.
- = means not available in literature and insufficient data in literature to enable calculation.

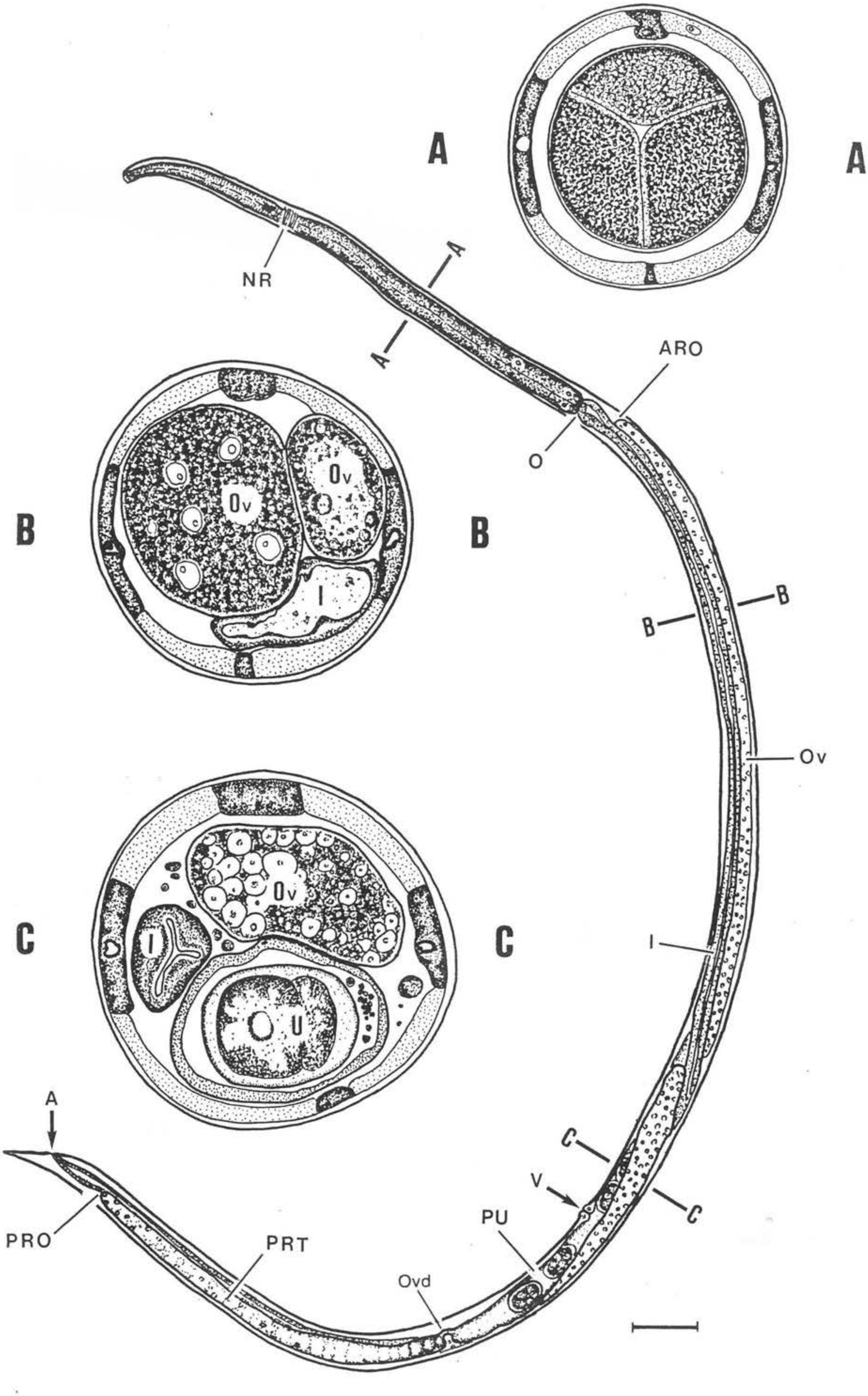


FIG.2:1. Parasitic female : *Strongyloides felis* from duodenum of cat. Scale line, for whole worm = 100μm; for transverse sections = 10μm.

2.2 DEFINITION.

STRONGYLOIDES Grassi, 1879.

2.2.1 Parasitic Female (Fig.2:1).

2.2.1.1 Description. -

Slender nematode, from 1.5mm to 10mm in length by 27 to 95µm in maximum width, average for genus 3013 by 44.8µm; width less than 4% of length. Cylindrical, slightly attenuated at anterior end, abruptly tapered at tail. Body wall thin, cuticle finely striated. Tail short, cone shaped. Head with circumoral elevation, lips absent. Stoma shallow, bilaterally symmetrical. No cephalic papillae, amphids at lateral margin of head (Fig.2:2).

FIG.2:2. *En face* view of parasitic female of *Strongyloides westeri* from small intestine of foal. Arrows mark amphids. SEM.

FIG.2:3. Vulva of parasitic female of *Strongyloides westeri* from small intestine of foal. SEM.

Single, dome shaped cervical papilla, bilaterally at level of excretory pore. Nerve ring crosses oesophagus in anterior 25%. Oesophagus cylindrical, portion anterior to nerve ring primarily muscular; portion posterior chiefly composed of a dorsal and two subventral glands each with a large nucleus near base of oesophagus; dorsal nucleus anterior to subventral nuclei which lie close together. Subventral glands drain into lumen of oesophagus at junction of glandular and muscular portions; dorsal gland empties into lumen near stoma. Intestine composed of 40 cells arranged in two rows (dorsal and ventral), each with a single nucleus; rectum short.

Excretory system composed of a single renette cell and lateral canals extending anteriorly and posteriorly in lateral chords. Excretory duct opens ventrally just posterior to nerve ring. Lateral chords larger than dorsal and ventral (Fig.2:1 A-C). Musculature meromyarian and platymyarian with one or two muscle cells per sector.

Reproductive system didelphic with opposed, equal uteri and reflexed ovaries; no seminal receptacles. Vulva two-thirds body length from anterior end, transverse slit (Fig.2:3), with a prominent cell forming anterior and posterior margins. Vagina very short, oviducts short with cellular walls (Fig.2:4), distal ends of ovaries lie near vulva.

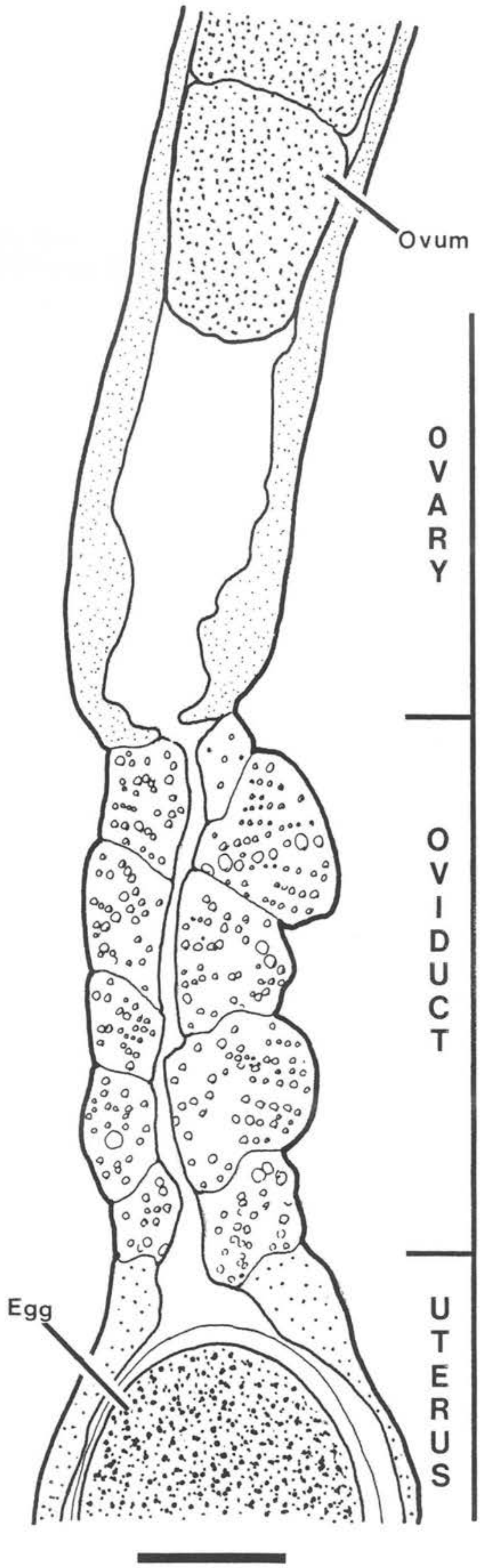


FIG.2:4. Oviduct region of parasitic female of *Strongyloides* sp from stomach of spectacled hare wallaby, *Lagorchestes conspicillatus*. Scale line = 10µm.

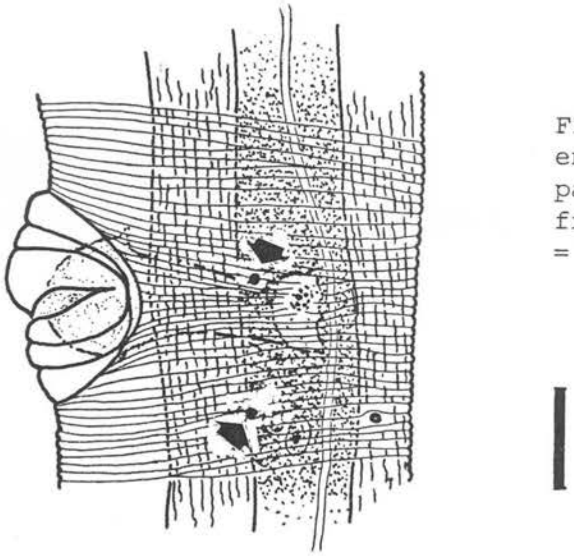


FIG.2:5. Perivulval papillae or nerve endings (arrows) lateral to vulva of parasitic female of *Strongyloides suis* from small intestine of pig. Scale line = 20µm.

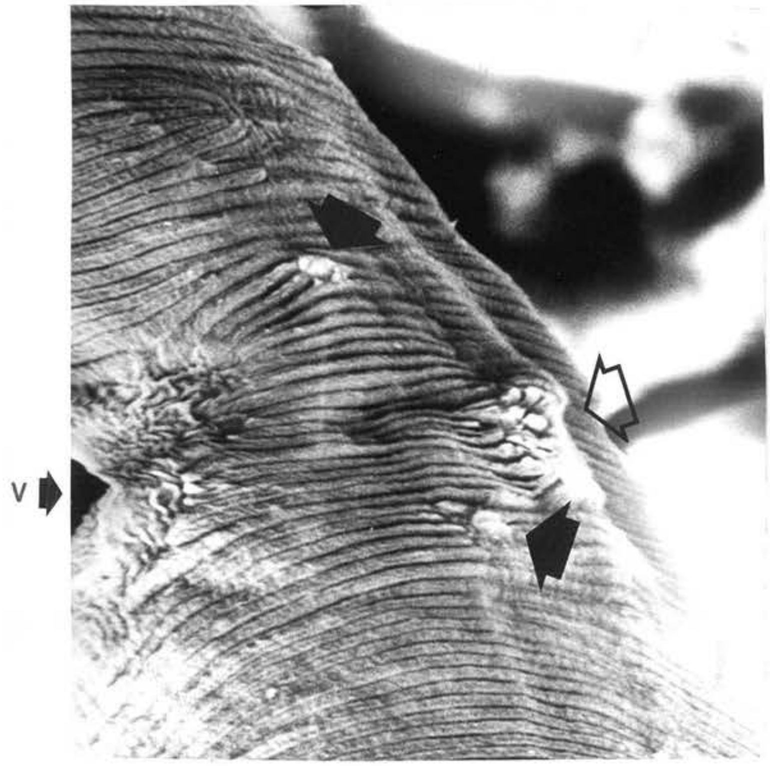


FIG.2:6. Perivulval papillae (solid arrows) and cuticular modification (open arrow) lateral to vulva of parasitic female of *Strongyloides westeri* from small intestine of foal.

Paired nerve endings bilateral to vulva (Fig.2:5). Cuticle dorsal to these modified where vulval cells insert into hypodermis (Fig.2:6). Phasmids bilaterally on tail, offset (Fig.2:7). Parasitic in the mucosa of the gastrointestinal tract of vertebrates.

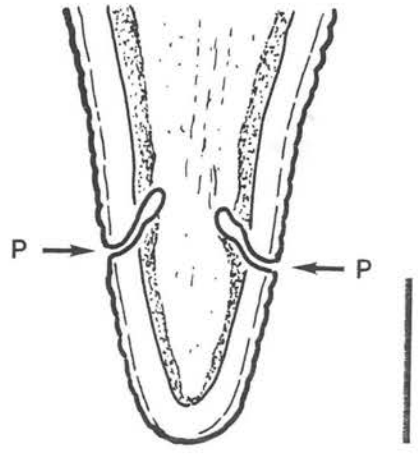


FIG.2:7. Phasmids, of parasitic female : *Strongyloides* sp from stomach of rufous rat kangaroo, *Aepyprymnus rufescens*. Dorso-lateral view. Scale line = 10µm.

2.2.1.2 Additions to Little's definition. -

Cervical Papillae.

All parasitic females have a small, dome shaped papilla bilaterally at the level of the nerve ring. Nerve fibres can be seen passing from the ring through the cuticle to each papilla. These papillae were noted by Arizono et al (1976) in *S.cati* (syn.*S.planiceps*) and by Sakamoto et al (1981) in *S.pavonis*. Both groups used SEM. The papillae are difficult to see using light microscopy, appear more prominent in some species (e.g., *S.suis*), but with care can be found in all. Little omitted this structure in his generic definition.

Position of vulva.

Many authors in the descriptions of their particular species have noted that the vulva divides the body in the proportions of 2:1. Little (1966a) included this in his definition of the genus. It is a point, however, which deserves greater emphasis. Fig.2:8 shows the plot of distance from mouth to vulva (M-V) against body length for valid species of *Strongyloides*. The regression coefficient is 0.991 and R squared is 0.981 indicating a very high degree of fit to the regression line. M-V/length is, therefore, a significant generic feature.

S.bovis has a M-V/length of 79% (calculated from Vryberg (1908, Plate 1, Fig 1) and the value for *S.viviparus* is 50% (Yorke and Maplestone, 1926). On the basis of other criteria, these two species were transfered from *Strongyloides*. Any species considered for placement in *Strongyloides*, and having a M-V/length not falling on the regression line, must be critically reassessed as to its true generic identity.

Perivulval Papillae.

The parasitic female has several cuticular structures lateral to the vulva. There is a pair of small papillae found bilaterally. Nerve fibres can be seen passing through the cuticle to each. The papillae appear as very small nerve endings just projecting above the cuticular surface (Fig.2:6) and are refractile under light microscopy.

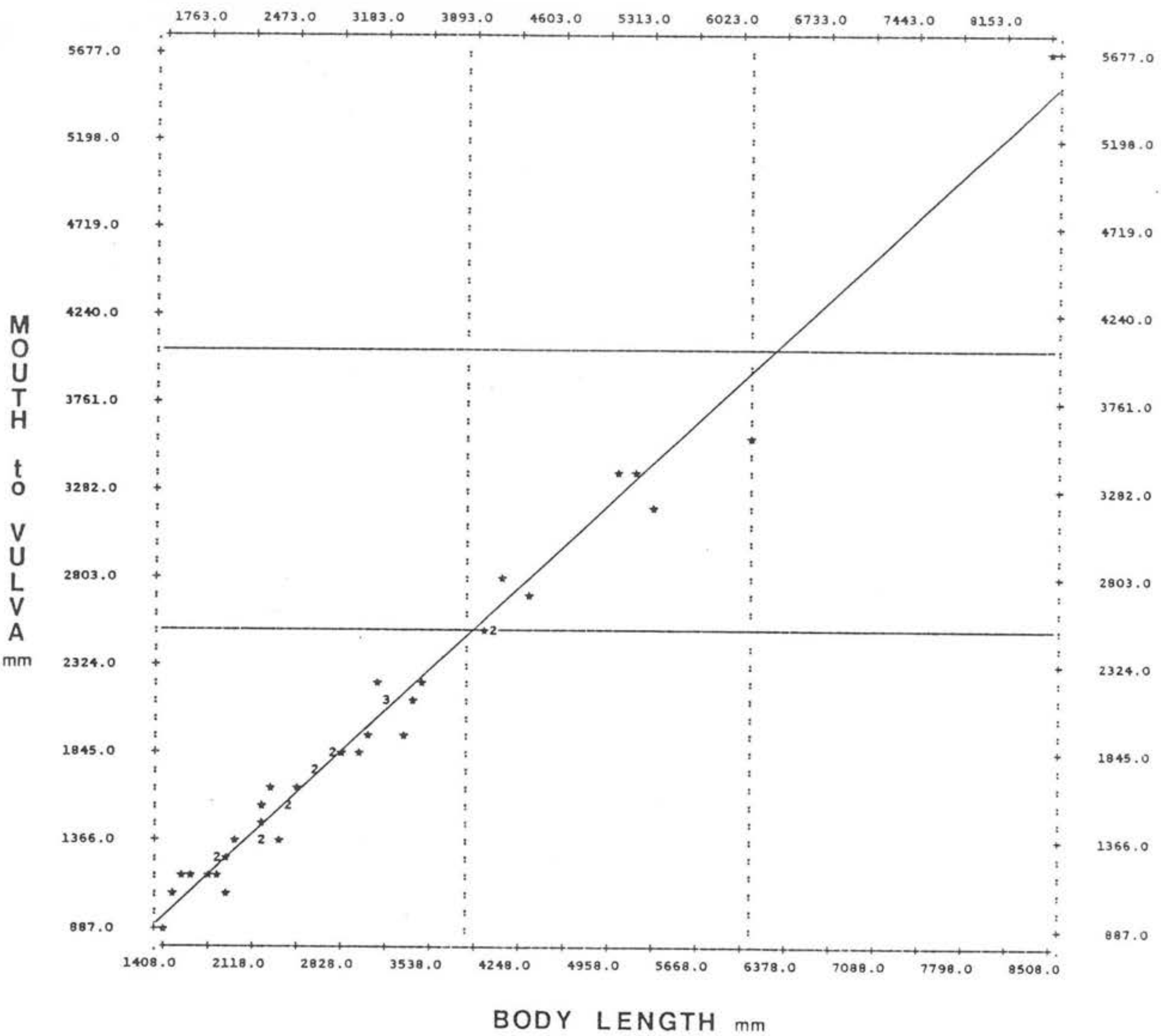


FIG.2:8. Regression of M-V against length for valid species of *Strongyloides*. Data from literature. R = 0.99058
R^2 = 0.98125, y = 0.63357x + 52.13136.

The members of each pair are in the same longitudinal line usually where the ventral border of the lateral chord meets the ventro-lateral muscle bundle (Fig.2:5). They are always within about 100μm of the position of the vulva. These papillae have not been noted previously, but in suitable specimens can be seen in all species.

A larger dome shaped papillae is seen in some species in the dorso-lateral position, usually bilaterally. This is refractile under light microscopy, and nerve fibres can be seen to pass through the cuticle to it. It does not occur in all species of *Strongyloides*, however, so it is not a generic character.

The cuticle at about the mid-lateral point at the level of the vulva is modified in some way in all species. This is the area where the cells forming the anterior and posterior lips of the vulva terminate and appear to be attached into the hypodermis. The nature of the cuticle at this point varies with the species, but ranges from a depression to a dome. Nerve fibres are not apparent and so the structure seems to be solely cuticular and not sensory. These cuticular structures were described by Arizono et al (1976) and Sakamoto *et al* (1981) for *S.cati* (syn. *S.planiceps*) and S.pavonis respectively. The presence of a cuticular modification is a generic feature, while its nature is specific.

The paired perivulval papillae and the cuticular modification lateral to the vulva were not included by Little (1966a) in his redefinition.

Phasmids.

All parasitic females have a phasmid situated bilaterally at about the middle of the tail. These are pocket-like with a nerve fibre passing obliquely in a posterior direction through the cuticle. In some species they are difficult to make out by light microscopy, while in others they are very prominent in ventral or dorsal views (Fig.2:7). The phasmids are not found equidistant from the tail tip; they are always offset by about 1-2μm. McLaren (1976) suggested phasmids may function with amphids to detect differences in the intensity of a stimulus, thus helping to maintain the worm in a favourable environment. The fact that the phasmids of *Strongyloides* are offset may allow directional localisation of a stimulus.

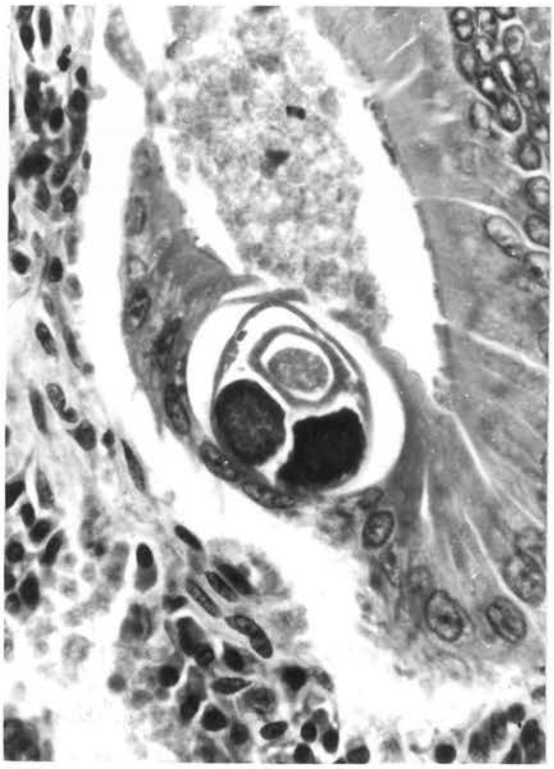


FIG.2:9. Parasitic female of *Strongyloides felis* in a mucosal tunnel in duodenum of cat. H & E X 400.

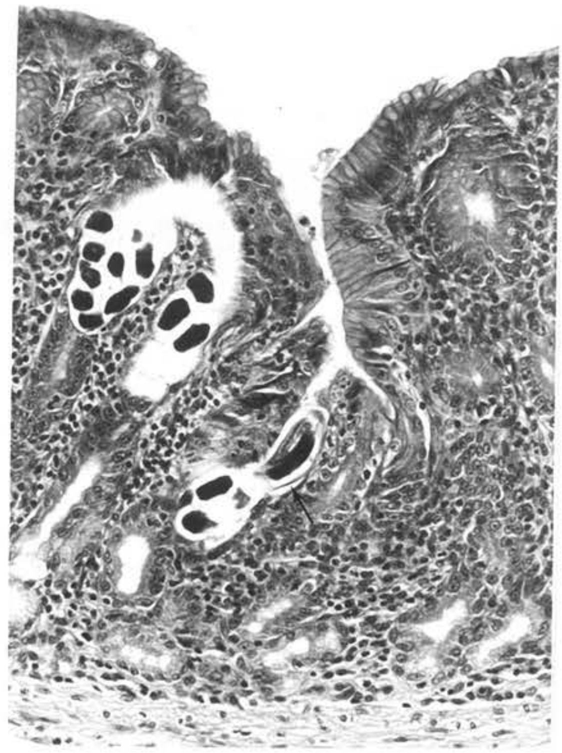


FIG.2:10. Mucosal tunnel containing eggs and parasitic female (arrow) in stomach of agile wallaby, *Macropus agilis*. H & E X 125.

Location of Parasite.

The parasitic female is a tissue parasite, living within the epithelium of the mucosa of the gastrointestinal tract (Fig.2:9) and forming tunnels in which eggs are laid (Fig.2:10). This has been noted in the literature for some species (Cram, 1929; Reesal, 1951; Worley and Barrett, 1964; Wertheim, 1970; Rego, 1972) but has not been stated to be a general trait of the genus. All the species examined by histological and dissection studies (see Appendix I) live for the most part in mucosal tunnels. No species have been found to occur outside the mucosa in the absence of a pathological response from the host.

Body Proportions.

The parasitic female is a slender , cylindrical nematode, much longer than wide, width 0.6% to 2.68% of length (Table 2:1). A serpentine body form, where width is less than 4% of total length, is associated in nematodes with mobility (Geraert, 1979), and in adult nematodes indicates a need to move in seeking nourishment. Confirmation of the mobility of the parasitic female is provided by biological data.

The hypothesis that the parasitic female is constantly mobile was examined morphologically by using its tunneling behaviour. Infected mucosa was freed and examined intact in mucosal squashes by light microscopy. The eggs were arranged in a linear fashion, indicating the worm had moved forward as egg laying occurred (Fig.2:11). Wertheim (1970) made a similar observation for S.ratti. The progressive development of the embryos from one end of the line to the other confirmed this mobility, indicating that the more developed eggs were laid earlier, eggs being deposited in a temporal as well as a spacial sequence. The linear arrangement of eggs in the mucosa was seen during dissection for all species.

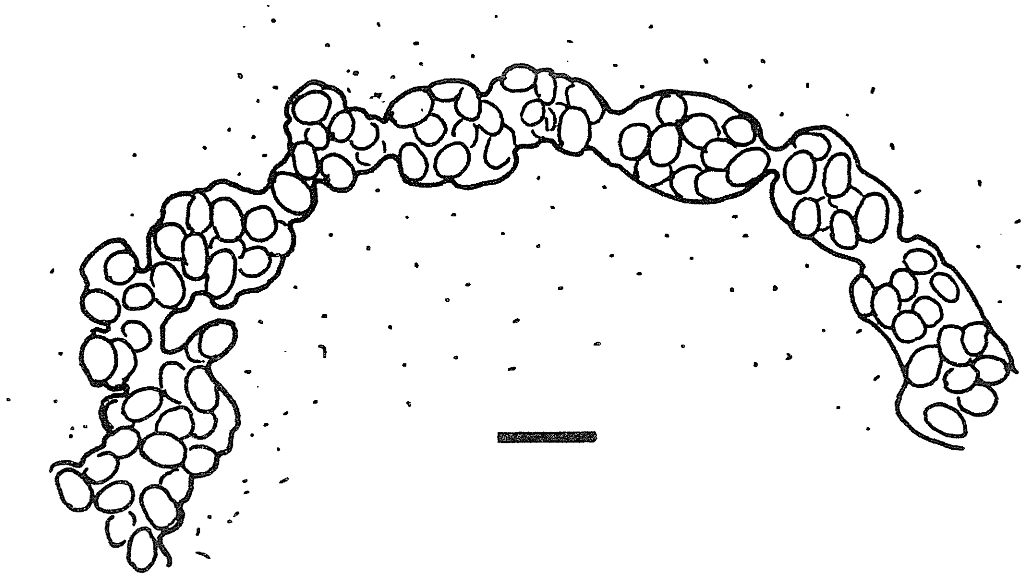


FIG.2:11. Mucosal squash from small intestine of foal infected with *Strongyloides westeri*. The eggs are laid in a linear sequence as the worm moves through the mucosa. Scale line = 100μm.

The parasitic female is mobile. Its general body shape is an expression of this. The body shape of the parasitic female is, therefore, a character of vital biological importance, and is an essential generic feature. A width/length ratio greater than 4% is atypical. Specimens or taxa considered for placement in Strongyloides, but with a width/length ratio greater than 4%, must be critically assessed as to their correct identities.

2.2.1.3 Points of Disagreement. -

Dimensions.

The upper limit of total body length has been increased from the six mm given by Little (1966a) to 10mm, as the average lengths of three species, *S.erschowi*, *S.robustus* and *S.westeri* exceeded the former upper limit (Table 2:1).

Similarly, the upper limit of maximum body width has also been raised from 75μm to 95μm, since *S.erschowi*, *S.tumefaciens* and *S.westeri* were wider. *S.tumefaciens* was reported to have a maximum body width of 109μm (Price and Dikmans, 1941). This was larger than it should have been since the specimens were squashed (see Chapter 5.3.1.1). The true diameter of 77μm has been substituted in Table 2:1. The largest species, *S.westeri*, sets the upper limits with maximum length of 10mm and width of 95μm.

The body dimensions, however, are only minor taxonomic criteria and specimens which fall outside these ranges should not be excluded on the basis of this character alone. The limits should be adjusted if other criteria are met.

Cephalic Papillae.

The number of cephalic papillae in the parasitic female has been a controversial point. Only 14 of the 51 original descriptions consulted gave the number of cephalic papillae. Little (1966b) was the author of seven of these. The literature contains comments on the number of cephalic papillae in 22 species, eight species having a more complete description subsequent to the original description (Table 2:2). The number of cephalic papillae ranged from four to eight, although in an unpublished dissertation Ballantyne (1971) stated the parasitic female had 10 cephalic papillae.

Little in his definition of the genus settled for four papillae, in subventral and subdorsal positions. Subsequently, some authors followed this convention (Rao and Singh, 1968) others proposed their species had six cephalic papillae (Sakamoto and Yamashita, 1970; Grabda-Kazubska, 1978), while others failed to state a number (Greve, 1969). None commented on Little's generic definition. The only point of agreement in the literature is that the cephalic papillae are very small and difficult to enumerate with confidence.

TABLE 2:2. Number of cephalic papillae reported for parasitic females.

(If original and subsequent descriptions lacked no.of papillae, species has been omitted from list. If original description lacked number but it was given in subsequent descriptions, the deficit in original description has been indicated by NS).

SPECIES	No.of PAPILLAE	REFERENCE
S.agoutii	6	Griffiths, 1940
S.ardeae	4	Little, 1966b
S.cati	NS	Rogers, 1939
	(see text)	Arizono et al, 1976
S.cebus	6	Darling, 1911
	4	Little, 1966a
S.dasypodis	4	Little, 1966b
S.erschowi	8	Popova, 1938
S.eryxi	NS	Mirza & Narayan, 1935
	4	Singh, 1954
S.fuelleborni	NS	von Linstow, 1905
	4	Little, 1966a
S.gulae	4	Little, 1966b
S.lutrae	4	Little, 1966b
S.martis	6	Petrov, 1940
S.myopotami	NS	Artigas & Pacheco, 1933
	4	Little, 1966b
S.papillosus	NS	Wedl, 1856
	4	Basir, 1950
S.pavonis	6	Sakamoto & Yamashita, 1970
	(see text)	Sakamoto *et al*, 1981
S.physali	4	Little, 1966b
S.procyonis	4	Little, 1966b
S.ratti	NS	Sandground, 1925
	4	Little, 1966a
S.serpentis	4	Little, 1966b
S.spiralis	6	Grabda-Kazubska, 1978
S.stercoralis	NS	Bavay, 1876
	4	Desportes, 1945
	4	Little, 1966a
S.venezuelensis	NS	Brumpt, 1949
	4	Little, 1966a

SEM studies provided an opportunity to resolve this point. Cephalic papillae, however, were not detected in expected locations. Arizono et al (1976) found papillae-like projections in *S.cati* (syn. *S.planiceps*) in lateral and ventral positions, while *S.pavonis* was reported to have papilliform projections in lateral, ventral and dorsal positions on the circumoral elevation (Sakamoto et al, 1981). Unfortunately, the latter authors did not illustrate this. None of these workers, committed themselves to stating whether cephalic papillae did or did not occur. In Figs 1,2 (p471) of Arizono et al (1976), no typical papilla can be seen, the papillae-like structures possibly being solely cuticular. In my SEM studies on *S.westeri* and *Strongyloides* sp. from the agile wallaby, Macropus agilis, no cephalic papillae were detected, and I have not been able to see papillae by light microscopy in en face views of any of the species studied.

I therefore disagree with Little"s proposal that the parasitic female has four cephalic papillae. I consider that the parasitic female has no cephalic papillae, and that this is a generic character.

2.2.2 Free-living Female (Fig 2:12).

2.2.2.1 Description. -

Body small, up to 1.5 mm long by 85μm wide, spindle-shaped. Body wall thin, cuticle with fine transverse striations. Lateral chords broad, flat. Head with two lateral cephalic lobes projecting beyond mouth, each bearing a small inconspicuous papilla in subdorsal, lateral, and subventral positions. Lateral papillae difficult to distinguish from slightly more posterior amphids from lateral view but distinct in *en face* and dorsal views. Mouth dorsoventrally elongated; stoma subglobular, laterally compressed, with thickened posterior wall. Collar-like, apparently cuticular structure, best seen in stained or glycerin mounts surrounding anterior part of stoma.

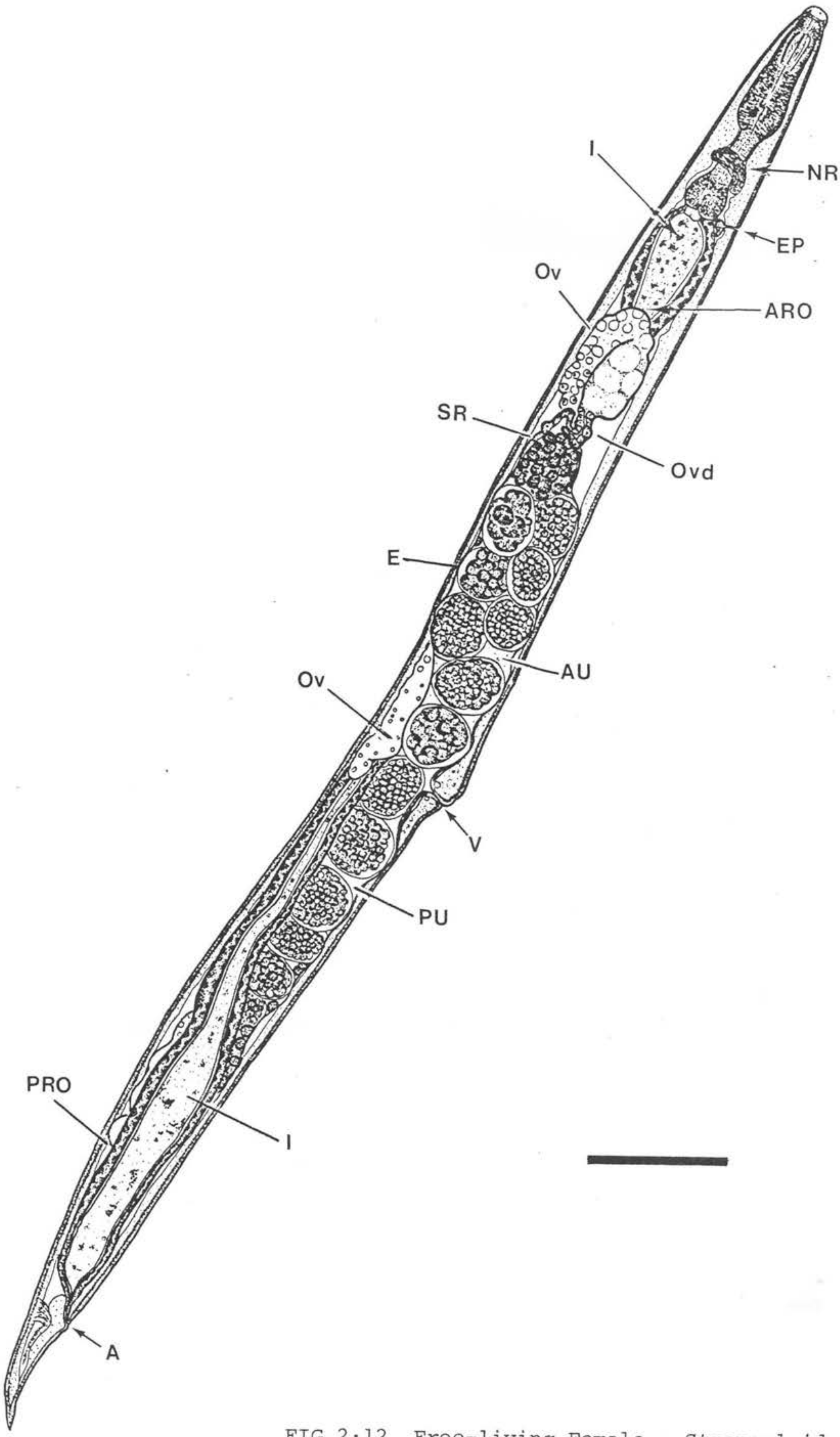


FIG.2:12. Free-living Female : *Strongyloides felis* from faecal culture of cat, 5 days at 23^{0}C. Scale line 100μm.

Oesophagus rhabditoid (Fig.2:13); a short, anterior, muscular portion, set off from corpus by slight constriction; muscles of corpus and bulb coarser than those of isthmus. In anterior portion of corpus, radii of esophageal lumen terminate distally in incomplete tubelike structures with thickened cuticular walls. These "tubes" (referred to by some authors as "spears") arch distally and decrease in caliber as they extend posteriorly.

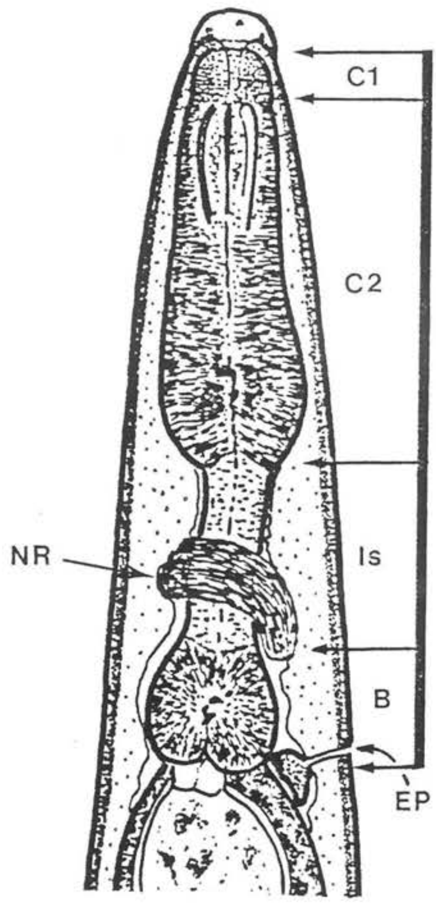


FIG.2:13. Oesophagus of free-living female : *Strongyloides felis* from faecal culture from cat. Scale line = 20µm.

Isthmus about one-half as long as corpus. Bulb with well-developed valvular apparatus. Short gastroesophageal sphincter present. Nucleus of dorsal oesophageal gland in anterior part of bulb, those of two subventral oesophageal glands at its base.

Intestine composed of 22 intestinal cells in two rows (dorsal and ventral), each with a single nucleus. Rectum short, compressed dorsoventrally. Anus subterminal, with small liplike swelling along posterior edge of transverse opening. Phasmids lateral, near middle of gradually tapering, finely pointed tail.

Nerve ring at posterior end of oesophageal isthmus. Excretory system composed of single renette cell located short distance behind oesophageal bulb, a duct extending anteriorly to pore just posterior to nerve ring. Deirids very inconspicuous, on lateral surfaces near level of excretory pore.

Reproductive system didelphic with opposed, equal uteri and reflexed ovaries; anterior branch on right side of intestine, posterior branch on left. Vulva near middle of body; vagina very short, oviduct enters subterminally, with end of uterus , serving as seminal receptacle (Fig.2:34).

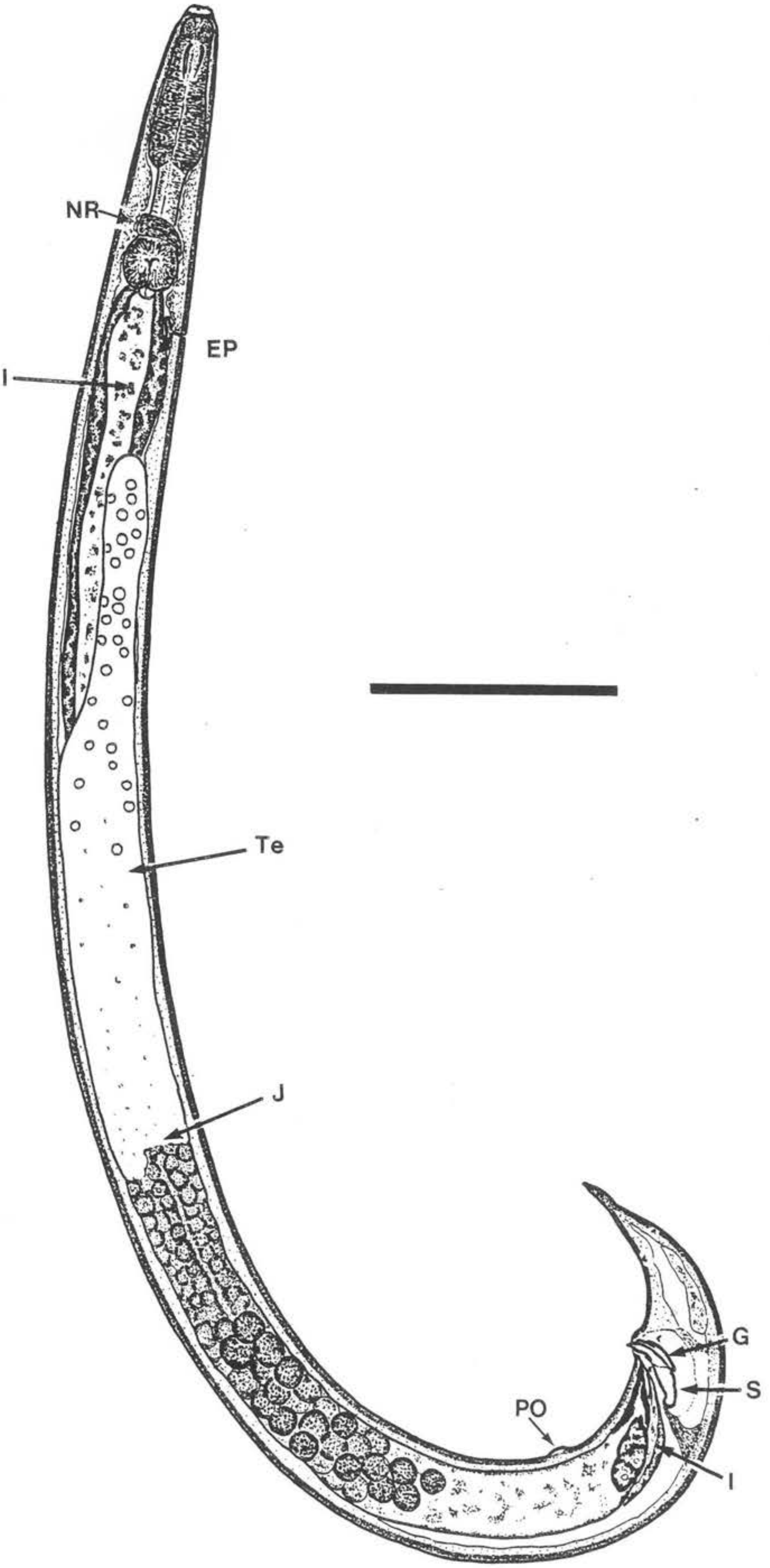


FIG.2:14. Free-living male : *Strongyloides felis* from 5 day faecal culture from cat. Scale line = 100μm.

2.2.3 Free-living Male (Fig.2:14).

2.2.3.1 Description. -

Slightly smaller than female, up to 1.2mm in length by 55μm wide, with shorter, broader tail ventrally curved when fixed. Body wall, cuticle, head, oesophagus, intestine, and excretory system as described for female.

Reproductive system single, straight. Testis blunt at anterior end, not reflexed, begins shortly behind oesophagus, extends to near middle of body. Seminal vesicle and vas deferens composing remainder of system not well differentiated. Cloaca short. Spicules equal, short, blade-like with laterally bent, knob-like anterior ends. Each spicule with two supporting ribs extending from base to near tip. Posterior part of spicule ventrally curved; thin membrane extending along curved portion of ventral edge gives spicule bow-like appearance. Gubernaculum laterally compressed with short wing-like structures extending laterally from posterior half of dorsal edge giving posterior end T-shaped appearance in cross-section with stem lying between spicules.

Caudal papillae (Fig.2:15) are one unpaired nerve ending on midpoint of anterior cloacal lip, six papillae bilaterally (one subventral preanal, two subventral adanal (anterior and posterior), one subventral postanal, one subdorsal postanal), and a dome shaped projection in midventral preanal position (preanal organ).

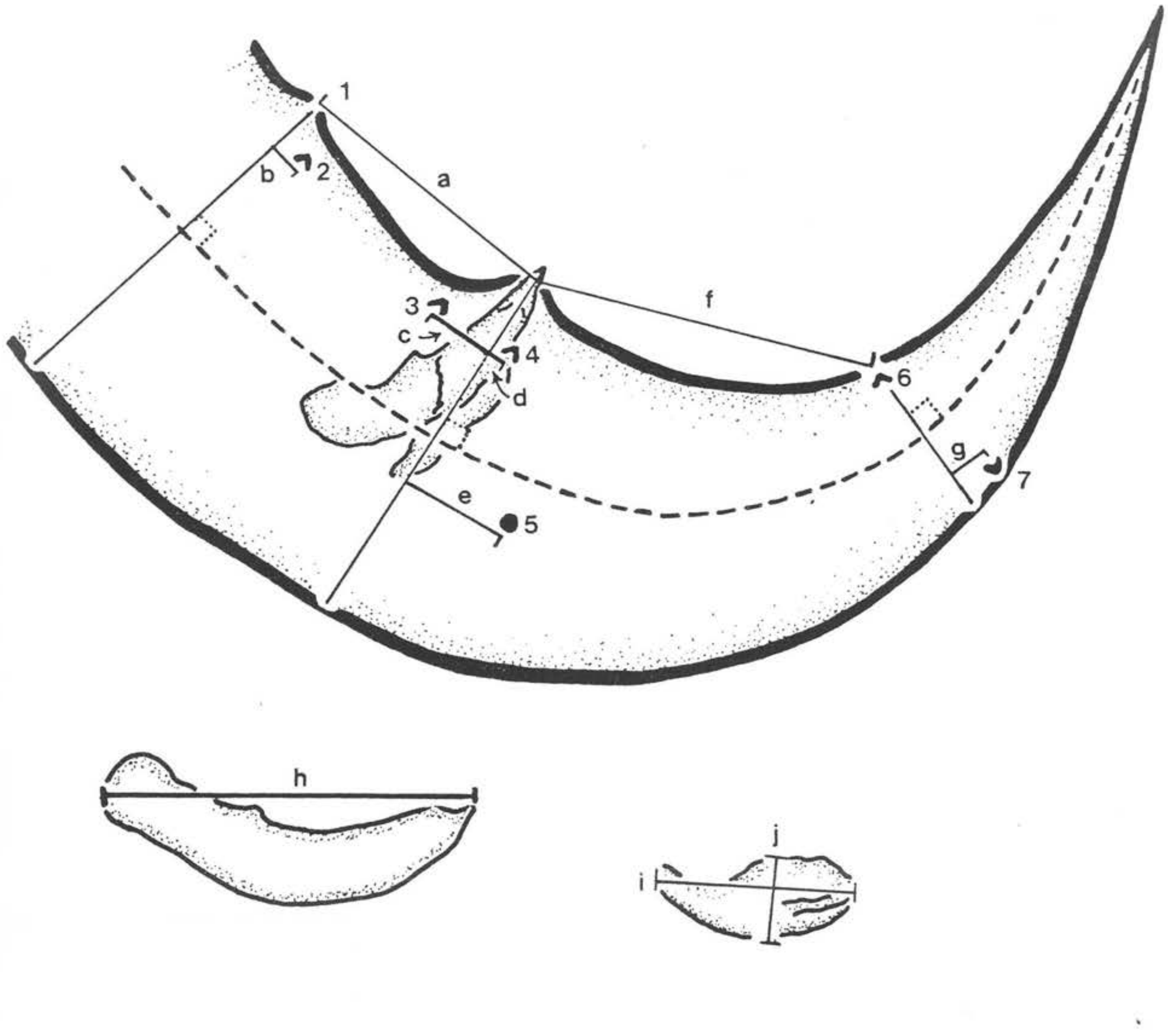
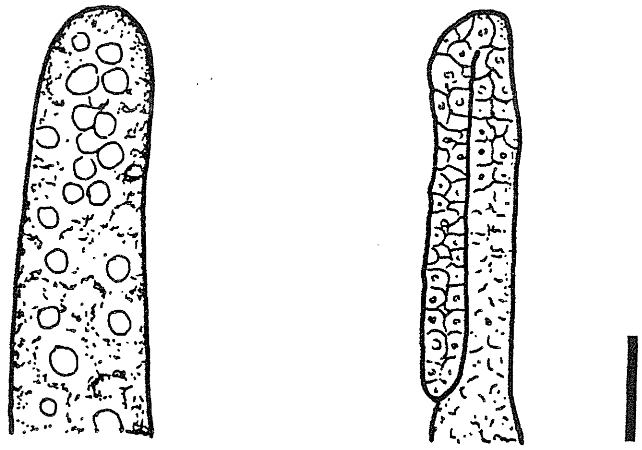


FIG.2:15. Caudal papillae, spicules and gubernaculum of free-living male and technique for quantifying positions and measuring dimensions. Key : 1 = preanal organ (PO); 2 = subventral preanal papilla (SVP); 3 = anterior adanal papilla (AD1); 4 = posterior adanal papilla (AD2); 5 = lateral papilla (LP); 6 = subventral postanal papilla (SVPo); 7 = subdorsal postanal (SDPo); a = distance from PO to cloaca; b = distance from SVP to transverse plane through PO; c = distance from AD1 to transverse plane through cloaca; d = distance from AD2 to transverse plane through cloaca; e = distance from LP to transverse plane through cloaca; f = distance from SVPo to cloaca; g = distance from SDPo to transverse plane through SVPo; h = spicule length; i = length of gubernaculum; j = width of gubernaculum.

2.2.3.2 Additions to Little's Definition. -

Testicular Shape.

A feature which allows the free-living male of *Strongyloides* to be easily distinguished from those of free-living rhabditoids is the simple rounded anterior end of the testis of *Strongyloides* (Fig.2:16A).



A B

FIG.2:16 Anterior ends of testicles : A. free-living male of *Strongyloides westeri* from faecal culture from foal at 23^{0}C for 5 days; B. free-living male of unidentified rhabditoid from faecal culture from foal. Scale line = 20μm.

Most rhabditoids encountered as contaminants in faecal cultures have a more tapered end which is reflexed (Fig.2:16B). On superficial examination this frequently appears similar to the rounded end of the testis in *Strongyloides*, but that of *Strongyloides* is never reflexed.

Papilla on Anterior Cloacal Lip.

Free-living males of all species examined had a single papilla on the midpoint of the anterior lip of the cloaca. Its degree of development varied with particular species. In many species, e.g., *S.stercoralis*, the papilla was not readily apparent, but could be detected in the lateral view as a small nerve ending projecting beyond the level of the cloacal lip. Other species, e.g., *S.westeri*, had a well developed papilla which appeared as a nerve ending in the centre of a small dome of cuticle (Fig.2:17). The only author to describe this papilla previously was Sandosham (1952) in a description of *S.stercoralis*. It was omitted by Little, but since it occurs in all species, it should be included in the definition of *Strongyloides*. The name anterior anal papilla is suggested for this papilla.

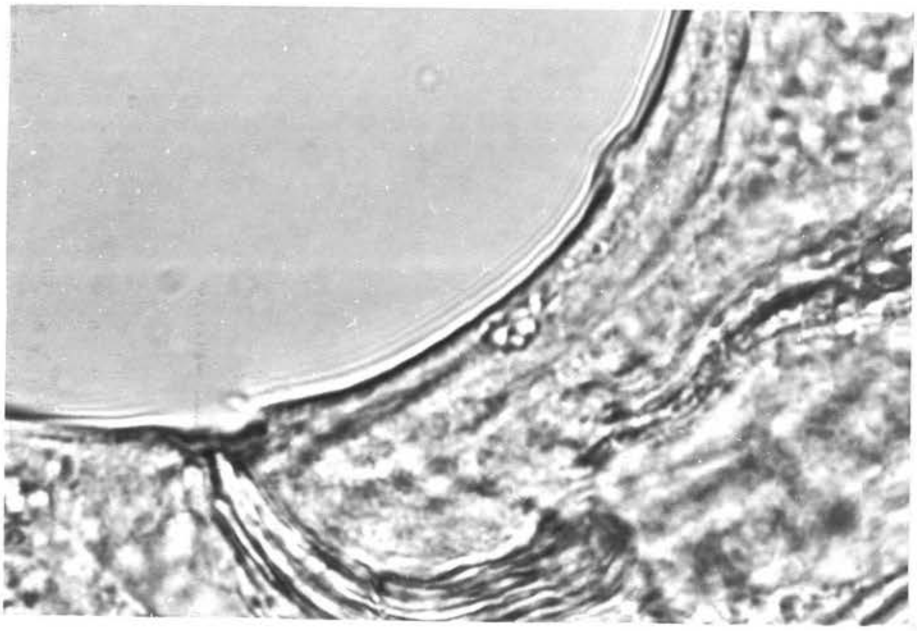


FIG.2:17. Free-living male of *Strongyloides westeri* showing anterior anal papilla, preanal organ and spicules. Scale line = 10µm.

2.2.3.3 Disagreements with Little's Definition. -

Spicule Tip.

The spicules of most species terminate in a sharp point. The nature of the tip is, however, not constant throughout the genus and is a specific character (Fig.6:7, Table 6:2)). It is not a generic feature, and therefore "sharply pointed" has been omitted from the definition.

Preanal Organ.

The structure Little named the midventral preanal papilla differs from the other 13 caudal papillae. The 12 paired papillae appear as small, domed cuticular projections with a refractile, centrally placed nerve ending, slightly elevated above the surface of the dome. The nerve fibre can usually be traced a short distance through the cuticle and into the hypodermis. The midventral preanal structure is larger, and the deeper layers of the cuticle and adjacent hypodermis are modified (Fig.2:17). A nerve ending or nerve fibres passing through the cuticle could not be discerned in any specimen. This structure may not be a papilla, but may be solely a cuticular modification. Since the point has not been definitely resolved, however, the structure has been retained in the definition as a caudal papilla. To avoid confusion with the papilla on the cloacal lip the terminology used by Little has been replaced by the term "preanal organ" used by Cram (1936 p297 fig.3). This is more appropriate since it recognises that the structure is different from the typical bilateral caudal papilla.

2.2.4 Eggs (Fig.2:18 & 2:19).

2.2.4.1 Description. -

Eggs of parasitic and free-living females superficially identical in appearance though slightly variable in size, ellipsoidal with slightly flattened poles and extremely thin walls. Medium sized, 40-85μm in length with dimension of width about half that of length. The eggs of the free-living female possess a vitelline membrane, while the eggs of the parasitic female do not.

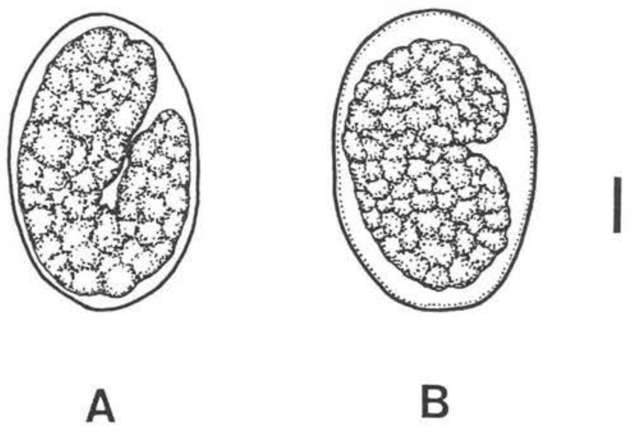


FIG.2:18. Eggs of *Strongyloides* : A. from parasitic female ex *Strongyloides* sp from large intestine of green tree frog, *Litoria caerulea*; B. from free-living female of same species. Scale line 10μm.

FIG.2:19. Eggs of parasitic female of *Strongyloides westeri* on the surface of the duodenal mucosa of foal. SEM.

2.2.4.2 Comment. -

Stage of Development.

Little (1966a) included information on the stage of development of the eggs at the time of laying for both adult female stages. He stated the parasitic female laid eggs in the stage of early cleavage. The eggs of *S.akbari* and *S.felis* have been reported to hatch in utero (Chandler, 1925b; Mirza and Narayan, 1935).

This phenomenon was not seen in any specimen examined, eggs usually containing a morula when laid. Many specimens of *S.felis* were examined, although none of *S.akbari* were available. Owing to the probability of some species proving exceptions, this point has been omitted from the definition.

Little (1966a) stated (p73) that the eggs of the free-living female were "usually in early cleavage when laid but may develop to larvae in utero". This is correct, younger females laying eggs in early cleavage, while hatching occurs inside the occasional effete female (Mackerras, 1959). This information, however, adds nothing to the definition since both options (oviparity or viviparity) are given. It has been omitted.

Vitelline Membrane.

The eggs of the parasitic female of *S.ratti* lack a vitelline membrane, while those of the free-living female posses one (Chitwood and Graham, 1940). Since the absence of a vitelline membrane is a consequence of parthenogensis (Chitwood and Graham, 1940), it is reasonable to predict that this situation would hold for all species in the genus.

Size.

The upper limit of 70μ has been increased to 85μ to accomodate the eggs of the parasitic female of *S.felis*.

2.2.5 First Stage Larva (Fig.2:20).

Body up to 400μm long by 20μm wide. Oesophagus of newly hatched larva nearly one-third body length, structurely similar to that of free-living adult. Head with two cephalic lobes separated by transversely elongated, oval mouth. Although not evident at first, four cephalic papillae, a right and left subdorsal and a right and left lateral amphids appear later in this stage.

Cephalic lobes, apparently formed by inflations of cuticle, increase in size as larva progresses towards first molt. Stoma about 8μm long, cylindrical; posterior wall slightly thicker than anterior. Nerve ring in newly hatched larva at anterior end; at time of first molt near posterior end of isthmus.

Excretory system like that of free-living adult. Intestine patent, composed of 22 uninucleated cells in two rows (dorsal and ventral). Rectum short, anus about 60μm from tip of tail. Genital primordium prominent, with five to nine nuclei, lying along ventral side near middle of intestine.

Although length of larva nearly doubles before first moult, depending upon culture conditions, oesophageal length increases very little. No morphological differences could be detected between first-stage larvae developing from eggs of parasitic and free-living females.

2.2.6 Second Stage Larva.

Just after the first moult second stage larvae are similar, but the morphology of larva at the second moult differs depending upon whether development is towards the direct or the indirect life cycle (Fig.I).

2.2.6.1 Second Stage Rhabditoid Larva (Fig.2:21). -

Body about 400μm long by 23μm wide Morphology similar to L1,

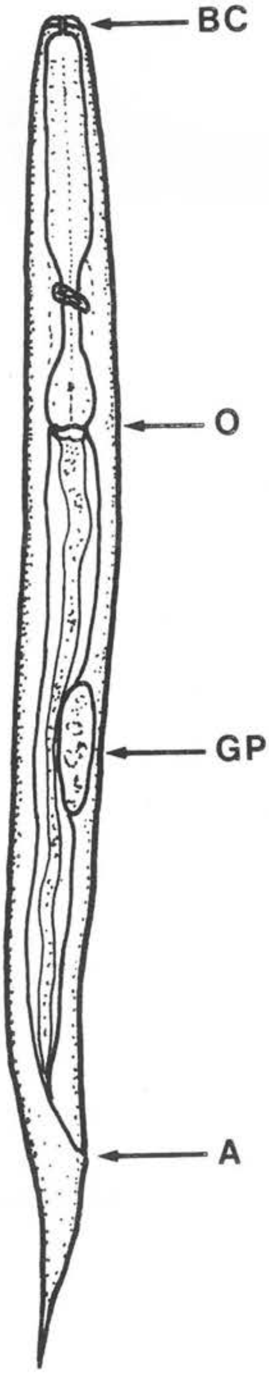


FIG.2:20. First stage larva of *Strongyloides felis* from faeces of cat immediately after voiding.

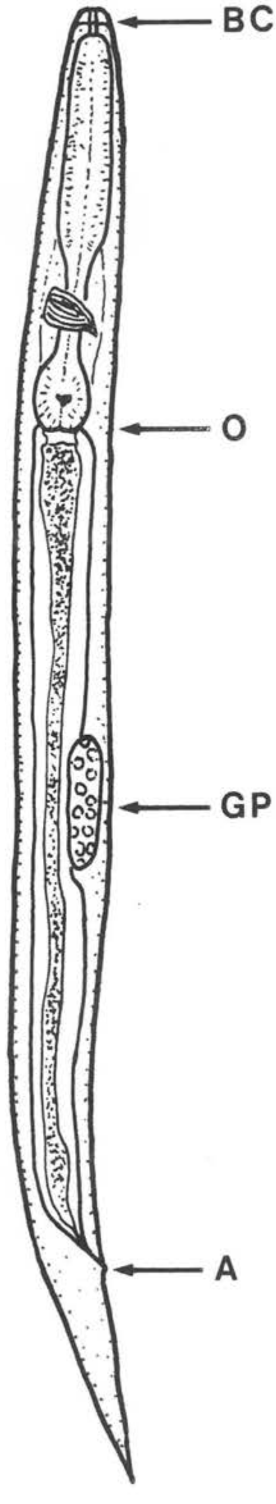


FIG.2:21. Second stage larva of *Strongyloides felis* from faeces of cat 6hr after voiding, 23^0C.

Scale line = 50µm.

but organs more easily discerned. Buccal capsule still cylindrical, cuticle inflated anteriorly (Fig.2:22). Genital primordium increased in size but still oval in outline. In male cellular mass forms dorsal to rectum, thickening body; female lacks this mass and is thinner here (Fig.2:23).

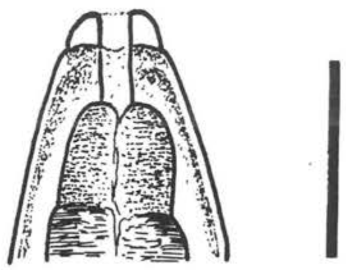


FIG.2:22. Anterior end of second stage larva of *Strongyloides felis*, lateral view. Note parallel sides to buccal capsule and inflated cuticle anteriorly, as well as typical anterior segment of oesophageal corpus. Scale line 10µm.

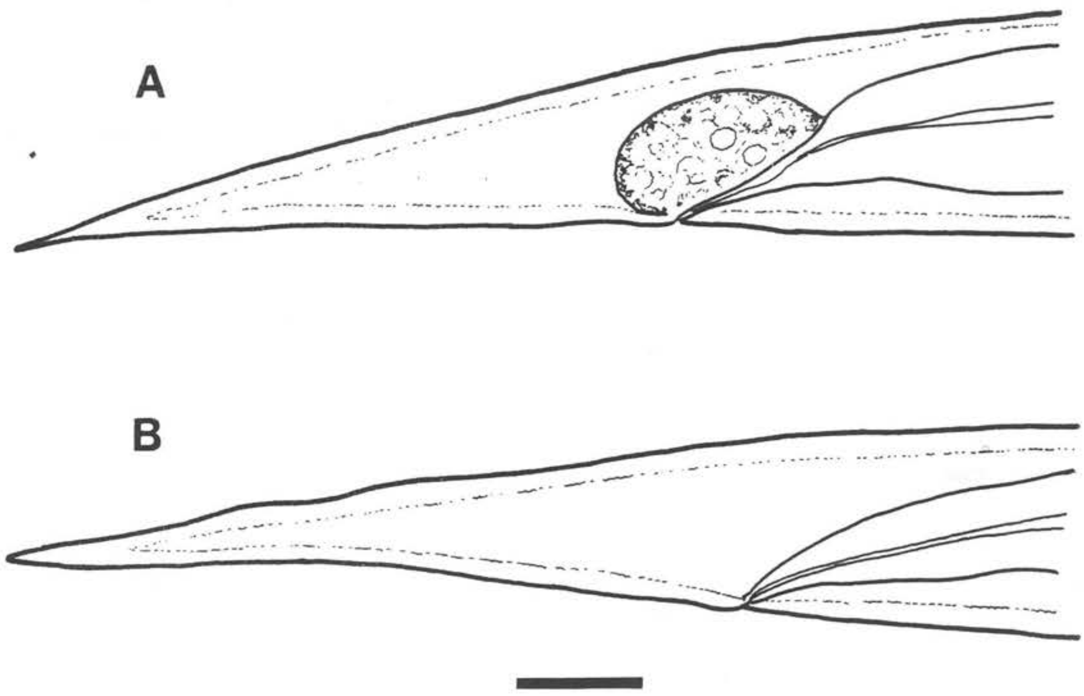


FIG.6:23. Tails of late second stage rhabditoid larvae of *Strongyloides felis* : A. male with primordium of sexual apparatus dorsal to rectum; B. female. Scale line = 10µm.

2.2.6.2 Second Stage Filariform Larva. (Fig.2:24). -

Size at second ecdysis larger than for indirect; same as infective larva. In early second stage, morphology is similar to rhabditoid second stage. Later oesophagus elongates from 30 % to 40 % body length, posterior part is less muscular and more glandular; divisions less distinct; oesophageal gland nuclei become more prominent; nuclei dividing in all intestinal cells except first and last pair, increasing the number from 22 to 40. Genital primordium does not increase in size. Notched tail of filariform larva forms within the old cuticle of second stage, but cuticle has not separated from body to form a sheath (Fig.2:25). Some of these larvae have an elongated oesophagus, largely cylindrical, but with a terminal bulb. End of second stage is marked by moulting or by separation of cuticle to form a sheath.

2.2.6.3 Comment. -

Little emphasised that the morphology of the L2 depended on the route of development. He did not, however, describe the stages in such a way that they could be confidently identified. Separate descriptions for indirect and direct developing L2 have been given and additional morphological features included.

2.2.7 Third Stage Filariform Larva (Fig.2:26)

Larva slender, about 400–700μm long by about 12–20μm wide; oesophagus filariform as in parasitic female with length about 40% that of body; tail notched. Cuticle finely striated; lateral alae double, about 4μm apart (Fig.2:27). Head bearing two inconspicuous lateral cephalic lobes, each with small subdorsal and subventral papilla and lateral amphid. Mouth small, pore-like; stoma shallow, laterally compressed. Excretory system similar to that of free-living adult. Deirids between lateral alae near level of

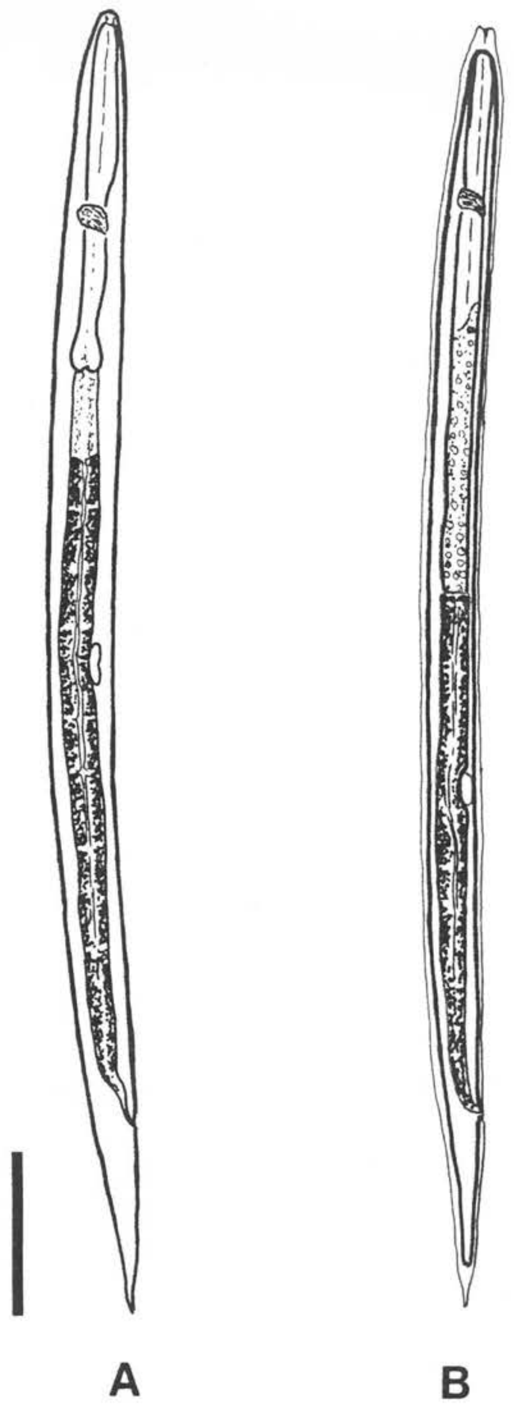


FIG.2:24. Filariform second stage larvae of *Strongyloides* sp from spectacled hare wallaby; faecal culture at 25^0C for 48hrs : A. with rhabditoid oesophagus; B. with filariform oesophagus and sheath. Scale line = 50µm.

FIG.2:25. Tail of filariform second stage prior to sheath formation. *Strongyloides* sp from 48hr faecal culture at 25^0C from spectacled hare wallaby. Scale line = 10µm.

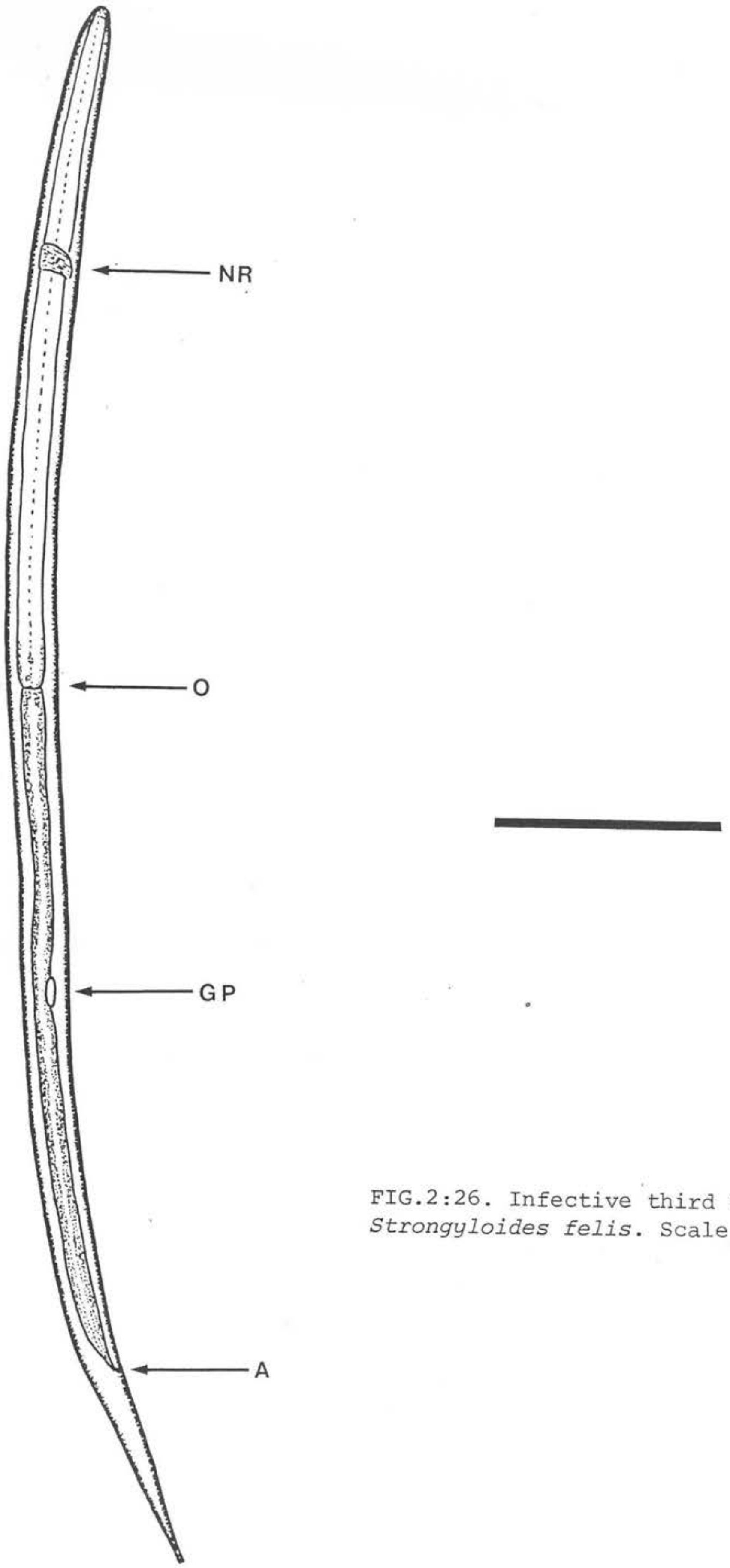


FIG.2:26. Infective third stage larva of *Strongyloides felis*. Scale line = 50μm.

excretory pore. Pbasmids between lateral alae near middle of tail. Double lateral alae, extending to end of tail form tetafurcated tip; however, tail usually slightly twisted and may have trifurcated appearance (Fig.2:28). Intestinal cells 22, arranged in two rows (dorsal and ventral), the first and last pairs uninucleate, the remain ing are binucleate, making altogether 40 nuclei.

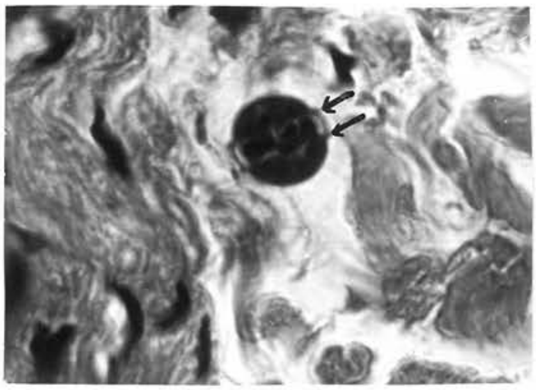


FIG.2:27. Transverse section of infective third stage larva in dermis of agile wallaby, *Macropus agilis*. Double lateral alae demarcated by arrows. Experimental percutaneous infection with *Strongyloides* sp. H & E X 1250.

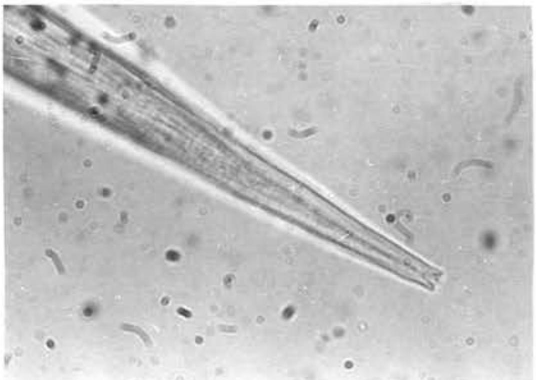


FIG.2:28. Tail of infective third stage larva of *Strongyloides felis*. Note truncated and notched tip.

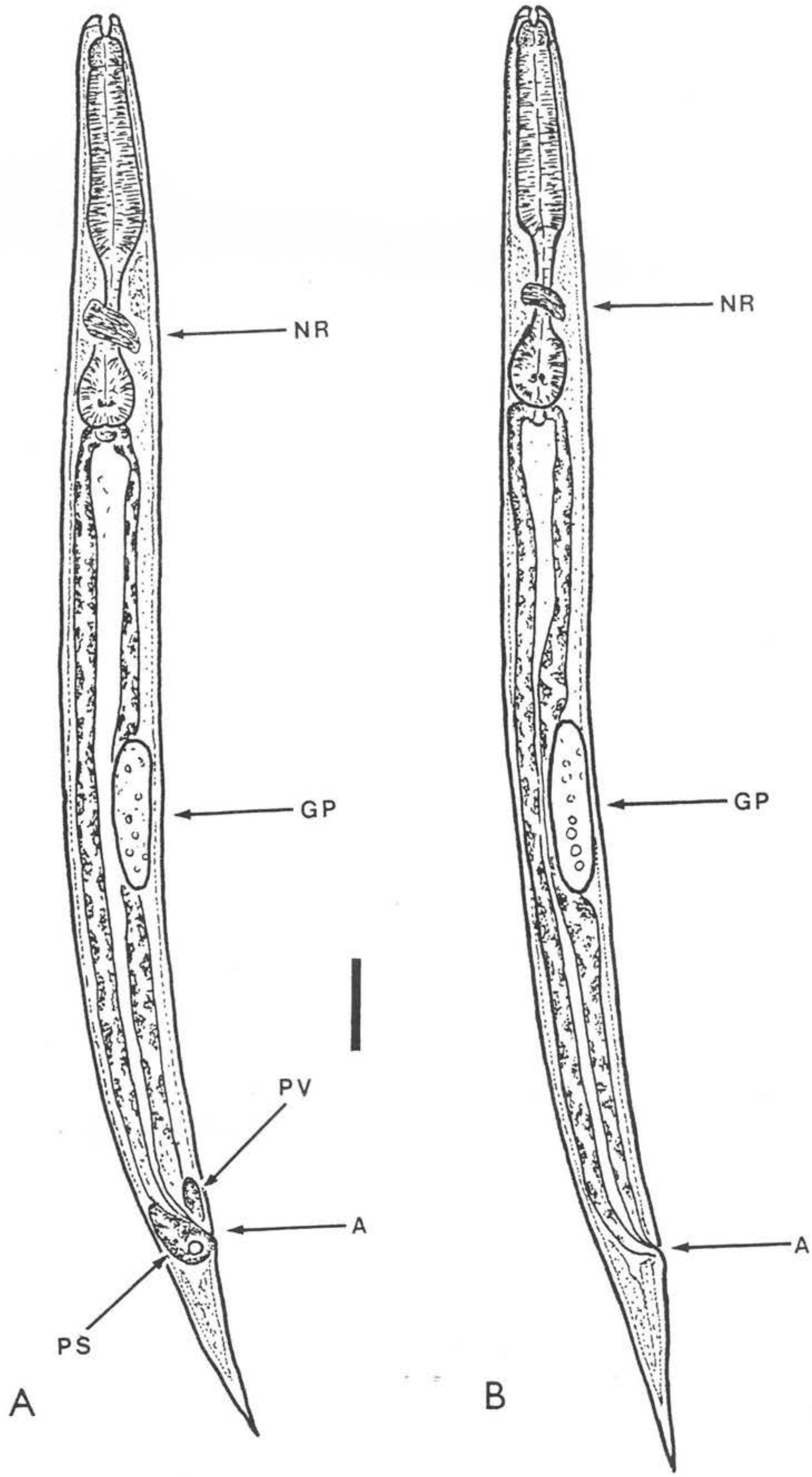


FIG.2:29. Third stage rhabditoid larva of *Strongyloides felis*.
A. male; B. female. Scale line = 20µm.

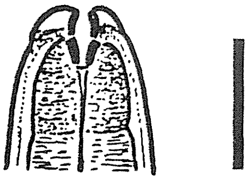


FIG.2:30. Head of third stage rhabditoid larva of *Strongyloides felis*, lateral view. Note cone shaped buccal capsule. Scale line = 10μm.

2.2.8 Third Stage Rhabditoid Larvae (Fig.2:29).

Body about 450μm by 22μm wide. Morphological differences from L2 involve head and reproductive system. Walls of buccal capsule deviate anteriorly, giving a cone shaped buccal capsule in lateral view (Fig.2:30). Genital primordium elongated in both sexes. Cellular mass dorsal to rectum in male more distinct than in L2.

2.2.9 Fourth Stage Rhabditoid Larvae (Fig 2:31).

2.2.9.1 Description -

Morphology of head similar to adult, with two lateral lips. In female, the anterior and posterior ends of genital primordium are reflexed, vulval slit has formed under cuticle, and cells forming uterus have become vacuolated to form a lumen. In male, spicules have formed and become progressively sclerotised, genital primordium has elongated anteriorly and posteriorly, meeting posteriorly with a cord of cells growing from the rectum. At time of moult morphology is that of adult.

2.2.9.2 Comment. -

The fourth stage rhabditoid larva was not described by Little (1966a) in his redefinition.

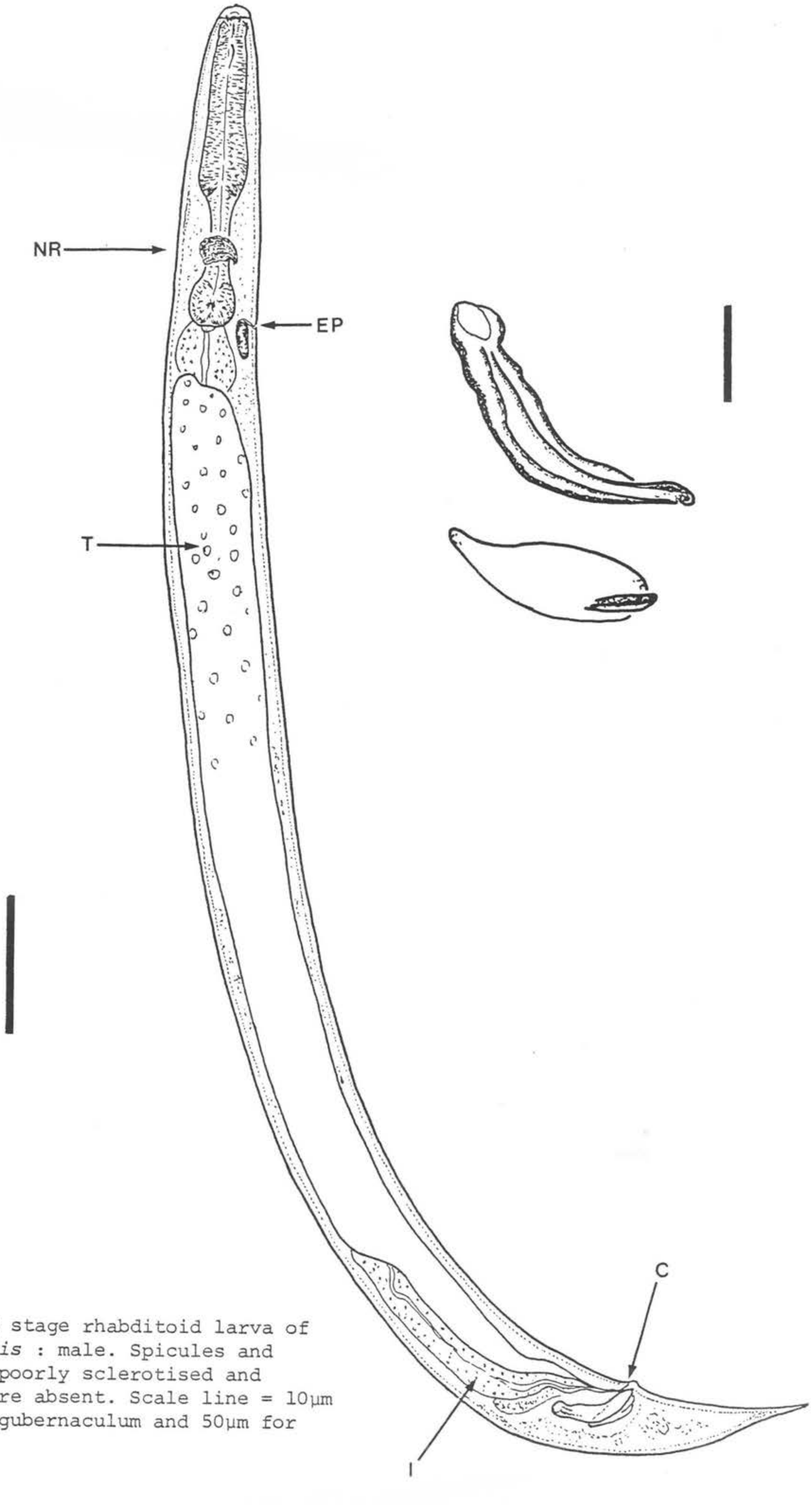


FIG.2:31A. Fourth stage rhabditoid larva of *Strongyloides felis* : male. Spicules and gubernaculum are poorly sclerotised and caudal papillae are absent. Scale line = 10μm for spicules and gubernaculum and 50μm for worm.

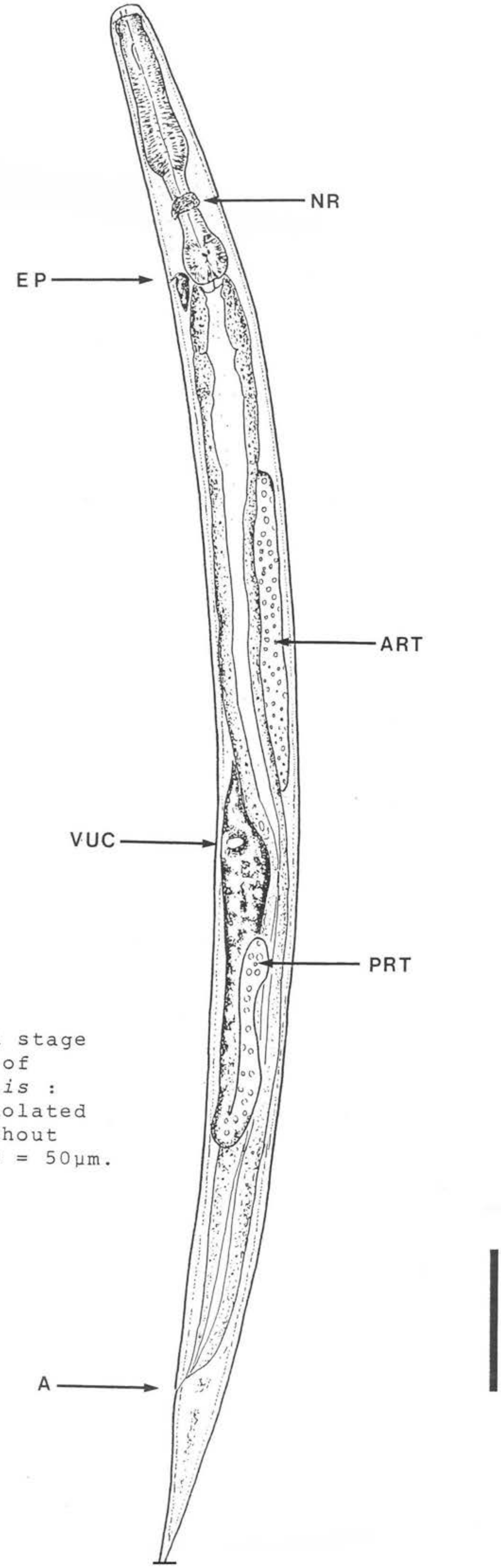


FIG.2:31B. Fourth stage rhabditoid larva of *Strongyloides felis* : female. Note vacuolated uterine cells without vulva. Scale line = 50μm.

2.2.10 Fourth Stage Parasitic Female (Fig 2:32).

2.2.10.1 Description -

Slender, size ranging from that of filariform larva to adult female. Oesophagus cylindrical, tail not notched. Reproductive system ranges from mass just larger than genital primordium of filariform larva to reflexed ovaries and uterus of adult. In those species in which the parasitic female has spiral ovaries the ovaries remain directly recurrent in L4. Vulva forms as transverse slit but has overlying layer of cuticle.

2.2.10.2 Comment. -

This stage was not included in Little's definition.

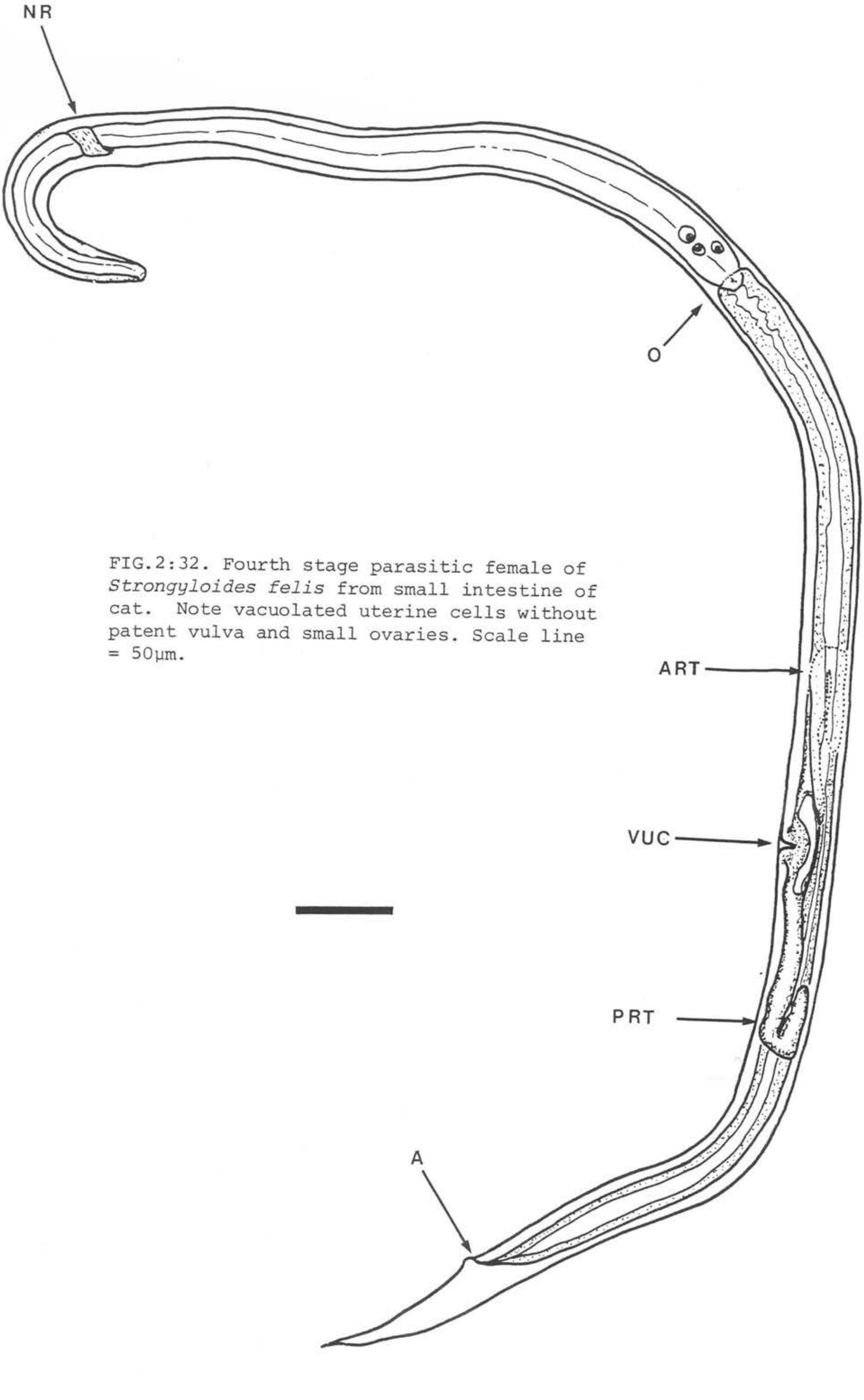


FIG.2:32. Fourth stage parasitic female of *Strongyloides felis* from small intestine of cat. Note vacuolated uterine cells without patent vulva and small ovaries. Scale line = 50µm.

2.3 GENERIC BOUNDARIES.

Strongyloididae contains three genera, *Strongyloides* Grassi, 1879, *Parastrongyloides* Morgan, 1928 and *Leipernema* Singh, 1976. They can be distinguished using a number of criteria (Table 2:3). Some points warrant comment.

TABLE 2:3. Criteria used to distinguish between members of the Strongyloididae.

CRITERIA	*STRONGYLOIDES*	*PARASTRONGYLOIDES*	*LEIPERNEMA*
PARASITIC FEMALE			
Buccal capsule	shallow	globular	conical
Buccal teeth	occas.present (1 pair)	absent	3 pairs
Cephalic annulation	absent	absent	present
Seminal receptacle	absent	present	?absent
PARASITIC MALE			
	absent	present	absent
FREE-LIVING ADULTS			
Relative body lengths	♀>♂	♀>♂	♀=♂
Buccal teeth	absent	absent	3 pairs
FREE-LIVING MALE			
No. caudal papillae	13 (1 single, 6 pairs)	?variable	24 (12 pairs)
Preanal organ	present	present	?absent

2.3.1 Buccal Capsule.

Although Singh (1976) did not describe the shape of the buccal capsule of *Leipernema*, his Fig.2 (p270) shows it to be cone shaped, narrower anteriorly. This is unlike the buccal capsule of *Strongyloides* which is very shallow, and that of *Parastrongyloides* which is globular in longitudinal section (Fig.1:1).

2.3.2 Buccal Teeth.

Singh (1976) reported three pairs of teeth in the buccal cavity of *Leipernema* in all adult stages. Although not stated, they were located in submedian and lateral positions (Singh, 1976: Figs 1&2, p270). Buccal teeth have not been reported for the other two genera, but the parasitic females of several species of *Strongyloides* have projections arising from the anterior ends of the oesophagus. These occur in dorsal and ventral positions (Fig.6:1).

2.3.3 Seminal Receptacle.

Morgan (1928) described a seminal receptacle in *Parastrongyloides winchesi*. This was at the distal end of the uteri and ended as a blind sac with the oviduct entering subterminally. It usually contained sperm. The oviduct in *Parastrongyloides* is a narrow, thick walled and sometimes coiled duct (Morgan, 1928) and at its point of entry into the uterus is expanded to form a sphincter-like apparatus within the uterine wall (Fig.2:33). This is situated ventro-medially about 30μm from the distal end of the uterus. The free-living female also has a similar arrangement, with the oviduct entering the uterus subterminally on its ventro-medial side. The oviduct of the free-living female is abruptly narrowed just distal to the point of entry into the uterus and then expanded in the uterine wall into a bulb-like structure with a central lumen and several peripheral nuclei (Fig.2:34). This morphology is seen also in unfertilised female L5's and in L4's, although the length of the blind end of the uterus is reduced (30 vs 10μm). The oviducts of *Strongyloides* in the parasitic female pass directly into the terminal point of the uteri (Fig.2:4) and lack any obvious sphincter. The free-living female *Strongyloides* has a morphology similar to that of the free-living female of *Parastrongyloides* (Fig.2:34). Singh (1976) did not comment on the presence of a seminal receptacle in *Leipernema*, but in the absence of a parasitic male, the seminal receptacle is presumably lacking.

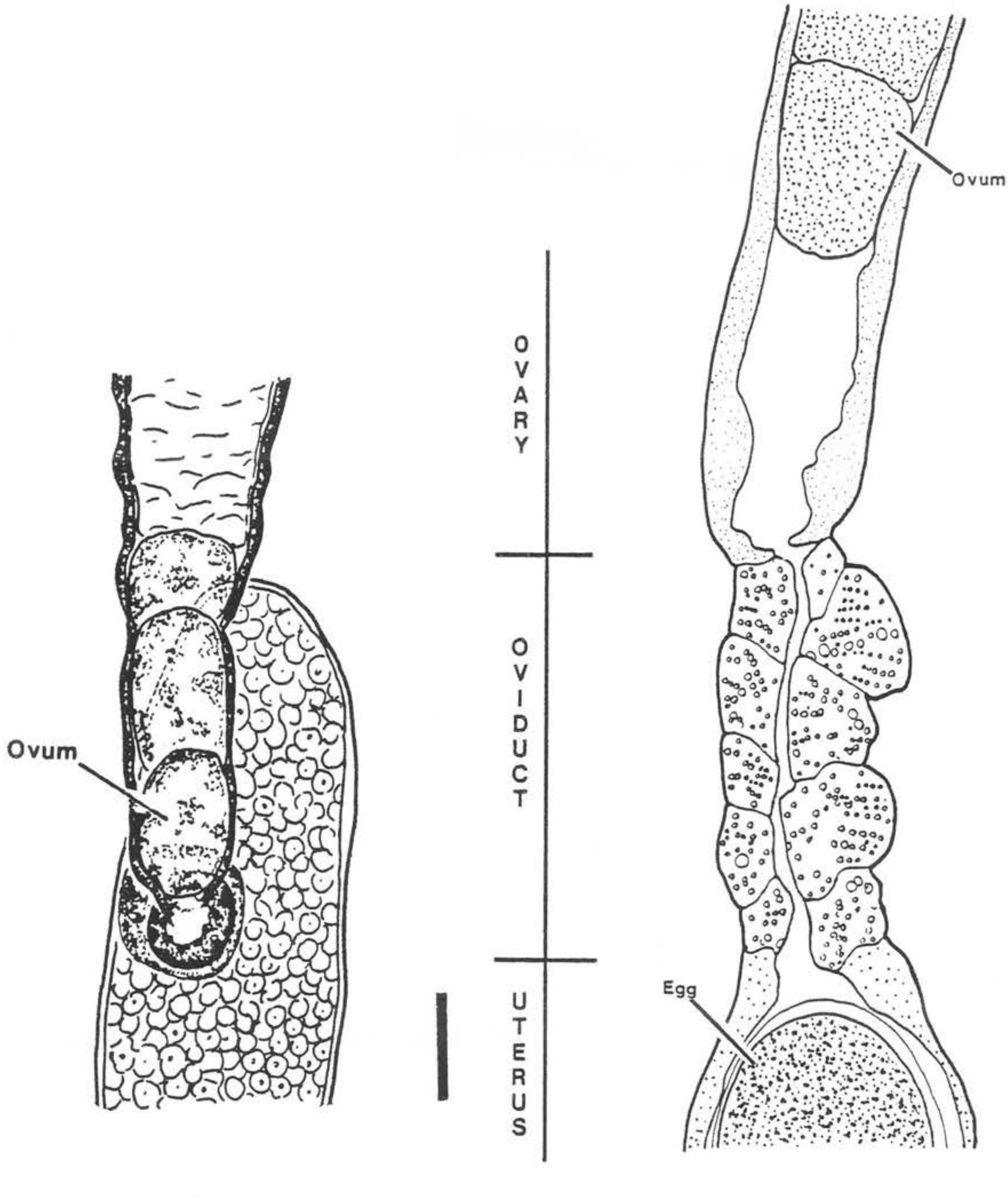


FIG.2:33. Distal uteri of parasitic females of *Strongyloides* and *Parastrongyloides* : A. *Parastrongyloides* sp from small intestine of echidna; B. *Strongyloides* sp from stomach of spectacled hare wallaby. Lateral views. Scale line = 10µm.

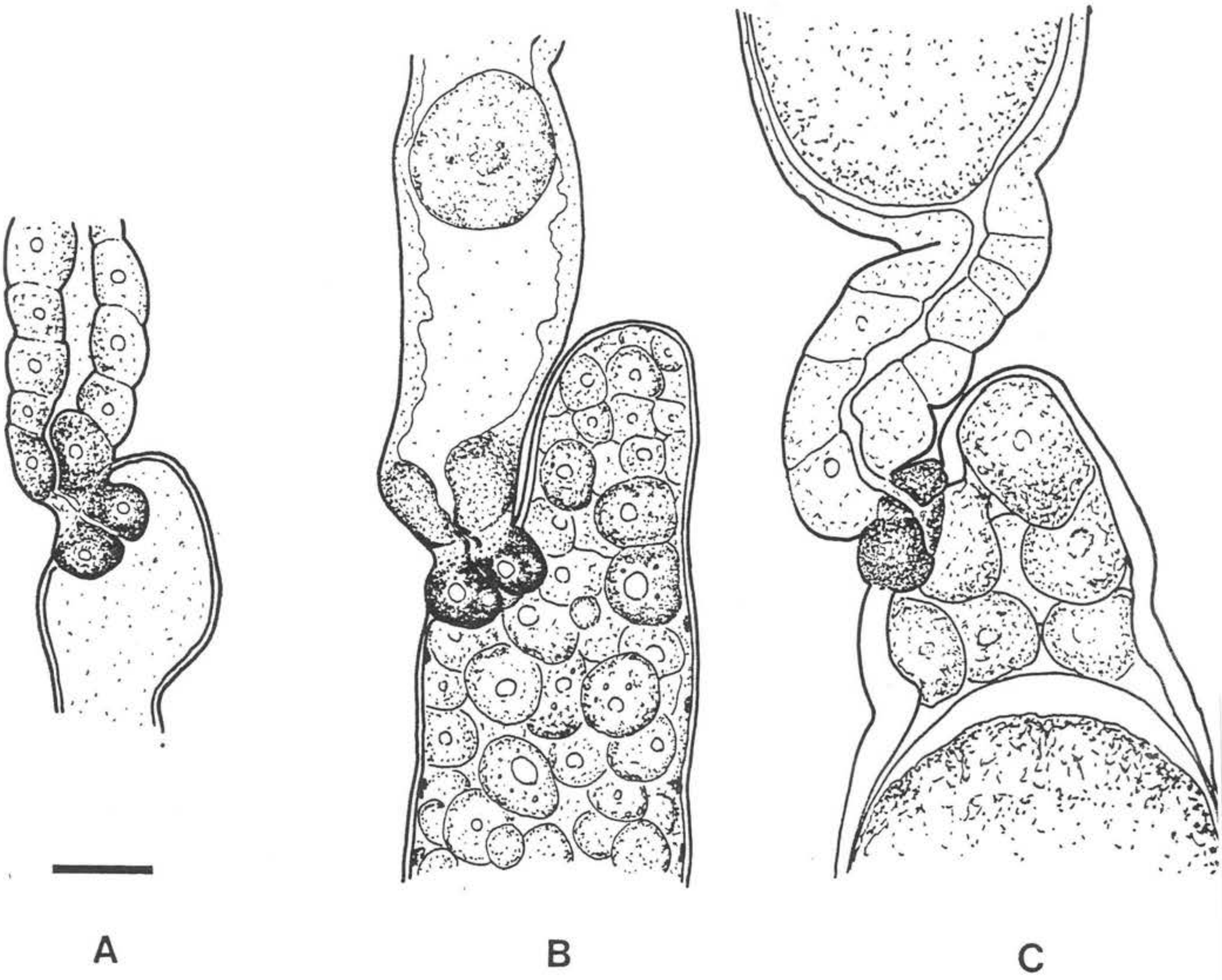


FIG.2:34. Distal ends of uteri of free-living females of : *Parastrongyloides* sp from echidna A. virgin fifth stage; B. inseminated free-living female; and C. *Strongyloides felis* inseminated free-living adult female. Scale line = 10μm.

2.3.4 Caudal Papillae.

The number and positions of caudal papillae in the free-living male of *Strongyloides* is constant for the genus. Different numbers of caudal papillae have been reported for species of *Parastrongyloides*. This genus, however, has not been reviewed, and the apparent variation in number of caudal papillae in the genus may be a result of observer error. This was the situation existing for *Strongyloides* prior to Little's review and redefinition (Little, 1966a&b). The free-living males of both *Strongyloides* and *Parastrongyloides* have the preanal organ. Singh (1976) did not comment on this feature in *Leipernema*.

2.3.5 Clarity of Generic Boundaries.

The limits of the genus *Strongyloides* have been precisely defined. Thus, any newly discovered nematodes which do not fall within these boundaries can be assigned to different genera. As the genus has become more clearly defined, there has been less confusion about which species should be included. With the passage of the years the morphology of those species originally considered for inclusion in *Strongyloides* and subsequently placed elsewhere has approached closer to that of *Strongyloides*. In other words, the new genera proposed show a greater degree of relationship to *Strongyloides* than those proposed in former times. Probstmayria vivipara (syn. *S.viviparus*) and Cooperia punctata (syn. *S.bovis*) were included when the generic boundaries were still unclear (1905 and 1907, respectively). Morgan's (1928) proposal that only those species with no parasitic male be included in *Strongyloides* was a major benchmark. He also highlighted the importance of the shape and depth of the buccal capsule in separating *Strongyloides* from other genera. Little (1966a) also stressed this point. Boyd (1966) inadvertently trangressed this generic boundary by listing as a feature of her *S.herodiae* (syn. *S.ardeae*) the occurrence of a deep buccal capsule (Fig.5:9). This is dealt with in Chapter 5.2.1.3 and was an artifact due to degeneration of the specimens. Singh's justification of *Leipernema* to accommodate his L.leiperi rested on the occurrence of buccal teeth in both the parasitic female and the free-living adults. The shape of the buccal capsule in the parasitic female also differed from that found in *Strongyloides*.

Little's review and redefinition established the generic boundaries of *Strongyloides* with great precision. *Parastrongyloides* now contains five species, but has not been reviewed. Consequently, in some areas, e.g. free-living stages, the generic boundaries are not clear, and when a host is infected with both *Strongyloides* and *Parastrongyloides* assignment to the correct genera is difficult (Mackerras, 1959). *Leipernema* contains only the single species *L. leiperi* from the pangolin, *Manus pentadactylus*. The free-living stages possess buccal teeth (Singh, 1976 p269 figs.9,10,11).

2.4 SUMMARY.

This chapter has dealt with the definition of the genus. Little's definition has been shown to be essentially correct. It has been modified in some respects. Larval stages have been more precisely defined, and minor additions and corrections made to his descriptions of other stages. The major theoretical modification has been to propose that the parasitic female lacks cephalic papillae. In the practical sense this is of no importance, since although Little's definition stated the parasitic female had four cephalic papillae, most authors had found them to be so small as to be indistinguishable. In no species had the number of cephalic papillae been of taxonomic weight.

The generic boundaries have been defined so precisely that closely related genera can now be confidently separated from *Strongyloides*.

CHAPTER 3

STATUS OF NAMES USED FOR SPECIES OF *STRONGYLOIDES*.

3.1 LIST OF PUBLISHED NAMES

A list of published names used for species of *Strongyloides* is given in Table 3:1. The authority proposing or first using the name is included as well as the scientific and common names of the type host, or if the name proposed for the parasite has no taxonomic status, the host name given is that associated with the use of the name. Names not used previously in the literature but considered by me to be the valid name of a taxon are also included. Unpublished names refering to new taxa are not listed. Where the scientific name of the host has been subsequently amended, the currently accepted scientific name is given followed by the binomial used by the parasitologist in parenthesis.

There have been several attempts to publish comprehensive lists of species of *Strongyloides* (von Linstow, 1905; Stiles and Hassall, 1920; Hung and Höeppli, 1923; Sandground, 1925; Travassos, 1930a; Tomita, 1939; Griffiths, 1940; Yamaguti, 1961; Tanaka, 1966). The last list which included all names in the literature was by Sandground (1925) when 12 species had been named. Table 3:1 is the first complete list since 1925.

The original description or paper containing first use of a particular name was viewed and evaluated for conformity with the International Code of Zoological Nomenclature, 1985. Names were initially assigned to one of two categories, "available" and "unavailable".

3.2 UNAVAILABLE NAMES

An unavailable name is one whose original use does not comply with Articles 10 to 20 of the Code, or which has been introduced into the literature through an inadvertent error, a *lapsus calami*. Mayr (1971) suggests such names should not be listed, even in synonymy, in case such a listing constitutes an "indication" under Articles 12 and 13, and therefore makes the name valid. This is the extreme view, but certainly care is required in their use in publications (see Chap.3.1, *S.martis* and S.mustelorum). The status of such names can be clarified only by listing and critical evaluation. Unavailable names are listed in Table 3:2.

TABLE 3:1. List of Published Names for *Strongyloides*.

SPECIES	AUTHORS	HOST SCIENTIFIC NAME	HOST COMMON NAME
S.agouti	Enigk, 1950	not given	not given
S.agoutii	Griffiths, 1940	*Dasyprocta agouti*	golden rumped agouti
S.akbari	Mirza & Narayan, 1935	*Crocidura coerula*	musk rat
S.amphibiophilus	Perez Vigueras, 1942	*Bufo peltocephalus*	toad
S.ardeae	Little, 1966	*Butorides virescens virescens*	eastern green heron
S.ardeae	Boyd, 1966	*Ardea herodius herodius*	great blue heron
S.avium	Cram, 1929	*Gallus gallus*	domestic fowl
S.bovis	Vryjburg, 1907	not given	domestic ox
S.bufonis	Rao & Singh, 1954	*Bufo melanosticus*	toad
S.bufonis	Anon, 1962	*Bufo valiceps*	Weigman's toad
S.bufonis	Rao & Singh, 1968	*Bufo melanostictus*	toad
S.canis	Brumpt, 1922	*Canis familiaris*	domestic dog
S.carini	Pereira, 1935	*Leptodactylus gracilis*	frog
S.carinii	Pereira, 1935	*Leptodactylus gracilis*	frog
S.cati	Brumpt, 1927	*Felis catus*	domestic cat
S.cati	Rogers, 1939	*Felis catus*	domestic cat
		Felis planiceps	rusty tiger cat
S.cebi	Travassos, 1930	*Cebus capucinus* (*Cebus hypoleucus*)	white -throated capucin monkey
S.cebus	Darling, 1911	*Cebus capucinus* (*Cebus hypoleucus*)	white-throated capucin monkey
S.chapini	Sandground, 1925	*Hydrochoerus hydrochaeris* (*Hydrochoerus hydrochoera*)	capybara
S.chitwoodi	Srivastava, 1971	not given	poultry
S.cruzi	Rodrigues, 1968	*Hemidactylus mabouia*	skink
S.cubaensis	Perez Vigueras, 1942	*Butorides virescens maculatus*	Cuban green heron
S.cubäensis	Perez Vigueras, 1942	*Butorides virescens maculatus*	Cuban green heron
S.cubanensis	Barus, 1968	not given	not given
S.darevskyi	Shapilo, 1976	*Lacerta saxicola*	skink
S.elephantis	Greve, 1969	*Elephas indicus*	Indian elephant
S.erschowi	Popova, 1938	*Nyctereutes procyonoides usuriensis*	raccoon dog
S.erycis	Baylis, 1923	*Eryx jaculus*	sand boa
S.eryxi	Mirza & Narayan, 1935	*Eryx johnii*	John's sand boa
S.felis	Chandler, 1925	*Felis catus*	domestic cat
S.fuelliborni	Knight *et al*	*Homo sapiens*	man
S.fuelleborni	von Linstow, 1905	*Pan troglodytes*	chimpanzee
		Papio cyanocephalus	yellow baboon

SPECIES	AUTHORS	HOST SCIENTIFIC NAME	COMMON NAME
S.füleborni	Panaitescu & Potorac, 1981	*Cercopithecus pygerethus*	vervet monkey
		Macaca irus	cymologus monkey
		(*Macaca fascicularis*)	
		Macaca mulatta	rhesus monkey
S.fullbornii	Held & Whitney, 1978	not given	non-human primates
S.fulleborni	Brumpt, 1949		
S.fülleborni	von Linstow, 1905	*Pan troglodytes*	chimpanzee
		(*Anthropopithecus troglodytes*)	
		Papio cyanocephalus	yellow baboon
		(*Cyanocephalus babuin*)	
*S.fülleborni*i	Shulman, 1980	not given	??
S.gulae	Little, 1966	*Natrix cyclopyon cyclopyon*	green water snake
S.herodiae	Boyd, 1966	*Ardea herodius herodius*	great blue heron
S.hominis	Reisinger, 1915	*Homo sapiens*	man
S.intestinalis	(Bavay, 1876) Grassi, 1879	*Homo sapiens*	man
S.longus	(Grassi & Segre, 1887) Rovelli, 1888	*Ovis aries*	domestic sheep
S.longus bovis	de Gaspari, 1912	*Bos taurus*	domestic ox
S.longus ovis	Reisinger, 1915	*Ovis aries*	domestic sheep
S.longus suis	Reisinger, 1915	*Sus scrofa*	domestic pig
S.lutrae	Little, 1966	*Lutra canadensis*	common otter
S.martis	Petrov, 1940	*Martes zibellina*	sable
		Mustela ermina	stoat
		(*Arctogale ermina*)	
S.martis	Little, 1966	*Martes zibellina*	sable
		Mustela ermina	stoat
		(*Arctogale ermina*)	
S.minimum	Travassos, 1930	*Dafilia bahamensis*	duck
S.mirzai	Singh, 1954	Zamensis mucosus	rat snake
		(*Ptyas mucosus*)	
S.mustelarum	Yamaguti, 1961	*Mustela erinacea*	not given
S.mustelorum	Cameron & Parnell, 1933	*Mustela ermina*	stoat
S.mustelorum	Little, 1966	*Mustela ermina*	stoat
S.musterolum	Fukase *et al*, 1985	Mustelidae	
S.myopotami	Artigas & Pacheco, 1933	*Myocastor coypus*	coipu rat
		(*Myopotamus coipus*)	
S.nasua	Darling, 1911	*Nasua narica panamensis*	coatimundi
		(*Nasua nasica panamensis*)	

SPECIES	AUTHORS	HOST SCIENTIFIC NAME	HOST COMMON NAME
S.nutriae	Enigk, 1933	*Myocastor coypus*	coypu rat
S.ophidae	Pereira, 1929	*Drymobius bifossatus*	snake
S.oswaldei	Boyd, 1966	*Gallus gallus*	domestic fowl
S.oswaldi	Travassos, 1930	*Gallus gallus*	domestic fowl
		(*Gallus domesticus*)	
S.oswaldoi	Travassos, 1930	*Gallus gallus*	domestic fowl
		(*Gallus domesticus*)	
S.ovocinctus	Ransom, 1911	*Antilocapra americana*	prong horned antelope
S.pallosus	Smits and Jacobi, 1965	*Okapia johnstoni*	okapi
S.papilosus	Lim and Lee, 1977	not given	deer
S.papillosus	(Wedl, 1856) Ransom, 1911	*Ovis aries*	domestic sheep
S.papillousus	Miyamoto, 1929	not given	not given
S.pappillosus	Tomita, 1939	*Sus scrofa*	domestic pig
S.pavonis	Sakamoto and Yamashita, 1970	*Pavo muticus*	green peafowl
S.pereirai	Travassos, 1932	*Elosia rustica*	
S.petrovi	Ryjova and Dubov, 1955		
S.physali	Little, 1966	*Bufo valiceps*	Wiegman's toad
S.planiceps	Rogers, 1943	*Felis catus*	domestic cat
		Felis planiceps	rusty tiger cat
S.procyonis	Little, 1966	*Procyon lotor*	raccoon
S.putorii	Morosov, 1939	*Mustela putorius*	polecat
		(*Putorius putorius*)	
S.quiscali	Barus, 1969	*Quiscalus niger caribaeus*	bird
S.ramsomi	Fukase *et al*, 1985	not given	
S.ransomi	Schwartz and Alicata, 1930	*Sus scrofa*	domestic pig
S.rasomi	Travassos, 1930	*Sus scrofa*	domestic pig
S.ratti	Sandground, 1925	*Rattus norvegicus*	brown rat
S.ratti v.ondatrae	Chandler, 1941	*Ondatra zibethicus*	musk rat
S.robustus	Chandler, 1942	*Scirius niger rufiventer*	fox squirrel
S.rostombekovi	Yamaguti, 1961	not given	hedgehog
S.rostombekowi	Gamzemlidse, 1941	*Erinaceus europea*	hedgehog
S.serpentis	Little, 1966	*Natrix cyclopyon cyclopyon*	green water snake
S.sigmodontis	Melvin and Chandler, 1950	*Sigmodon hispidus*	cotton rat
S.simiae	Hung and Höeppli, 1923	not given	"makaken"
S.spiralis	Grabda-Kazubska, 1978	*Rana esculenta*	edible frog
		Rana lessoni	edible frog

SPECIES	AUTHORS	HOST SCIENTIFIC NAME	HOST COMMON NAME
S.stercolaris	Ito *et al*, 1962	*Canis familiaris*	dog
S.stercoralis	(Bavay, 1876) Grassi, 1879	*Homo sapiens*	man
S.stercoralis v.eryxi	Mirza and Narayan, 1935	*Eryx johnii*	John's sand boa
S.stercoralis v.felis	Chandler, 1925	*Felis catus*	domestic cat
S.stercoralis v.vulpi	Mirza and Narayan, 1935	*Vulpes alopex*	artic fox
S.suis	von Linstow, 1905	*Sus scrofa*	domestic pig
S.thylacis	Mackerras, 1959	*Isoodon macrouris* (*Thylacis obesulus*)	short nosed bandicoot
S.tumefaciens	Price and Dikmans, 1941	*Felis catus*	domestic cat
S.turkmenica	Kurtieva, 1953	*Himantopus candidus*	stilt
S.turkmenicus	Barus *et al*, 1978	*Larus canus*	common gull
S.venezuelensis	Brumpt, 1934	*Rattus norvegicus*	brown rat
S.vesteri	Chilimoniuk, 1958		horse
S.vituli	Brumpt, 1921	*Bos taurus*	domestic ox
S.viviparus	(Probstmayr, 1865) von Linstow, 1905	*Equus caballus*	domestic horse
S.vulpis	Petrov, 1940	*Vulpes vulpes*	red fox
S.westeri	Ihle, 1917	*Equus caballus*	domestic horse

TABLE 3:2. Unavailable names.

NAME	AUTHOR	STATUS	REFERENCE
S.agouti	Enigk, 1950	*lapsus calami*	this thesis
S.bufonis	Rao & Singh, 1954	no differential diagnosis	this thesis
S.bufonis	Anon, 1962	*nomen nudum*	(see text
S.carini	Pereira, 1935	*lapsus calami*	this thesis
S.cati	Brumpt, 1927	*nomen nudum*	Rogers, 1943
S.cebi	Travassos, 1930	*lapsus calami*	this thesis
S.chitwoodi	Srivastava, 1971	*nomen nudum*	this thesis
*S.cub*üensis	Perez Vigueras, 1942	unacceptable spelling	this thesis
S.cubanensis	Barus, 1968	*lapsus calami*	this thesis
S.fuellborni	Knight *et al*, 1979	*lapsus calami*	this thesis
*S.f*üleborni	Panaitescu & Potorac, 1981	*lapsus calami*	this thesis
S.fullbornii	Held & Whitney, 1978	*lapsus calami*	this thesis
S.fulleborni	Brumpt, 1949	*lapsus calami*	this thesis
*S.f*ülleborni	von Linstow, 1905	unacceptable spelling	this thesis
*S.f*üllebornii	Shulman, 1980	*lapsus calami*	this thesis
S.hominis	Reisinger, 1915	*nomen nudum*	this thesis
S.martis	Petrov, 1940	no differential diagnosis	this thesis
S.mustelarum	Yamaguti, 1961	*lapsus calami*	this thesis
S.mustelorum	Cameron & Parnell, 1933	no differential diagnosis	this thesis
S.musterolum	Fukase et al, 1985	*lapsus calami*	this thesis
S.oswaldei	Boyd, 1966	*lapsus calami*	this thesis
S.pallosus	Smits & Jacobi, 1965	*lapsus calami*	this thesis
S.papilosus	Lim & Lee, 1977	*lapsus calami*	this thesis
S.papillousus	Miyamoto, 1929	*lapsus calami*	this thesis

NAME	AUTHOR	STATUS	REFERENCE
S.pappillosus	Tomita, 1939	*lapsus calami*	this thesis
S.ramsomi	Fukase *et al*, 1985	*lapsus calami*	this thesis
S.rasomi	Travassos, 1930	*lapsus calami*	this thesis
S.rostombekovi	Yamaguti, 1961	*lapsus calami*	this thesis
S.stercolaris	Ito *et al* , 1962	*lapsus calami*	this thesis
S.turkmenicus	Barus *et al*	*lapsus calami*	this thesis
S.vesteri	Chilimoniuk, 1958	*lapsus calami*	this thesis
S.vituli	Brumpt, 1921	*nomen nudum*	Sandground, 1925

3.2.1 Comment on Unavailable Names.

S.agouti.

This name was used (p132) in a review by Enigk (1950), and again by Tanaka (1966 p593). It is obvious that they meant to refer to *S.agoutii*. It is a *lapsus calami*.

S.bufonis.

Little (1961) used this name in his PhD dissertation for a species from Wiegmann's toad, *Bufo valiceps*. The name had been used previously by Rao and Singh (1954) for a species from *Bufo melanosticus*, a toad from India. (In the 1954 abstract the host specific name was spelt "*melanosticus*"; but the 1968 paper gave it as "*melanostictus*", with an additional "t". I was unable to determine which was correct.) Little discovered this prior to publication of his species and instead used the name *S.physali*. The dissertation did not constitute a valid publication, but an abstract, including a list of new species names without descriptions, was published in Helminthological Abstracts (vol 31, 1962, no.2953), four years before publication of the descriptions (Little, 1966b). This action introduced *S.bufonis* into the literature with Little as author. The U.S.D.A. Index-Catalogue of Medical and Veterinary Zoology Suppl. 17, Part 4, 1969 (p202-204) gave the names of all seven new species named by Little in his dissertation, including *S.bufonis*, the status of *nomina nuda*. The other names were subsequently published (Little, 1966b), but this use of *S.bufonis* remains a *nomen nudum*. This sequence of events serves to illustrate the problems caused by abstraction of proposed species names from dissertations prior to their publication in full.

The name *S.bufonis* as proposed by Rao and Singh (1954) was not accompanied by any attempt to differentiate the species from others. It was originally published as an abstract, listing the host and several measurements and proportions. Article 13a(i) states that a name published after 1930 must be :

> "accompanied by a description or definition that states in words characters that are purported to differentiate the taxon,"

Clearly, Rao and Singh (1954) had failed to do this and the name was unavailable. Had Little chosen to use *S.bufonis* instead of *S.physali* in his 1966 paper, *S.bufonis* Little would have been available and valid. Little (1966b) suggested that *S.bufonis* Rao and Singh was not "valid" on the grounds of an inadequate description. This opinion is open to debate, but under Article 13a(i) there can be no doubt that *S.bufonis* as used by Rao and Singh (1954) is not an available name. In response to Little's criticsm Rao and Singh (1968) subsequently described the species more fully and provided a brief differential diagnosis. The correct citation for the species is *S.bufonis* Rao and Singh, 1968.

S.carini.

This name was used once (p20) in the original paper by Pereira (1935). The author intended the parasite to be known as *S.carinii*, named after A.Carini, and the name *S.carinii*, was used on four occasions in the same paper (pp 19,20 and 21). *S.carini* was obviously an inadvertent error and is therefore unavailable under Article 32c(ii).

S.cati.

Brumpt (1927) originally used the name in a footnote on page 662, "au Bengale, le chat presente, dans 20 pour 100 des cas sur 250 examines, un *Strongyloides* identifie au stercoralis par A.Chandler (1925) et considere comme une espece particuliere, *S.cati*, par d'auteurs." These other authors could not be found by Rogers (1943) or myself. Brumpt was apparently refering to *S.stercoralis* v.*felis* described by Chandler (1925a&b) from cats in Calcutta, not "Bengale". *S.stercoralis* v.*felis* was an available name, so if Brumpt's *S.cati* was available it was first published as a junior synonym. *S.cati* as used by Brumpt, however, was unaccompanied by a description, and lacking an indication, under Article 12, the name is a *nomen nudum*. Unaware of this prior use Rogers (1939) used the name to describe a species originating from the rusty tiger cat, *Felis planiceps*, and maintained experimentally in the domestic cat. Since Brumpt's use was invalid, his *S.cati* had no taxonomic standing, and *S.cati* Rogers, 1939 was not in homonymy. The latter was the only available name. Rogers (1943), however, discovered the former use of *S.cati* by Brumpt, suggested that this was a *nomen* *nudum*, but then proposed an alternative name for his species, *S.planiceps* Rogers, 1939. This latter name has become universally accepted. An original name can be changed only if the error is inadvertent. *S.cati* Rogers, 1939 was valid. Consequently, his proposal to rename the species does not conform to the Code. *S.planiceps* Rogers, 1939 is therefore a junior synonym of *S.cati* Rogers, 1939.

S.cati has been used by several authors, mainly of veterinary reviews or textbooks (Soulsby, 1968; Prescott, 1972; 1977; Mason, 1980; Wilkinson, 1984), but only Soulsby (1968) listed *S.cati* and *S.planiceps* as synonyms. The other authors failed to make clear to which taxon they were referring in their use of *S.cati*. Wilkinson (1984 p466) clumsily indicated *S.cati* to be a junior synonym of *S.stercoralis*, when he listed them as "*S.stercoralis*, (*cati*)". He failed to give taxonomic references for this synonymy. This use is an error and of no taxonomic standing.

S.cebi.

Travassos (1930b p176) used this name in error for *S.cebus*. It is a *lapsus calami*.

S.chitwoodi.

This name was proposed as a *comb.nov*. by Srivastava (1971). No details were given, but reference was made to the author's dissertation. Unfortunately, a copy could not be viewed. This use is a *nomen nudum* and unavailable.

*S.cub*ä*ensis*.

Article 32c(vi) of the 1985 Code forbad the use of diacritic marks. Under Article 32d(i)2 the correct spelling is *S.cubaensis*. Little (1966b) and Boyd (1966) used the correct form without comment.

S.cubanensis.

Barus (1969) used this name twice (pp132,133). It is a *lapsus calami* for *S.cubaensis*.

S.erycis.

Baylis (1923 p35) introduced this name when he reported on the *Strongyloides* collected by Looss. Looss had labelled specimens collected from a sand boa as *Rhabdonema erycis*. *Rhabdonema* is a synonym of *Strongyloides*. The name had not been published prior to Baylis's use. Baylis provided no description, so the name is a *nomen nudum* and unavailable.

*S.fü*elleborni.

This name was proposed by von Linstow (1905) for a species from the chimpanzee and a baboon. Article 32c(i) of the 1964 Code was a new provision and forbade the use of the umlaut, and replacement by the original vowel followed by "e". This provision is maintained in the 1985 Code. The correct spelling is *S.fuelleborni*. Many authors have persisted in using the unavailable form (Jaros et al, 1966; Little, 1966a; Gretillat et al, 1967; Beg, 1968; Wong and Conrad, 1968; Hansen et al, 1969, 1975; Pampiglione and Riccardi, 1971,1972; Healy and Myers, 1973; Myers and Kuntz, 1973; Arambulo et al, 1974; Goldsmid, 1974; Kagei and Hasegawa, 1974; Arizono, 1976a&b; Hira and Patel, 1977; Schultze, 1977; Hira, 1978; Prosl and Tamer, 1979; Karr et al, 1980; Rutherford, 1981; Horii et al, 1982; Usui and Horii, 1982; Fukase et al, 1985). Others have omitted the umlaut and used *S.fulleborni* (Brumpt, 1949; Lefrou and Michard, 1957; Guilloud et al, 1965; Gorkhali and Basir, 1968; Wong and Conrad, 1968; Rego, 1972; Kelly et al, 1976; Remfrey, 1978; Ashford et al, 1979; Vince et al, 1979; 1982; Eberhard, 1981). This latter spelling is also invalid as under section 32d(i)2, "ü" becomes "ue". *S.fulleborni* does not have the status of a junior synonym since the uses were inadvertent errors.

S.fuellborni, *S.fü*leborni, *S.fullbornii* and *S.fü*llebornii are *lapsa calamorum*.

S.hominis.

This name was used by Reisinger (1915); no authority was given and no details provided. The only other similar name found was *Rhabdonema hominis*, used by Lutz (1885 p387). *Rhabdonema* is a synonym of *Strongyloides*. In both cases the implication was that the name referred to the *Strongyloides* of man. The name as used is a *nomen nudum* since a definition or description was not given.

S.martis.

Petrov (1940a) proposed the name *S.martis* for specimens collected from the intestines of *Martes zibellina* and *Mustela ermina*. The description (pp221-222) was of the parasitic female only, and lacked key taxonomic features. An illustration of the whole worm (p221, unnumbered fig.) suggested that the ovaries were directly recurrent, and that the tail was narrowly tapered. The text contained no reference to ovary type, but stated that the tail was conical and bluntly rounded. Some measurements were given. There was no attempt to give a differential diagnosis; no other species of *Strongyloides* was mentioned in the paper. A name proposed after 1930 must be accompanied by a differential diagnosis (Article 13a(i)). Petrov (1940) made no attempt to do so. *S.martis* Petrov is therefore unavailable.

S.martis Little, 1966 is an available name, since Little (1966b p87) , in discussing Petrov's description, gave an indication and a differential diagnosis in his proposal for *S.lutrae*.

S.mustelarum.

Yamaguti (1961) used this name in his list in error for *S.mustelorum* Cameron and Parnell, 1933, a species from the stoat, *Mustela ermina*. Yamaguti (1961) also erred in giving the host as *Mustela erinacea*. The name is a *lapsus calami*.

S.mustelorum.

This name was proposed by Cameron and Parnell (1933) to accommodate two parasitic females found in the small intestine of a stoat, *Mustela ermina*. A brief description, some dimensions, and an illustration of the whole worm was given (pp143,144 fig.8). No attempt to differentiate the taxon was made. Justification for the new species was (p144):

> "We consider it advisable to have two names for a single species rather than have two species with the same name."

Arguments can be presented for and against this principle, but the point is that Cameron and Parnell provided no means whereby their specimen could be distinguished from another. Apparently they did not deposit it. Since *S.mustelorum* was proposed after 1930 and no differential diagnosis was given, under Article 13a(i) of the Code, the name is unavailable.

Little used the name *S.mustelorum* in his discussion on *S,lutrae* (1966a p85,87). He gave the dimensions published by Cameron and Parnell (1933), and attempted to give a differential diagnosis. *S.mustelorum* Little is therefore an available name.

S.musterolum.

In a comprehensive paper on *Strongyloides* from *Mustela sibirica* Fukase et al (1985) used the name "*musterolum*" in error for "*mustelorum*" (p630). It is a *lapsus calami.*

S.oswaldei.

Boyd (1966) used this name for a species from "*Gallus* in Brazil", and gave as authority Freitas and Almeida (1936). These latter authors did not propose or use this name. Boyd apparently meant to refer to *S.oswaldi* Travassos, 1930. *S.oswaldei* is a *lapsus calami.*

S.pallosus.

This name was used by Smits and Jacobi (1965) (p146, Table 3) in a paper on the parasites of okapi, *Okapia johnsoni.* It is obvious the authors meant to record the presence of *S.papillosus,* a species found commonly in ruminants. *S.pallosus* is a *lapsus calami.*

S.papilosus.

Lim and Lee (1977) gave this name for specimens found in captive deer (species not stated). It is a *lapsus calami* for *S.papillosus.*

S.papillousus.

This name was used by Miyamoto (1929) when comparing the shape of the tail of *S.suis* from Formosan pigs. He meant to use *S.papillosus* group *sensu* Chandler (1925b). This use is a *lapsus calami.*

S.pappillosus.

In a comprehensive paper on the *Strongyloides* of pigs on Formosa, Tomita (1939) assigned the species found to *S.papillosus*. He used this consistently throughout, but erred in the abstract (p1624) in using "*pappillosus*". This use is a *lapsus calami*. Tomita was probably dealing with *S.suis*, not *S.papillosus*.

S.ramsomi.

Fukase *et al* (1985) used this name in a general discussion on *Strongyloides* of Canidae, Felidae and Mustelidae. They obviuosly intended to use the name *S.ransomi*. *S.ramsomi* is a *lapsus calami*.

S.rasomi.

Travassos (1930b) used this name (p176) in discussing the species from pigs "named by Schwartz". It is a *lapsus calami* for *S.ransomi*.

S.rostombekovi.

This name was used by Yamaguti (1961) in error for *S.rostombekowi* Gamzemlidse, 1941 from the hedgehog. It is a *lapsus calami*.

S.stercolaris.

The first to use the name *S.stercolaris* was Ito *et al* (1962; pp55,57,58,60 Tables 2 and 6) for specimens from a dog in Bangkok. Presumably, they meant to use the specific name "*stercoralis*". Hayama and Nigi (1963) also consistently used the name *S.stercolaris* (pp104,106, Tables 3 and 4) for a species from gibbons and chimpanzees. It is obvious from the text that they meant to refer to the parasite of primates, *S.stercoralis*. Hayama and Nigi (1963) did not refer to the earlier use. *S.stercolaris* is a *lapsus calami*.

S.turkmenicus.

This is a *lapsus calami* for *S.turkmenica* Kurtieva, 1953. It was used without comment by Barus *et al* (1978 pp46,47).

S.vesteri.

This name was used by Chilimoniuk (1958 p169), presumably in error for *S.westeri.* It is a *lapsus calami.*

S.vituli.

Brumpt (1921) used this name for a parasite of calves in France. No morphological details were given and it is therefore a *nomen nudum* (Sandground, 1925).

3.3 INVALID NAMES.

Validity is a term that refers to the rights of names in relation to homonyms and synonyms (Mayr, 1971). At any particular time only one name can be the valid name of a taxon. Synonyms are different names for the same thing. The synonym which was published the earliest is the senior synonym and is the only valid name for the taxon. The synonyms published subsequently are junior synonyms and invalid. A name becomes a senior synonym at the time when a second name for the same taxon is made available. Names first published as synonyms may be available, that is fulfil the provisions of the Code, but will not be valid. A homonym is the same name for different taxa. The earliest name is the senior homonym and is valid ; the other names are the junior homonyms and are invalid. A primary homonym is a name originally published as a junior homonym. It must be renamed. Provisions governing the replacement of rejected primary homonyms are given in Article 60 of the Code, and give the author of the rejected name an opportunity to propose an alternative valid name.

Arguments about validity depend on whether the species in question are actually the same and priority. The date of publication is the important date when deciding on priority. The date of publication is the date on which the publication was mailed to subscribers, placed on sale, or, where the edition is distributed free of charge, mailed to institutions and individuals to whom such free copies are normally distrubited (Mayr, 1971). This date is not necessarily the date printed on the cover of the journal or book. The revelent provisions are dealt with in Articles 21 -24. Invalid names are listed in Table 3:3.

TABLE 3:3. Invalid names.

INVALID NAME	STATUS	VALID NAME	REFERENCE
S.ardeae Boyd,1966	junior homonym	*S.herodiae* Boyd,1966	Boyd(1967)
S.bovis Vrijburg,1907	not *Strongyloides*	*Cooperia punctata* Ransom,1911	Ransom(1911)
S.canis Brumpt, 1922	*nomen dubium*	-	this thesis
S.intestinalis (Bavay,1876) Grassi,1879	junior synonym	*S.stercoralis* (Bavay,1876) Grassi,1879	Stiles&Hassall(1902)
S.longus (Grassi&Segre,1887) Rovelli,1888	junior synonym	*S.papillosus* (Wedl,1856) Ransom,1911	Ransom(1911)
S.longus bovis de Gaspari, 1912	junior synonym	*S.papillosus* (Wedl, 1856) Ransom, 1911	this thesis
S.longus ovis Reisinger,1915	junior synonym	*S.papillosus* (Wedl,1856) Ransom,1911	this thesis
S.longus suis Reisinger,1915	junior synonym	*S.suis* vonLinstow,1905	this thesis
S.mirzai Singh,1954	junior synonym	*S.eryxi* Mirza&Narayan,1935	this thesis
S.nutriae Enigk,1933	junior synonym	*S.myopotami* Artigas&Pacheco,1933	this thesis
S.oswaldoi Travassos,1930	junior synonym	*S.oswaldi* Travassos,1930	this thesis
S.ovocinctus Ransom,1911	junior synonym	*S.papillosus* (Wedl,1856) Ransom,1911	Sandground(1925)
S.planiceps Rogers,1943	junior synonym	*S.cati* Rogers,1939	this thesis
S.ransomi Schwartz&Alicata,1930	junior synonym	*S.suis* VonLinstow,1905	this thesis
S.simiae Hung&Höeppli,1923	*nomen dubium*	-	this thesis
S.stercoralis v.*eryxi* Mirza&Narayan,1935	elevation in rank	*S.eryxi* Mirza&Narayan,1935	Rodrigues, 1968
S.stercoralis v.*felis* Chandler,1925	elevation in rank	*S.felis* Chandler,1925	Goodey(1926)
S.viviparus von Linstow,1905	not *Strongyloides*	*Probstmayria vivipara* (Probstmayr,1865) (Probstmayr,1865) Ransom,1907	Ransom(1907b)

3.3.1 Comment on Invalid Names.

S.ardeae Boyd, 1966.

Boyd published a description of *S.ardeae* from the eastern green heron, *Butorides virescens virescens*, in the Journal of Parasitology, 52, part 3, p503, June, 1966. Little in February of the same year published his description of *S.ardeae* from the yellow crowned night heron, *Nyctanassa violacea* in Journal of Parasitology, 52, part 1, p85. *S.ardeae* Little had priority and *S.ardeae* Boyd was therefore a primary homonym. Boyd (1967) considered her species was distinct from *S.ardeae* Little and renamed it *S.herodiae* Boyd, 1966.

S.bovis Vryjburg, 1907.

The original description of *S.bovis* (Vryjburg, 1907) consisted of fairly comprehensive descriptions and illustrations of male and female trichostrongyloid nematodes. Ransom (1911) commented that *S.bovis* "is very clearly not a *Strongyloides*. His description and figures indicate that he was dealing with *Cooperia punctata*, in part at least.".

S.canis Brumpt, 1922.

Fülleborn (1914) was the first to report *Strongyloides* in dogs. He proposed that the parasite in Chinese dogs was a biological variety of *S.stercoralis*. Brumpt (1922) considered that this variety should be given specific status, and proposed the name *S.canis*. His grounds for so doing were based solely on biological criteria :

(i) Differences in geographic ranges of the two species in their respective hosts. *S.canis* was found mainly in dogs in the "Orient", presumably China and Japan, and had a very low prevalence elsewhere. *S.stercoralis* in man was cosmopolitan, and occurred at high prevalences in areas where dogs were rarely affected.

(ii) Difficulty in infecting dogs with *S.stercoralis*. In general this point still holds; *S.stercoralis* can infect dogs, but the patency, intensity, and longevity of the infection varies with the strain used and the age of the dog (Galliard, 1951; Dawkins and Grove, 1982;). Puppies are more susceptible (Horie et al, 1974;?). Faust (1933) and Augustine (1940) produced persistent experimental infections in dogs using natural canine strains. Both, however, failed to give any morphological details of their strains.

(iii) Differences in the type of development in culture. Fülleborn (1914) found only indirect development with the canine strain, while Brumpt (1922) obtained mixed development with *S.stercoralis*. This point is of no significance, as with most species the type of development varies with factors other than the specific identity of the worm.

The status of *S.canis* has been uncertain since its proposal. It is an available name, since an indication, the "work" of the animal, was given (Article 16a(viii). The validity of *S.canis* is the point to be considered. The major weakness of Brumpt's argument, and of those supporting the validity of *S.canis* (Augustine, 1940), is that, apart from its "works", the parasite has not been well described. The key feature known is that larvae are found in faeces. Brumpt's argument rests mainly on biological criteria, and he and Augustine seem to adopt the approach that any *Strongyloides* found in a dog is *S.canis* by virtue of it being found as a natural infection in a dog. This is incorrect. *S.cati* (syn.*S.planiceps*) is a natural parasite of dogs in Japan (Arizono *et al*, 1976; Horie *et al*, 1980). Infection of dogs over three months of age with a species passing eggs in faeces is prevelant in Fiji (Munro and Munro, 1978). *S.cati* may be the parasite involved, but a more complete examination is required. An unidentified parasite, morphologically similar to *S.stercoralis* was described by Lucker (1942) from natural infections in seven dogs in USA. This was not *S.cati* since larvae were passed in faeces. *S.stercoralis* has been reported as natural infections in dogs (Ware and Ware, 1923; Whitney, 1936; Ito et al, 1962; Enyenihi, 1972; Georgi and Sprinkle, 1974; Ohder and Hurni, 1978; Horie et al, 1980), but none of the reports have given sufficient major criteria by which the identification can be evaluated. A group of dogs examined by me in Townsville, north Queensland, had larvae in faeces, and free-living adults consistent with *S.felis* were cultured. Naturally infected dogs in USA have had either eggs (Chandler, 1939) or larvae (Augustine and Davey, 1939; Augustine, 1940; Lucker, 1942) in faeces. Patent experimental infections of dogs have been reported for *S.fuelleborni* (Sandground, 1925) and *S.suis* (Kotlan and Vadja, 1934).

Consequently, to assume that the dog is naturally infected by only one species is incorrect. The clarification of the status of *S.canis*, even by means of a comprehensive investigation, is probably impossible since there are too few clues to indicate its morphology. The name, *S.canis*, is therefore a *nomen dubium*.

S.intestinalis (Bavay, 1876) Grassi, 1879.

Grassi (1879b) proposed this name for the species now known as *S.stercoralis*. The taxonomic history has been discussed under Section 1:2. The generic name *Strongiloides* was not widely accepted, even Grassi failed to use it after 1879, and the specific epithets *stercoralis* and *intestinalis* were used interchangeably often in the same publication (Golgi and Monti, 1884; Lutz, 1855; Grassi and Segre, 1887). Strict adherence to the generic case for the specific name was not followed, "stercorale" and "intestinale" also being used interchangeably (Grassi and Segre, 1887). The specific name "stercoralis" had priority over "intestinalis", and priority had been established in principle by Linneaus. Linneaus and his followers, however, were inveterate name changers ; often for quite minor reasons (Mayr, 1971). The principle of priority had been formalised in the Strickland Code (Strickland, 1842) backed by the British Association for the Advancement of Science, but was not adopted on an international scale until 1905. This may explain why one binomial had not been adopted to the exclusion of the other. By the late 1890's - early 1900's Anguillula intestinalis seemed to be the favourite in Europe ; but in American literature *Strongyloides intestinalis* was prefered (Strong 1901a&b; Thayer, 1902; Ginsburg, 1920). Stiles and Hassall (1902) discussed the naming of this species and proposed *Strongyloides stercoralis* as the correct binomial. They deemed their effort to be worthy of taxonomic recognition, *S.stercoralis* to be followed by (Bavay, 1876) Stiles and Hassall, 1902. Stiles and Hassall merely played the role of adjudicator, however, and had not contributed taxonomically. The credit should have been given to Grassi, the author who proposed the change in the generic name from Anguillula to *Strongiloides*. The correct name is *Strongiloides stercoralis* (Bavay, 1876) Grassi, 1879 and *Strongiloides intestinalis* is a junior synonym. If however *Strongiloides* is suppressed, the correct citation of authors should be *Strongyloides stercoralis* (Bavay, 1876) Anon, 1879. Miyamoto (1929) may have been the last to use *Strongyloides intestinalis*.

S. nutriae Enigk, 1933.

Enigk (1933) described a species from a South American rodent, the nutria or coypu rat, *Myocastor coypus*, and proposed the name *S.nutriae* in Zeitschrift fur Parasitenkunde 6, distributed on 18th December, 1933. Earlier in the same year Artigas and Pacheco had described the same species in Comptes Rendus de la Societe de Biologe, Sao Paulo 112, issued on 3rd February. The latter species was named *S.myopotami* and has priority. Consequently, *S.nutriae* is a junior synonym. Enigk's (1933) new name was provisional since he considered the specimens he described may have belonged to *S.chapini* Sandground, 1925 whose type host was another South American rodent, the capabaya, *Hydrochoerus hydrochaeris*. The original description of *S.chapini* was incomplete and the specimens so degenerate (Sandground, 1925) that comparison is not possible without further collecting.

S.longus (Grassi and Segre, 1887) Rovelli, 1888.

The name *Rhabdonema longus*, was used by Grassi and Segre (1887) for a species from sheep. The original description was incomplete but Ransom (1911) proposed that *S.longus* was a junior synonym of *Trichosoma papillosum*, a species which he transfered to *Strongyloides* thereby changing the name to *S.papillosus*. This was generally accepted; the last use of *S.longus* was in 1927 by Haupt. Rovelli (1888) was cited by Ransom (1911) as an author of *S.longus* , presumably responsible for change of name from *Rhabdonema* to *Strongyloides*. Unfortunately Rovelli's paper could not be located.

S.longus bovis de Gaspari, 1912.

Using the name *S.longus bovis* de Gaspari (1912) published a description of specimens collected from *Bos taurus* in Turin. The description is consistent with *S.papillosus* (Wedl, 1856), which has priority. *S.longus bovis* is a junior synonym.

S.longus ovis Reisinger, 1915.

In a paper dealing with the species of *Strongyloides* found in pigs Reisinger (1915) gave the parasites in their respective hosts subspecific status, naming that from sheep *S.longus ovis* and from pigs, *S.longus suis*. This convention has not been followed for sheep, as the species found in sheep readily infects goats (Turner, 1959; Bezubik, 1963), rabbits (Ransom, 1907a), and the springbok, *Antidorcas marsupialis*, an African antelope (Mönnig 1931). It is unlikely that the sheep strain is specific and the subspecific name should be considered a junior synonym of *S.papillosus*.

S.longus suis Reisinger, 1915.

See *S.suis*. Junior synonym of *S.suis*.

S.mirzai Singh, 1954.

See *S.stercoralis* var.*eryxi* below. Junior synonym of *S.eryxi*.

S.oswaldoi Travassos, 1930.

S.oswaldi was used in the original description of a species from the domestic fowl (Travassos, 1930a). In the same year Travassos (1930b) used the name *S.oswaldoi* and continued to use this latter form (Travassos, 1932) without commenting on the change. Subsequent parasitologists (Cram, 1936; Freitas and Almeida, 1936; Griffiths, 1940; Yamaguti, 1961; Little, 1966b; Barus, 1968) used *S.oswaldoi*. Tanaka (1966) appears to have been the only worker to use *S.oswaldi*. The species was obviously named after the Institute of Oswaldo Cruz, where the type specimens were first deposited in 1917 (Travassos 1930a), and "*oswaldoi*" is the correctly latinised form. The change of the former name is a justified emendation under Article 32a(ii) if *S.oswaldi* was a *lapsus calami* or inadvertent error, either on the part of the author or printer. It is not justified if the error is one of transliteration on the author's part. If Travassos (1930a) had meant to use *S.oswaldi* in his initial publication, had subsequently realised his incorrect latinisation and then changed it, the error would be one of transliteration and therefore change of name would be unjustified under Article 32b. If on the other hand, Travassos had used *S.oswaldoi* in the manuscript, but the printer had erred and used *S.oswaldi*, a *lapsus calami* would have occurred. *S.oswaldi* was used only once in the original publication. *S.oswaldoi* was not used. No comment was made in the subsequent paper (Travassos, 1930b) when *S.oswaldoi* was first used, but *S.oswaldi* was listed as a synonym (p177). Travassos by this action acknowledged the taxonomic status of *S.oswaldi*. Although *S.oswaldi* is not the correctly latinised form as the author intended, *S.oswaldi* is an available name. It is the senior synonym and *S.oswaldoi* the junior. The valid name of the taxon is therefore *S.oswaldi*.

S.ovocinctus Ransom, 1911.

Specimens from the prong-horned antelope, *Antilocapra americana*, were morphologically consistent with *S.papillosus*, but appeared to have an unusual method of egg laying. Eggs were deposited beneath a cuticle which was shed by the worm (Ransom, 1911). On this basis and several minor morphological differences Ransom (1911) proposed a new species, *S.ovocinctus*, but commented that the specimens may belong to *S.papillosus*. Sandground (1925) considered that Ransom's specimens were *S.papillosus*, and that *S.ovocinctus* was a junior synonym. This view has not been disputed.

S.planiceps Rogers, 1939.

The history of this name has been discussed under *S.cati* in Section 1:5. It is a junior synonym of *S.cati* Rogers, 1939.

S.ransomi Schwartz and Alicata, 1930.

This name was proposed for a species found in the small intestine of the domestic pig. *S.suis* had been used in the literature for *Strongyloides* from pigs, but the authors proposed that their species differed in several characteristics. This is discussed in full below under *S.suis*. *S.ransomi* is a junior synonym of *S.suis*.

S.simiae Hung and Hoeppli, 1923.

Specimens from a monkey, "makaken" (English "macaque"), were described as a new species, *S.simiae* (Hung and Hoeppli, 1923). They were morphologically similar to *S.fuelleborni* and *S.cebus*, previously described from non-human primates, but the parasitic females of these latter species had not been described with cuticular striations, while striations could be seen in *S.simiae*. Hung and Höeppli (1923) used this as the major criterion to justify their proposal for a new species. All *Strongyloides* have transverse striations and consequently it is not a useful feature for differentiation. Sandground (1925), Goodey (1926) and Premvati (1959) considered the species to be a junior synonym of *S.fuelleborni* . Premvati (1959) also synonymised *S.cebus* and *S.fuelleborni*. Little's (1966a) more definitive study showed *S.fuelleborni* and *S.cebus* to be distinct species. He suggested that only two spiral ovary species occurred in non-human primates, *S.cebus* in New World species and *S.fuelleborni* in Old World primates. He considered *S.simiae* was a junior synonym, but did not nominate a senior synonym. In view of the lack of details on the identity of the type host, the incompleteness of the original description and the lack of type specimens, the more accurate view is to regard *S.simiae* as a *nomen dubium*.

S.stercoralis var.*eryxi* Mirza and Narayan, 1935.

Singh (1954) proposed *S.mirzai* for a species from the rat-snake, *Ptyas mucosus* from India. Mirza and Narayan (1935) had described specimens from *Eryx johnii*, a boa from India, and had named the species *S.stercoralis* var.*eryxi*. Singh (1954), who previously had published as Narayan in Mirza and Narayan (1935) (Singh, 1954), stated *S.stercoralis* var. *eryxi* was a synonym of *S.mirzai*. The morphological details given in both descriptions were consistent ; the synonymy was justified. The occurrance of eggs in freshly voided faeces and spiral ovaries in the parasitic female indicated that the parasite was not *S.stercoralis*, which has directly recurrent ovaries and larvae in faeces (Little, 1966a). The initial proposal was in error. A name proposed as a variety prior to 1961 has the rank of a subspecies under Article 45g(ii) and is of taxonomic significance. The name "*eryxi*" was available for this particular species, although the specific identification was wrong. "*eryxi*" is the senior synonym and "*mirzai*" the junior. The valid name for the species is therefore *S.eryxi*. *S.mirzai* is invalid. *S.stercoralis* v.*eryxi* was first raised to specific status by Rodrigues (1968 p32).

S.stercoralis var.*felis* Chandler, 1925.

This variety was raised to specific rank by Goodey (1926). As discussed under *S.stercoralis* var.*eryxi* Article 45g(ii) gives a name proposed as a variety before 1961 subspecific rank. Goodey's action was consistent with the provisions of the Code.

S.suis von Linstow, 1905.

Both the availability and the validity of this name have caused controversy. It was originally used as a synonym for *S.longus* by von Linstow (1905), who gave Lutz as the author, but failed to give a date. The existence of *Strongyloides* in pigs was evidently well known prior to von linstow's (1905) paper (Grassi, 1885;?). Lutz had published on *Strongyloides* in pigs, but did not use the specific name "*suis*" in 1885 nor 1886. Travassos (1930a) listed *S.suis* (Lutz, 1894) von Linstow, 1905 as authors for *S.suis*, but stated the original use was a *nomen nudum*. An 1894 publication by Lutz could not be located. Von Linstow's description of *S.longus* and consequently *S.suis* consisted of a list of six hosts, the locality "Europa", and the clause "ist 6mm lang.". There were no illustrations. Under Article 12c mention of host or locality is not an indication, but the comment on length may have constituted an indication prior to 1931. Article 11e of the 1985 Code deals with publication in synonymy:

> "A name first published as a junior synonym is not thereby made available unless prior to 1961 it has been treated as an available name and either adopted as the name of a taxon or treated as a senior homonym; such a name dates from its first publication as a synonym "

S.suis had been treated as an available name prior to 1961 and had been used to designate a taxon. It was described as a subspecies by Reisinger (1915); defined as a species without reference to von Linstow's use by Marotel (1920), and used by several workers (Ransom, 1907a; Ransom 1911; Stiles and Hassall, 1920; Chandler, 1925b; Sandground, 1925; Miyamoto, 1929; Travassos, 1930b; Schwartz and Alicata, 1930; Kotlan and Vajda, 1934; Stefanski, 1947; Brumpt, 1949; Tarczynski, 1956). The major problem concerning availability was authorship of the name. Lutz appears not to have used it (Stiles and Hassall, 1920; Sandground, 1925; Schwartz and Alicata, 1930; Stefanski, 1947; Tarczynski, 1956). The original use had been assigned to von Linstow by several authors (Stiles and Hassall, 1920; Sandground, 1925; Schwartz and Alicata, 1930; Travassos, 1930b; Kotlan and Vajda 1934; Stefanski, 1947; Brumpt, 1949; Tarczynski, 1956). All provisions of Article 11d namely, publication prior to 1961, treatment as an available name with original date and authorship, and adoption as the name of a taxon are fulfilled. *S.suis* von Linstow, 1905 is therefore an available name.

Since *S.suis* is available, the problem of validity must be considered. Debate till the 1930's concerned its synonymy with *S.papillosus*. Several workers considered *S.suis* a junior synonym (von Linstow, 1905; Sandground, 1925; Travassos, 1930b). Reissinger (1915) regarded it as a subspecies of *S.papillosus* (syn.*S.longus*). Schwartz and Alicata (1930) stated that the species in pigs was distinct from *S.papillosus*. The criteria used to separate them was a blunter tail in *S.papillosus* and an inability of the Strongyloides from pigs to infect rabbits. Patent experimental infections of rabbits by *Strongyloides* from pigs were subsequently obtained (Kotlan and Vajda, 1934; Lucker, 1934; Oshio, 1956), making this an invalid criteria for differentiation of *S.papillosus* and the *Strongyloides* of pigs. Cytological studies by Triantaphyllou and Moncol (1977) showed the two species to be very closely related and that cross-mating of free-living stages were fertile. An attempt to infect a pig with *S.papillosus* was unsuccessful (Lucker, 1934), although this same pig was also refractory to infection with *Strongyloides* obtained from pigs, and consequently a negative result was of little significance. Morphologically, cytologically and biologically the two species are closely related, but insufficient data are available to designate them as synonyms.

The other aspect of nomenclatural significance is to decide which name, *S.suis* or *S.ransomi*, is valid. Schwartz and Alicata (1930) divided the *Strongyloides* of pigs into two species; that found most commonly in North American pigs which they named *S.ransomi* and a species with a longer, narrower tail which they designated *S.suis*. These authors suggested *S.suis* was the species found in European swine, although they had seen specimens of *S.suis* in American pigs. Brumpt (1949) had considered them synonymous, and had designated *S.suis* as the senior synonym, and *S.ransomi* as the junior. Kotlan and Vajda (1934) and Tarczynski (1956) considered the separation proposed by Shwartz and Alicata to be unjustified. The tail morphology in the *Strongyloides* of pigs was shown to vary to such an extent that in a population both types could be found. As this was the criteria on which speciation relied, these authors considered *S.suis* and *S.ransomi* to be synonymous. This opinion has been generally accepted, *S.suis* being last used in the literature by Tarczynski (1956) and *S.ransomi* being universally used as the name for the species in pigs. The reason for favouring *S.ransomi* was doubt concerning the availability of *S.suis* (Tarczynski, 1956). Since *S.suis* is available and it had priority, the species of *Strongyloides* in pigs should be known as *S.suis* with *S.ransomi* as its junior synonym.

S.viviparus (Probstmayr, 1865) von Linstow, 1905.

Only parasitic females of this species were originally discovered by Probstmayr (1865) in the caecum of the horse. Males are rare but were subsequently found by Jerke (1902).

Probstmayria (1865) proposed the name *Oxyuris vivipara*, but von Linstow (1905) listed the parasite as *S.viviparus*. Ransom (1907b) recognised that it did not belong to *Strongyloides* and proposed a new genus *Probstmayria* to accommodate it.

3.4 Descriptions not Sighted.

The original descriptions of *S.petrovi* and *S.vulpis* could not be obtained. Consequently their status was not able to be assessed. Since this was no fault of the authors, but a deficiency on my part, the names by default have been provisionally classed as valid. These two species were included with other valid species in Table 2:1, but no values given.

3.5 Summary.

The aim of Chapter 3 was to establish a basis for a comprehensive review of the species in the genus. This has been achieved by listing all names in the literature and eliminating those which are unavailable or need little further consideration since they are invalid. One hundred and three names were located and subdivided as shown in Fig.3:1.

The effects of most changes suggested in this review will be minor, since they concern species of little practical importance. The opinion that *S.planiceps* and particularly *S.ransomi* are junior synonyms and therefore invalid will cause some disruption, and perhaps controversy, particularly in the case of *S.suis* (syn.*S.ransomi*).

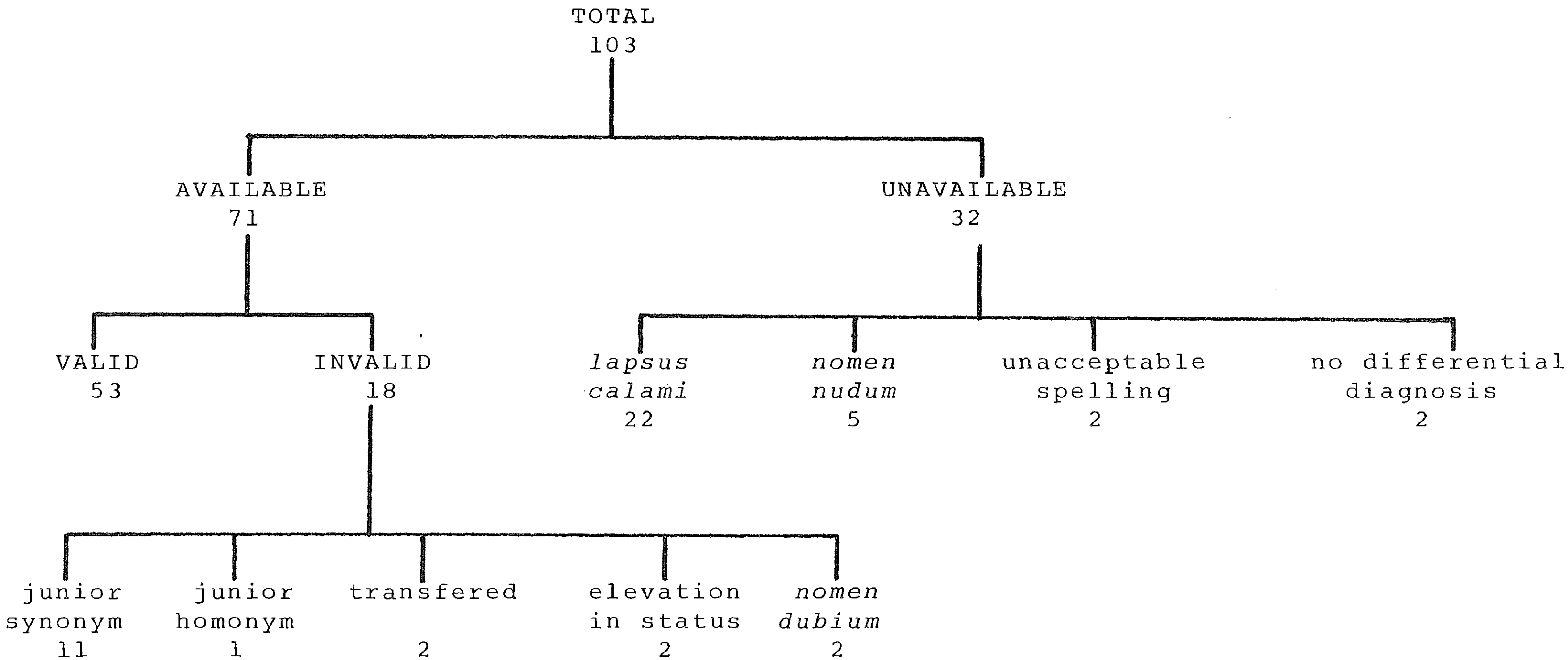


FIG.3:1. Subdivision of published names for *Strongyloides*.
(number in each category is shown)

3.5 FURTHER AIMS OF THIS THESIS.

The task of clarifying the status of species in *Strongyloides* has now been made easier by the removal of unavailable names and invalid species. These rejected names will not be examined further unless the specimens upon which the species was based serve to illustrate a point which holds true for the genus as a whole. The next step in this generic spring-cleaning is to identify and describe those processes which distort or change the morphology of *Strongyloides*, and which, if not recognised, can lead to errors in description or identification of species.

CHAPTER 4

TECHNIQUES AND EXPERIMENTS.

4.1 INTRODUCTION.

The first section of this chapter contains details of techniques used to collect, fix, preserve and study the various stages of *Strongyloides*. The second section contains details of experimental procedures and particular experiments.

4.2 TECHNIQUES.

4.2.1 Collection of *Strongyloides*.

4.2.1.1 Parasitic Female. -

Since the parasitic female is a tissue parasite, it is normally not found in the lumen of the gut. In rare circumstances, however, usually due to a pathological host response, worms may be recovered from the gut contents (Speare et al, 1982). Usually they have to be extracted from the mucosa.

Equipment needed:

1. dissecting microscope with transmitted light
2. microscope slides
3. glass petri dish
4. dissecting needles or jeweller's forceps
5. pasteur pipette and bulb
6. fine wire hook or single hair
7. 0.9% saline solution
8. collecting bottle

Technique:

1. Section of gut to be examined is opened longitudinally, placed flat, serosa down on a firm supporting surface.
2. Narrow end of microscope slide is used to scrape the mucosa off the muscularis.
3. Scraped mucosa placed in petri dish.
4. Moisten with saline and place a lake of saline on working edge.
5. Using dissecting microscope and transmitted light, tease mucosa apart.
6. Pick up worms by pipette, hair or hook.
7. Transfer to saline in bottle.

Juvenile stages in the gut were also obtained using his technique. Collection of parasitic females after anthelminic treatment was made by microscopic dissection of the fixed contents of the large intestine using transmitted light.

4.2.1.2 Other Parasitic Stages. -

Third-stage larvae were collected from skin by active migration from skin fragments. Equipment needed:

1. test tube

2. 0.9% saline

3. scalpel blade

Technique:

1. Cut skin into small pieces about 1-2mm diameter.

2. Place in saline at room temperature.

3. Remove after 12 hours.

4. Centrifuge at 1500rpm for 5 min.

5. Remove fluid from top, leaving 0.5cc in tube.

6. Examine under microscope.

7. Place larvae in saline prior to fixation.

Collection of larvae from lung was carried out using a Baermann technique similar to that described above but using .9% saline as the medium, cutting the lungs finely, floating the fragments on the surface of the saline and examining the sediment at 6 and 24 hours.

4.2.1.3 Free-living Stages -

All free-living stages as well as larvae in faeces can be collected by the Baermann technique. The technique used has been described by Speare and Tinsley (1986) and is illustrated in Fig 4:1. This technique relies on larvae moving through the faecal mass, passing into water and settling out.

Equipment needed:

1. funnel with flexible tube on the stem

2. clamp to close tube

3. wire shelf to fit into the funnel.

4. fine guaze or tissue paper

5. water at room temperature or greater than 25° but less than 38°.

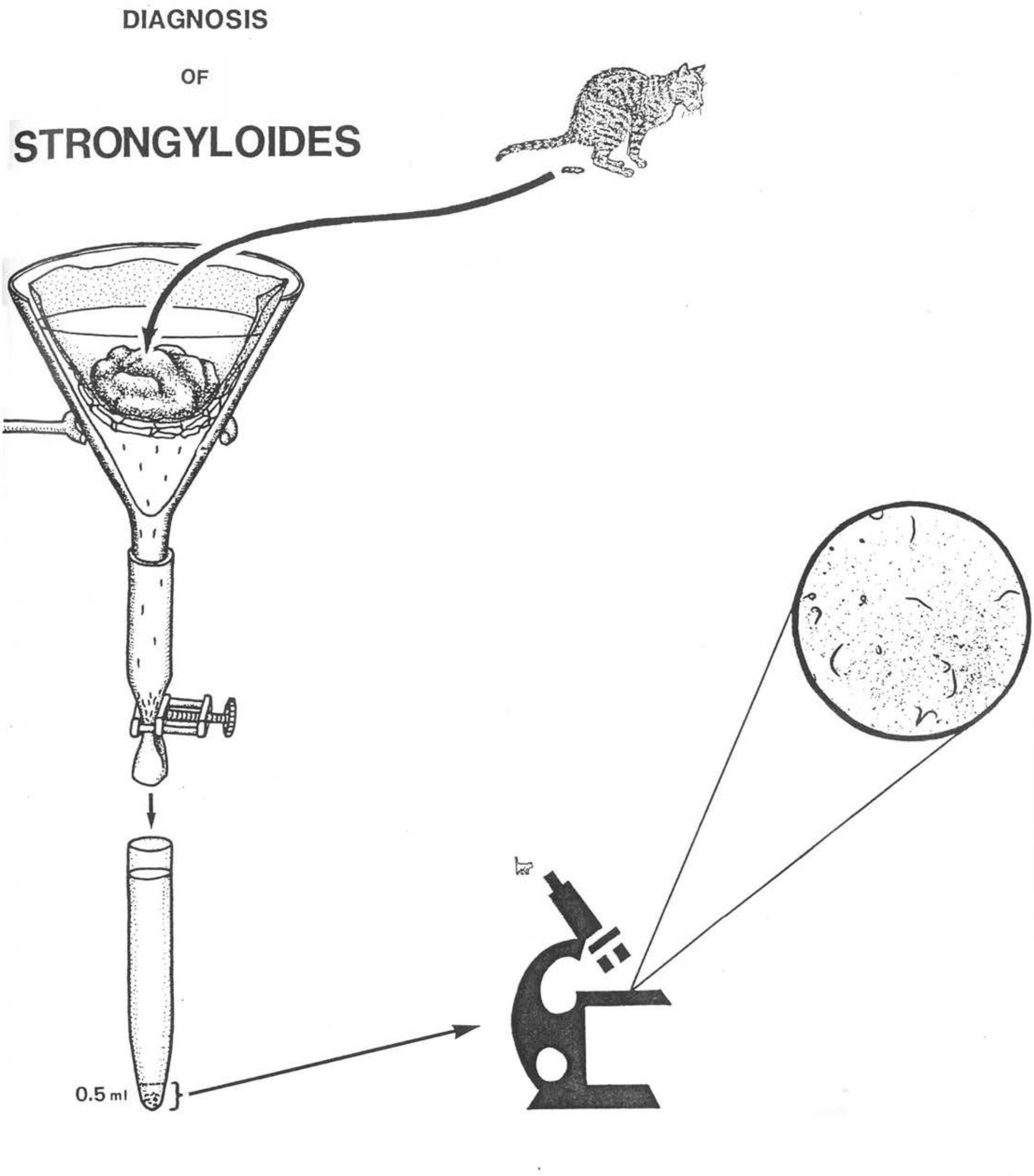


FIG.4:1. Baermann technique for the collection of larvae and adults. Diagram illustrates its use in the diagnosis of *Strongyloides felis* infection in cats (from Speare and Tinsley, 1986).

Technique:

1. Half-fill funnel with water.
2. Place wire shelf in funnel.
3. Place guaze or paper tissue on shelf.
4. Place matter containing worms on top.
5. Add sufficient water to cover the faeces.
6. Collect worms after 6hrs by running 5ml into a test tube.
7. Centrifuge at 1500r.p.m.
8. Discard top 4.5ml.
9. Collect worms from bottommost 0.5ml.

4.2.2 Fixation

All specimens when alive were fixed by the addition of hot fixative to parasites in a small amount of liquid, 0.9% saline for parasitic stages and water for free-living stages. The temperature of the fixative ranged from 60-100°C, and the volume added was always greater than the volume of liquid in which the parasites were contained. Specimens were stored in 10% buffered neutral formalin or 70% ethanol with 5% glycerol

4.2.3 EXAMINATION.

4.2.3.1 General. -

Most microscopic examinations were performed using water as a supporting medium. Contents of collecting bottles were placed into a cavity block, individual specimens transfered by a hair or pipette to water on a slide, and a coverslip applied. Sufficient water was used to prevent the specimen becoming flattened by pressure of the coverslip. If this was not possible, e.g. in some larger free-living females, fragments of glass coverslips were placed on the slide with the worms and a coverslip applied, the fragments supporting the weight of the coverslip. In most specimens, clearing was not required as the body was transparent.

4.2.3.2 Transfering into Glycerol. -

Glycerol was a good clearing medium and processing through glycerol was a necessary preliminary step prior to examination of the apical view. Specimens transfered directly from fixative into glycerol collapse badly. Wrinkling can also be a problem in some specimens transfered from formalin into alcohol. To maintain their shape, worms were transfered firstly from formalin into alcohol, then into glycerol. The following procedure was used for specimens fixed in 10% formalin:.

1. Place specimens in distilled water in a cavity block.
2. Place block above a 70% achohol solution in an enclosed container for 3 days.
3. Add 70% Ethanol with 5% glycerol drop by drop to cavity block, taking 24 hours to double the original volume.
4. Place cavity block under inverted petri dish which is not airtight or is in a dessicator and leave for 4 days or until only glycerol remains.

A more rapid technique involved:

1. Placing specimens in distilled water.
2. Adding 70% alcohol drop by drop over 12 hours until the volume was twice the original.
3. Adding glycerol drop by drop over 24hrs until the volume was increased by about 25%.
4. Dehydrating and dealcoholising at 32°C, this step taking 24hr.

Specimens in glycerol tended to become friable and care was needed in handling.

4.2.3.3 *En face* Preparation. -

Apical views were made using a modification of the method of Anderson (1958). Only specimens in glycerol could be used. Equipment needed:

1. glycerol
2. eye-surgeons scalpel or 22G disposable needle
3. cutting slide (glass or perspex)
4. microscope slide
5. coverslip
6. plasticine
7. glycerine jelly
8. single hair
9. dissecting microscope with transmitted light
10. spirit burner and means of lighting
11. compound microscope
12. jeweller's forceps

Technique:

1. Place worm in glycerol on cutting slide on plate of dissecting microscope, with head protruding peninsula like from edge of lake of glycerol.
2. Using eye-surgeon's scalpel or edge of bevel of needle, cut off anterior 10μm.
3. By means of the hair move the severed head back into the glycerol.
4. Place small amount of glycerine jelly on centre of coverslip and warm over spirit burner until the jelly liquifies.

5. Pick up the head on the hair and transfer it to the liquid jelly.

6. Push the head down into the jelly, so that the mouth is against the coverslip. It is now at the bottom of the drop.

7. When the jelly is tacky, invert the coverslip using the forceps.

8. Place the inverted coverslip on two walls of plasticine about 1mm high lying transversely across the microscope slide at a distance of one coverslip diameter apart.

9. Press the coverslip down until the glycerine jelly makes contact with the slide.

10. While the jelly is still malleable, orient the head using the compound microscope so that the mount is not viewed obliquely. This is done by gently moving the coverslip on its plasticine supports, allowing the tension from the adherence of the bottom of the jelly to the slide to change the orientation of the severed head at the top of the jelly.

11. If jelly has set, heat it very slightly, enough to enable deformation but not enought to cause it to become poorly viscous and allow the head to fall away from the coverslip. If the head drops down into the jelly, steps 6-10 have to be repeated.

12. Examine under oil immersion.

4.2.4 Depigmentation technique.

A technique adapted by L.Owens for removal of pigmentation from crustacea and nematodes was used in an attempt to remove brown-black pigmentation from specimens.

Materials.

1. 0.25% potassium permanganate
2. 1% oxalic acid
3. cavity block
4. pipettes

Technique:

1. Fill a cavity block with each solution.
2. Place specimens in potassium permangate in cavity block for 20mins.
3. Remove and place in oxalic acid for 1min.
4. Place in water and examine.
5. Repeat steps 2-4.

Specimens may break up with repeated treatments (Owens pers comm, 1986), so careful observation is needed. Only one repeat was used on specimens and no deleterious effects noted.

4.2.5 Measurement.

All measurements except those made using oil immersion were carried out using a calibrated eyepiece graticule. Measurements of various features on male tail were made from camera lucida drawings (see Fig.2:15),as was calculation for the free-living female of the angle of the vulva with the longitudinal axis (see Fig.6:15).

4.2.6 Drawings.

A drawing tube was used to make the initial outlines which were then completed free-hand by reference back to the specimen.

4.2.7 Photography.

Leitz and Zeiss photomicroscopes with Pan-X film were used for photomicroscopy.

4.2.8 Election Microscopy.

Specimens embedded partly in gut were prepared for SEM by stepwise dehydration in graded series of ethanol increasing in concentration to absolute, critical point drying and coating with gold-paladium. They were examined using an ETEC Autoscan and backscatter mode. Worms not in tissue were placed in a small bag made of plankton netting for critical point drying and treated similarly.

4.2.9 Histology.

Tissue for histology was fixed in either 10% BNF or Bouin's fixative, processed routinely by paraffin embedding, sectioned at 6μm and stained with haematoxylin and eosin (Culling, 1974).

4.2.10 Culture.

Free-living stages were cultured using various techniques, depending on the particular species of host involved. Species from poikilotherms e.g. snakes and frogs, grew best by placing faeces in the centre of a petri dish and adding sufficient water to form a small lake of fluid around the faecal mass. All stages could be collected by pipetting them up from the fluid. The faeces of herbivores were cultured by breaking up faecal pellets or faecal mass and placing them in containers in a slightly moist atmosphere. The faeces of omnivores and carnivores had to be mixed with an inert media e.g. sawdust or vermiculite, to allow aeration. These were then placed in a humid atmosphere. The culture technique for

S.felis described by Speare and Tinsley (1986) was used for cats, dogs, and humans. Unless otherwise stated culturing was performed at room temperature, 22–26°C.

4.2.11 Experimental Infections.

4.2.11.1 Percutaneous Penetration.

Strongyloides infective larvae can burrow through intact skin. Percutaneous penetration was carried out by placing infective larvae onto a moist pad of tissue paper in a shallow petri dish. The pad was held in contact with the area of penetration, usually for 15min. Remaining larvae were recovered by Baermannisation.

4.2.11.2 Subcutaneous Infection.

Infective larvae were injected subcutaneously usually in distilled water in a volume not greater than 1ml, using a 1ml syringe and 19G needle. The numbers of larvae were calculated either by counting individually or by dilution and counting of larvae in an aliquot.

4.2.12 Statistical Analyses.

Means, standard deviations, coefficients of variation and proportions were calculated using a pocket calculator, Casio fx-510. Other statistical analyses were performed using a main frame computer, DEC system-10, Digital Equipment Corporation, using programmes from SPSS Batch System, SPSS Inc.

4.3 SPECIFIC EXPERIMENTS

4.3.1 Post Mortem Degeneration.

Aim:

To study the morphological effects of the death of the host on the parasitic female.

Materials:

1. Host - 5 albino rats, 2 months old
2. Parasite - *S.ratti*
3. Infecting dose - 200
4. Route - Subcutaneous innoculation

Technique:

1. All rats killed by percussion to head on day 8.
2. Carcases held in 25°C ambient temperature.
3. One rat autopsied at each of following times, 0hr, 2hr, 6hr, 20hr, 25hr.
4. Parasites collected from first quarter of small intestine within 15min of rat being opened.
5. Fixed in 10% BNF at 90°C.
6. Examined by light micropscopy.

4.3.2 Host Immunity.

4.3.2.1 Experimental infection. -

Aims:

1. To determine the effects of immunity on the morphology of the parasitic female.

2. To determine the effects of immunity on the distribution of the parasitic female.

Materials:

1. Host - 5 albino rats, about 4 months of age

2. Parasite - *S.ratti*

3. Infecting Dose - 500

4. Route - Subcutaneous innoculation

Technique:

1. Daily output of eggs and larvae in faeces measured.

2. One rat killed by percussion at day 7 and 30.

3. Small intestine divided into quarters and parasites collected from each.

4. Parasites examined by light microscopy.

4.3.2.2 Natural infection. -

Aims:

1. To determine the effect of immunity in a natural infection on the morphology of the parasitic female.

2. To examine the distribution of specific antibody on the parasite and in the gut of the host.

Materials:

1. Host - foal (*Equus caballus*), 10 months of age, which died from paralytic ileus secondary to strongyloidiasis.

2. Parasite - *S.westeri*.

3. Reagents - Anti-equine IgG, IgA.

Technique:

1. Foal was euthanised in extremis, duodenum opened and fixed within 10min of death in 10% BNF.

2. Parasitic females obtained by dissection from the fixed gut and examined.

3. Fixed mucosal surface examined by SEM.

4. Histological sections prepared for routine examination.

5. Sections for immunoglobulin assessment stained by immunoperoxidase technique (Sinclair and Bourne, 1984) using modifications of Parsons (1984).

4.3.3 Fixation Experiments.

4.3.3.1 Type of Fixative. -

Aims:

1. To determine the effect of different fixatives on morphology of the parasitic female.

2. To determine the effect of different fixatives on dimensions of the parasitic female.

3. To determine the effect of different fixatives on the infective larvae.

Materials:

1. Parasite and Host: 1. *Strongyloides* sp. ex stomach of spectacled hare wallaby, *Lagorchestes conspicillatus*.
   2. *S.felis* ex small intestine of cat .
   3. *Strongyloides* infective larvae ex faecal culture of spectacled hare wallaby.

2. Fixatives: 10% buffered neutral formalin, 70% ethanol and Bles's fixative, following Gray, 1973.

Technique:

1. Parasitic females collected from mucosa by dissection; infective larvae from culture by Baermannisation.

   Experiment 1.

2. 10 parasitic females from wallaby measured and examined while unfixed.

3. 5 placed in each of 2 collection bottles with normal saline.

4. 70% alcohol and Bles's fixative at 80°C added to one bottle each.

5. Specimens re-examined and measured after 48 hours.

Experiment 2.

6. Parasitic females placed in normal saline in 3 collection bottles.

7. 70% alcohol, 10% BNFormalin and Bles's at 80°C added to separate bottles.

8. Specimens examined after 48 hours.

Experiment 3.

9. Infective larvae placed in water in 3 collection bottles.

10. 70% alcohol, 10% BNFormalin and Bles's at 80°C added to separate bottles.

11. Larvae examined and measured after 48 hours.

4.3.3.2 Temperature of Fixation. -

Aim: To determine the effect of temperature of fixation on the configuration of the parasitic female.

Materials:

1. Parasite and host: *S.ratti* ex small intestine of laboratory rat.

2. Fixative - 10% Buffered neutral formalin.

Technique:

1. Route of infection - subcutaneous injection of 5000 infective larve into laboratory rat.

2. Rat killed by cerebral percussion.

3. Worms dissected from mucosa of anterior quarter of small intestine.

4. 60 worms divided into 3 groups of 20.

5. One group per collecting bottle.

6. Each bottle containing 0.5ml normal saline.

7. 10% buffered neutral formalin at desired temperature added to each bottle to give final temperature of 50°C, 75°C and 90°C.

8. Fixed worms assessed for configuration using the following criteria.

9. Criteria: loose turn = diameter across circle formed by body is greater than 2 body widths; tight turn = diameter less than 2 body widths; usable = specimen has no tight turns, or not more than two loose turns.

4.3.4 Effect of Host.

4.3.5 Change in Morphology with Change in Host Species.

Aim: To determine the effect of species of host on the morphology of the parasitic female.

Materials:

1. Hosts: sheep, *Ovis aries*, goat, *Capra hircus*, pig, *Sus scrofa*, rabbit, *Oryctolagus cuniculus*.

2. Parasite: *S.papillosus*.

Technique:

1. Route of infection: subcutaneous.

2. Infecting doses: 1000 - 10,000.

3. Parasitic females collected from natural infections in small intestine of goats.

4. Infective larvae from faecal culture of goat faeces used to infect lamb, 9months old, pigs x 4, 10 weeks old, two rabbits (6mo and 2yr), two guinea pigs (approx.1yr old). No evidence of previous infection of any host with *Strongyloides* was found by repeated examination of and culture of faeces prior to infection.

5. Parasitic females collected from small intestines and examined.

4.3.6 Effect of Temperature on Morphology of Free-Living Stages.

Aim: To determine the effect of temperature on the morphology and dimensions of the free-living male, female and infective larvae.

Materials:

1. Parasite - *S.felis*.

Technique:

1. Faeces collected within one hour of defaecation from cats experimentally infected with *S.felis*.
2. Faecal mass divided into three and equal amounts cultured at 15°, 23° and 32°C.
3. Collection of free-living stages made daily from aliquots of faeces.
4. Free-living stages fixed and examined.
5. Comparison made between stages at similar physiological stages rather than on a chronological basis since rate of development is temperature dependent.

CHAPTER 5

ARTIFACTS

5.1 INTRODUCTION.

An artifact demands a natural state. Before defining the artifact the natural state must be defined. This is the "ideal" *Strongyloides* (Fig.5:1).

Fig.5:1. Criteria of the "ideal" *Strongyloides*.

1. same body shape as in life,
2. same morphology as in life,
3. same dimensions as in life,
4. all important features can be seen,
5. body is straight,
6. morphology is not obscured by extraneous material.

Artifacts are therefore changes in morphology which if not recognised for what they are may lead to the specimen in question being misidentified. All specimens are of necessity not natural.

The worms have to be killed to be examined, and once dead, decay has to be prevented. The "ideal" *Strongyloides* is, therefore, an artificial creation, but one whose morphology we come to accept as a baseline. Artifacts are changes induced in this baseline by forces other than the specific identity of the particular worm.

Mackerras (1959) and Little (1961) noted that the parasitic female degenerated rapidly after death of the host, but both failed to describe the changes seen. The morphological changes caused by the immune response of the host have been described for *S.ratti* (Moqbel and McLaren, 1980; Moqbel *et al*, 1980). This latter artifact is the only one which has been described as such.

Artifacts were studied in both the parasitic and free-living adults, with greater emphasis being placed on the parasitic female. Experimental infections in various hosts were used to study the artifacts in the parasitic female caused by the following: death of host, host immunity, anthelmintic therapy, fixatives. Details of experiments were given in Chapter 4. Worms collected from natural infections were also used and correlations made on a semi-quantative basis. Deposited specimens were examined and evaluated to determine the significance of artifacts in causing aberrant findings which had been described in the literature.

In this chapter the changes seen in particular organs are described under the organ, and a differential diagnosis of causes given. Summaries of changes due to particular artifactual processes are then presented. Emphasis is placed on those changes of significance to the taxonomy of *Strongyloides* and other changes are mentioned only.

5.2 PARASITIC FEMALE

5.2.1 Cuticle.

5.2.1.1 Wrinkling. -

Appearance.

The parasitic female is a cylinder with smooth parallel walls (Fig.2:1). Transverse striations occur at a periodicity which varies with the region of the worm (Fig.5:2), but ranges between 0.5 μm to 3.5μm. These striations do not distrupt the smooth contour of the "ideal" *Strongyloides*.

Wrinkling is detected as a deviation of the contour from this smooth outline. It gives the outline an irregular form, the sides in any one region losing their parallel disposition. It is often associated with shrinkage.

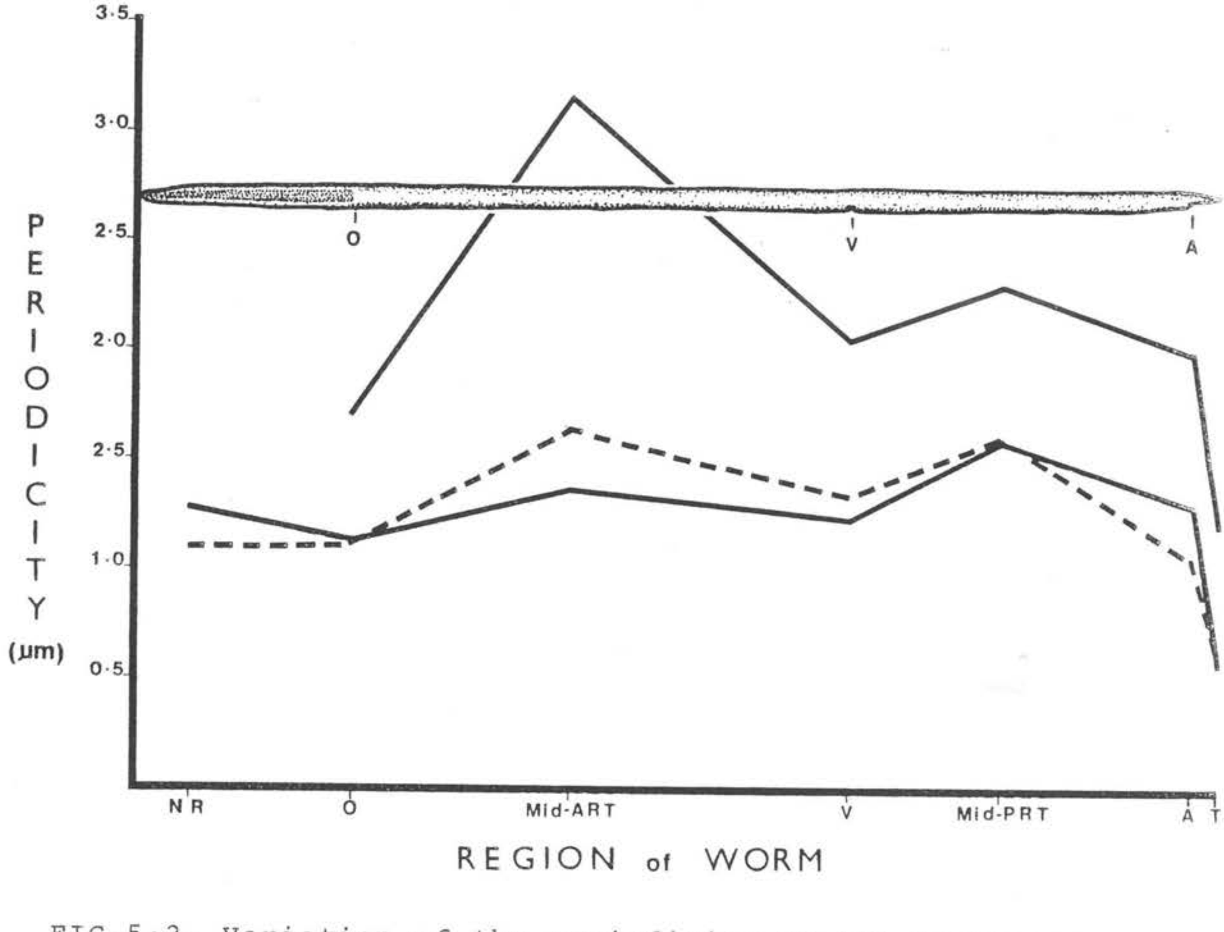


FIG.5:2. Variation of the periodicity of the transverse striations in the parasitic female. Periodicity varies between and within worms, according to region of the worm. Graph shows variation in periodicity for three paratypes of *Strongyloides elephantis*.

Causes.

Fixation.

Ten percent formalin causes less wrinkling than 70% alcohol or Bles's fixative (Table 5:1). Parasitic females in good condition fixed in 10% BNF have minimal wrinkling and maintain their cylindrical body shape. 70% alcohol can sometimes caused a marked distortion of specimens. Griffiths (1940), working with *S.agoutii*, found 5% formol-saline to be the most satisfactory fixative, with 70% alcohol containing 5% glycerol better than 70% alcohol alone.

Immunity.

Parasitic females affected by the immune response of the host are often wrinkled (see Chap.5.3.3) (and Moqbel and McLaren, 1980).

Autolysis.

The cuticle becomes wrinkled during autolysis.

TABLE 5:1A. Relative changes in dimensions of parasitic females from rufous rat kangaroo, *Aepyprymnus rufescens*. Measurements were made individually before and after fixation. (Chap.4.3.3.1 Experiment 1)

FIXATIVE	LENGTH (%)	MAX.WIDTH (%)	OES (%)	TAIL (%)	OES/L (%)	M-V/I (%)
Bles's	-7.8±0.4	-6.4±7.8	-10.7±3.3	-15.5±13.2	-1.0±1.0	-0.4±0.
70% alcohol	-14.9±2.8	-8.6±3.9	-17.2±3.6	-12.4±11.2	-0.8±1.3	+0.3±1.

TABLE 5:1B. Effect of fixation on the dimensions of infective larvae of *Strongyloides* sp from spectacled hare wallaby, *Lagorchestes conspicallatus*. (Chap.4.3.3.1 Experiment 3)

PARAMETER	HEAT KILLED UNFIXED	10% FORMALIN	BLES' FIXATIVE	70% ALCOHOL
n	10	10	10	10
length (μm)	531.2±15.2	491.3±27.2	468.6±25.6	459.6±19.9
change	-	-7.5%	-11.8%	-13.5%
oes (μm)	237.3±9.6	214.4±7.5	201.4±14.0	204.4±12.8
change	-	-9.6%	-15.1%	-13.9%
tail (μm)	62.2±1.8	58.5±2.8	57.9±4.1	57.3±3.0
change	-	-6.0%	-7.0%	-7.9%

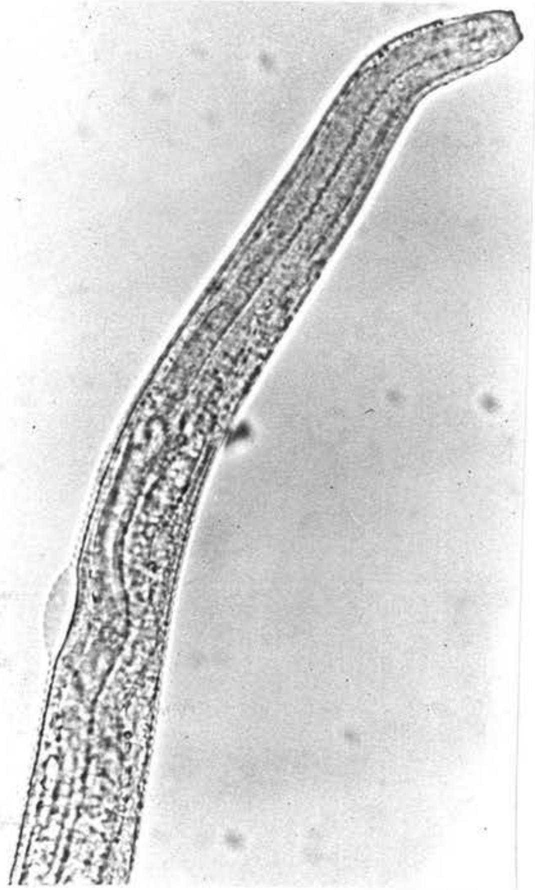


FIG.5:3. Early split with clear fluid in cuticle of *Strongyloides ratti* 6hr after death of host (Chap.4.3.1).

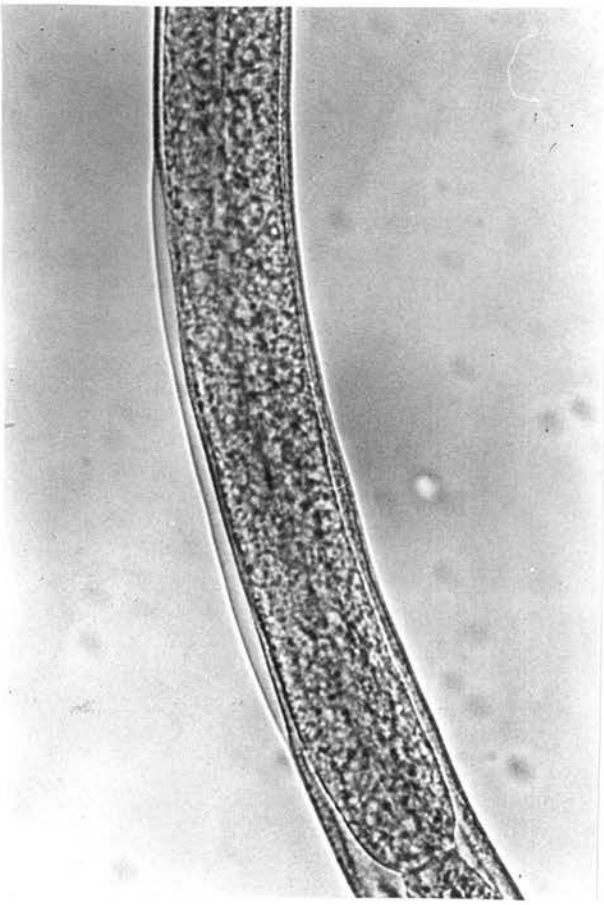


FIG.5:4. Larger split in cuticle of *Strongyloides ratti* 6hr after death of host (Chap.4.3.1).

5.2.1.2 Splitting. -

Appearance.

The cuticle of *Strongloides* has three layers, cortex, matrix and fibre layers (Colley, 1970). Splitting refers to a deviation of the outer and the inner boundaries of the cuticle with formation of a space between them. The space can be transparent (Fig.5:3&:4) or contain granular material (Fig.5:5). The site of the split on the ultrastructural level was not investigated. Splitting is a focal change and can occur at any region of the parasitic female.

Causes

Autolysis

After a host dies, its *Strongyloides* are doomed. One of the signs of autolysis is cuticular splitting. Initially only small areas of cuticle are involved and the space formed between the separated layers is clear (Fig.5:4). With increasing time after the death of the host, the area of cuticle showing splitting increases, more foci appear and the contents of the split become granular (Fig.5:5a). Granularity varies from fine to dense, irregular aggregations. Fragmentation of the outer cuticular layer may occur at a later stage (Fig.5:5b).

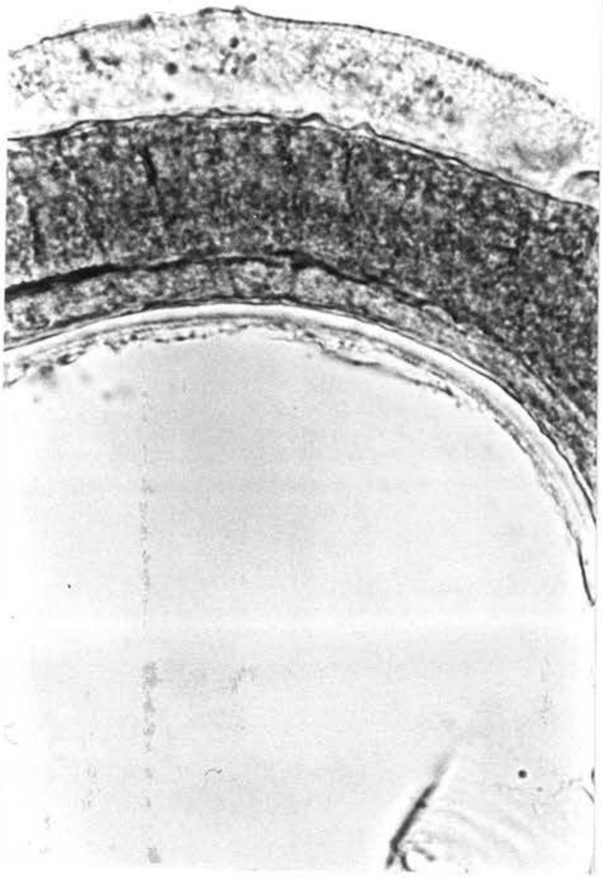


FIG.5:5A. Cuticular splitting with granular contents in paratypes of *Strongyloides ovocinctus*.

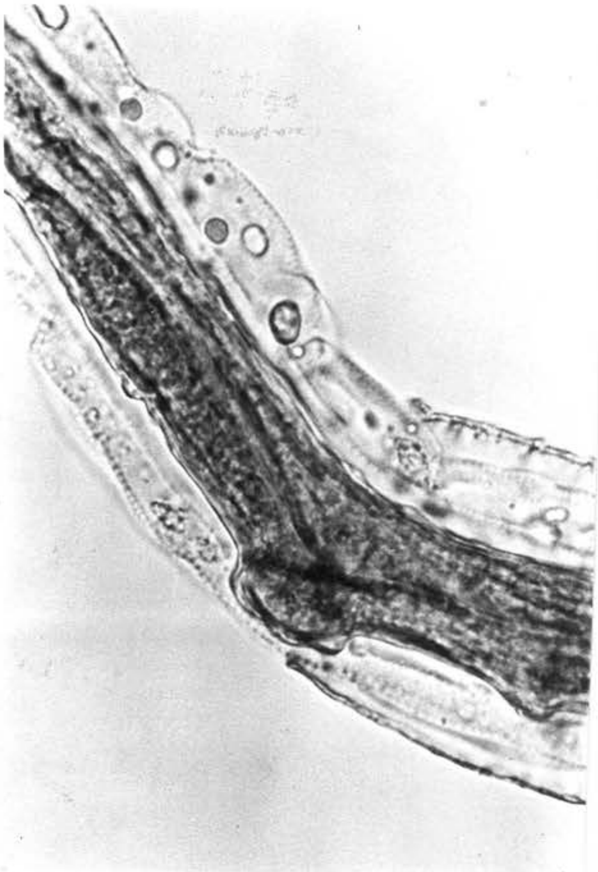


FIG.5:5B. Cuticular splitting with granular contents and dense aggregations in paratypes of *Strongyloides ovocinctus*. Contiguity of pseudocoelome is disrupted at one point, and ovary is herniating.

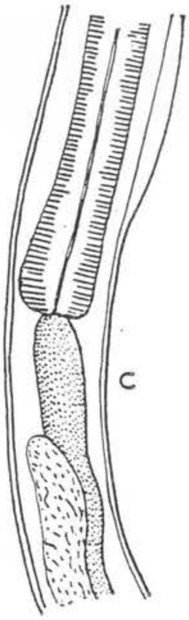


FIG.5:6. "Inflated cuticle" in *Strongyloides turkmenica* was splitting of cuticle due to autolysis (from Barus, 1979 Fig.13c).

Barus (1979) in a redescription of the parasitic female of *S.turkmenica* noted that the cuticle was inflated in some regions. He illustrated this in Fig.13c p 47. He was without doubt describing cuticular splitting and not a specific feature of the parasite (Fig.5:6).

Cuticular splitting is a common artifactural change encountered in the parasitic female. It is not confined solely to *Strongyloides*. A similar change, but to a lesser extent was noted in the trichostrongyloid nematodes included in the bottle (USNMHC 14647) containing the paratypes of *S.ovocinctus* (see Chap.5.5.4).

5.2.1.3 Anterior Prolopse.

Appearance.

In specimens showing other signs of degeneration (Table 5:2), the cuticle of the head and neck occasionly prolapses anteriorly to form a cylindrical tube having at its base or posterior end the buccal cavity of the worm (Fig 5:7). This sleeve is formed from thin, wrinkled cuticle and contains clear fluid or slightly granular material in its walls. It is a slipping forward of the cuticle of the head and neck, passing lateral to the cuticle of the circumoral elevation which remains anchored at the stomal edge. This artifact is seen nicely in the paratypes of *S.herodiae* and *S.ovocinctus*. Ransom (1911) ignored it in his specimens, but Boyd (1966;1967) listed "a deep buccal capsule" as a distinguishing feature in *S.herodiae*. The paratypes of *S.herodiae* (USNMHC 60530) show marked anterior prolapse (Fig.5:8). Boyd obviously failed to recognise it as an artifact. As discussed in Chapter 2.3.1 the feature as described by Boyd (1966) transgressed a generic boundary. If it had been real, either *S.herodiae* could not have been accomodated in *Strongyloides* or the generic definition was in error in stating *Strongyloides* had a shallow buccal capsule. Anterior prolapse of cuticle is seen commonly in degenerate specimens of *S.papillosus*, *S.westeri* and *Strongyloides* sp. from macropods.

Cause - Autolysis.

5.2.1.4 Loss of Transverse Striations.

Appearance.

All parasitic females have transverse striations (Fig. 2:3). The periodicity varies with the region of the worm (Fig.5:2) and the ease of detection under light microscopy varies with the species; e.g., striations are frequently difficult to see in *S.stercoralis* and *S.ratti*, but are easily seen in *S.suis*. Transverse striations can, however, become almost impossible to detect with light

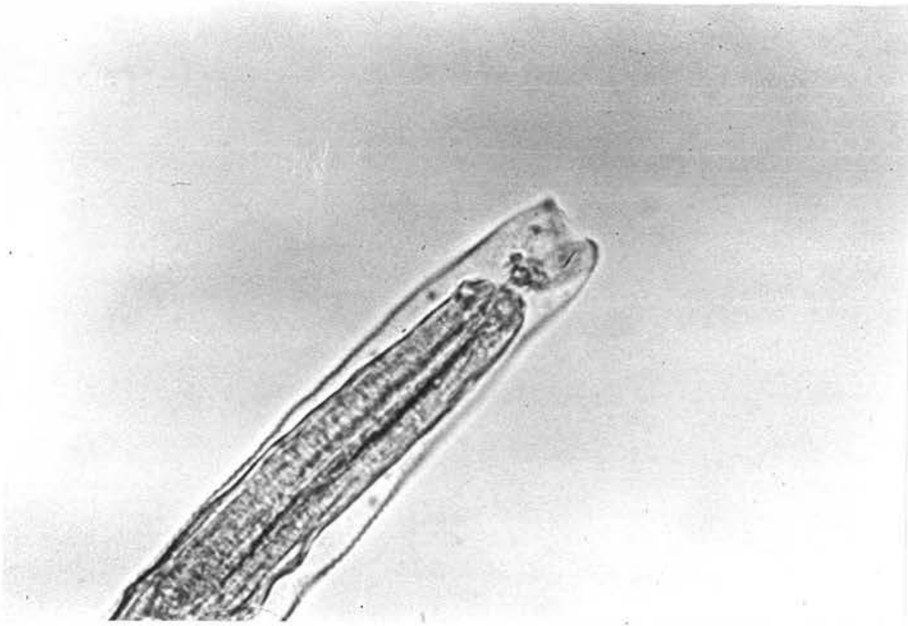


FIG.5:7A. Anterior prolapse of cuticle of head of paratype of *Strongyloides ovocinctus*.

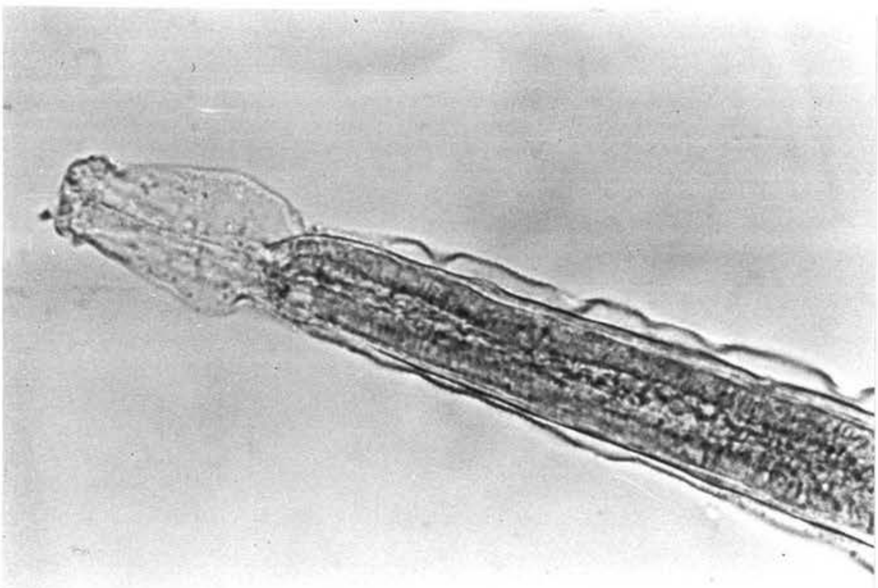
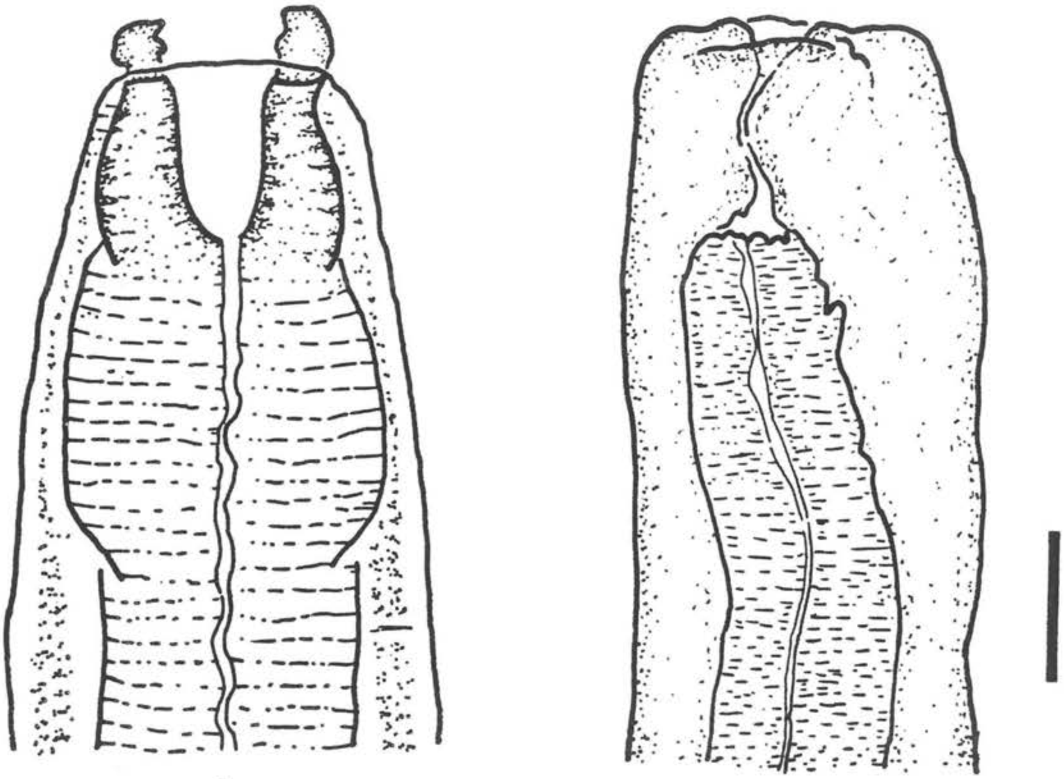


FIG.5:7B. Greater degree of anterior prolapse : paratype of *Strongyloides ovocinctus*.



A

B

FIG.5:8. Head of *Strongyloides herodiae*. A. from Boyd, 1967 showing "deep buccal capsule"; B. paratype showing anterior prolapse of cuticle. Scale line = 10μm.

microscopy owing to autolytic changes. In specimens so affected, striations are best looked for posterior to the posterior reflection of the ovary as this seems to be the area where they are least affected.

Cause.

Some species have striations which are much less distinct than in others. Degenerative changes occurring after death of the host are the major cause of loss of transverse striations.

5.2.1.5 "Cuticular Moulting". -

Appearance.

Ransom (1911) in *S.ovocinctus* described a phenomenon in which adult worms apparently experienced successive moults. The eggs passing out of the vulva lodged beneath an outer cuticular layer (p108 figs 135-136)(Fig.5:9). This was a combination of cuticular splitting and sheath formation (see Chap.5.5.4). Ransom failed to recognise that two artifacts were present and thought that each was part of the same process.

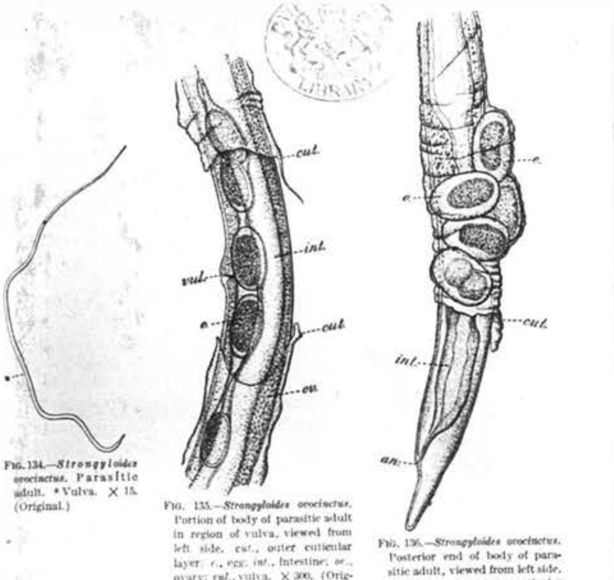


FIG. 134.—*Strongyloides ovocinctus*. Parasitic adult. * Vulva. × 15. (Original.)

FIG. 135.—*Strongyloides ovocinctus*. Portion of body of parasitic adult in region of vulva, viewed from left side. *cut.*, outer cuticular layer; *e.*, egg; *int.*, intestine; *ov.*, ovary; *vul.*, vulva. × 300. (Original.)

FIG. 136.—*Strongyloides ovocinctus*. Posterior end of body of parasitic adult, viewed from left side. *an.*, anus; *cut.*, outer cuticular layer; *e.*, eggs lodged beneath the outer loosened cuticle; *int.*, intestine. × 300. (Original.)

FIG.5:9. Original illustrations for *Strongyloides ovocinctus* from Ransom (1911 Fig. 134-136) showing sheaths and "moulting" of cuticle.

5.2.2 Reproductive Tract.

5.2.2.1 Degeneration. -

Appearance.

The type of ovary is a feature of major taxonomic importance in the parasitic female (Little, 1966a). Ovaries are classified into two classes; directly recurrent or spiral. Degeneration is marked by several changes in the reproductive tract (Table 5:2), but the only ones of taxonomic significance are those affecting the determination of the type of ovary. In severely degenerated worms, the ovaries are vacuolated, their outlines are indistinct, and the pseudocoelomic cavity contains debri. Occasional specimens are so affected that ovary type is difficult to determine with confidence.

Cause - Autolysis.

TABLE 5:2. Morphological changes of autolysis in parasitic female.

CUTICLE
Splitting and fragmentation
Wrinkling
Anterior prolapse
Loss of transverse striations

GUT
Granularity of oesophagus becomes coarse
Oesophageal nuclei disappear

REPRODUCTIVE TRACT
Vacuolation of ovary, particularly proximally
Outline of ovary less distinct
Oviduct cells not discernable
Uteri contain granular debri

PSEUDOCOELOME
Refractile granules increase in number and size

EXTRANEOUS MATERIAL
Sheath size and number increase

5.2.2.2 Misinterpretations of the Ovary Type. -

It is important to understand the geometery of a spiraled ovary. The literature fails to describe this, and from many of the illustrations provided the parasitologist also has not understood it (see Singh, 1954, fig.1; Rao and Singh, 1968, fig.4; Lichenfelds, 1975 p14 fig.2 ; Grabda-Kazubska, 1976, fig.1). The geometery of spiraled ovaries are amazingly uniform throughout the genus. The ovary does not spiral around the gut, it spirals with the gut; the intestine does not form a central axis, but participates completely in the spiraling process (Fig.6:4). Both distal and proximal arms of the ovary maintain the same relationship with each other and the gut. They do not cross over, out of position as it were, but form a unit of three, spiraling in a uniform manner. This point is important as it enables one to follow the individual units, e.g. distal ovary, and so determine the degree of spiraling for that particular unit.

The other key point is that the spiral is always in the same direction in all species of *Strongyloides*, and that is, anticlockwise from the anterior end. This direction is followed also in the posterior ovary. If these facts are heeded, it is not difficult to decide whether a species has or does not have spiral ovaries. Partial spirals can be identified from the tendency of the two ovarian arms and the gut to spiral as a unit.

In some specimens with directly recurrent ovaries the distal ovary is occasionally sinuous, and adopts a wandering course beside the gut (Fig.5:10). An inexperienced observer may mistake this for a spiraled ovary. Several early drawings show sinuous ovaries, and one cannot be sure of the ovary type (see Travassos, 1930b; Cameron and Parnell, 1933; Pereira, 1935; Perez Vigueras, 1942; Rao and Singh, 1968). These errors can be avoided if the generic geometery of the spiral is known.

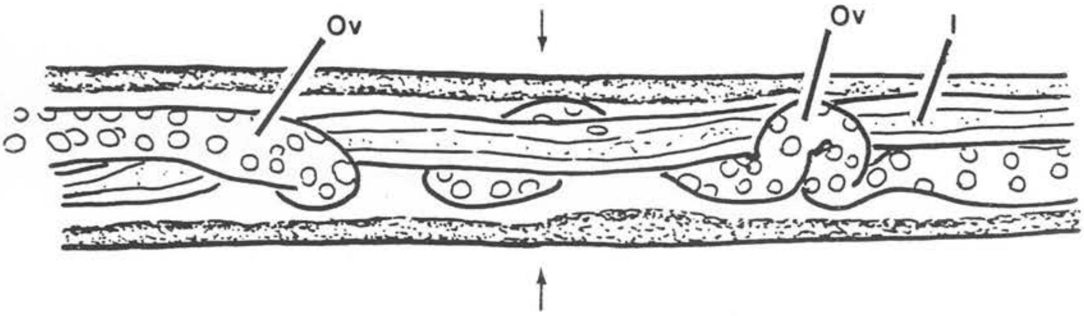


FIG.5:10. Appearance of sinuous path in distal ovary of *Strongyloides* sp from large intestine of green tree frog, *Litoria caerulea*. Dorsal view. Arrows mark level of vulva.

5.2.2.3 Failure of Ovaries to Spiral. -

The ovary spirals only in mature parasitic females. Prior to this, in the larval stages and the young adult stage, all females have directly recurrent ovaries. Egg production frequently begins before spiraling has been completed, and sometimes before it has commenced. Worms collected at this stage will, therefore, have directly recurrent ovaries. *S.cati* Rogers, 1939 has spiral ovaries (Rogers, 1939). Specimens (L d'V) obtained from a cat experimentally infected by Erhardt and Denecke (1939) using Rogers' strain had directly recurrent ovaries. These worms had been collected on day seven of the infection. They were mature but spiraling of ovaries had not commenced.

5.3 CHANGES IN DIMENSIONS.

5.3.1 Too Large.

5.3.1.1 Squashing. -

Specimens can be deformed by pressure of the coverslip. Their cylindrical cross-section then becomes a flattened ellipse, with the apparent diameter of the specimen approaching the theoretical maximum of half the circumference. An excellent example of this deformity is provided by the paratypes of *S.tumefaciens*. The width of 109μm given by Price and Dikmans (1941) is the greatest for the genus and far beyond the average of 44.3μm (Fig.5:11). The paratypes (USNHC nos. 28190, 28191, 28192) are specimens which were recovered from fixed tissues and permanently mounted on slides. All specimens are badly flattened. Nine fragments were examined and body widths measured. Widths were 120.9μm at the vulva (n=1) and 79.9±6.7 (75.0-87.6)μm at the base of the oesophagus (n= 3). This is not the true diameter, but in a flattened state more closely represents half the circumference. Since the parasitic female is circular in cross-section, body width can be calculated from "2 radius = circumference/π"; therefore, "body width = 2 radius = 1/2 circumference/π X 2". Calculated diameter for *S.tumefaciens* is, therefore, 77μm at the vulva and 50.9μm at the level of the posterior end of the oesophagus. Dubey and Pande (1964) reported *S.tumefaciens* from adenomas in the large intestine of the Indian wild cat (*Felis chaus*). Their specimens had length of 5.5mm and a diameter of 80μm, agreeing well with the calculated value for maximum body width.

The main visual clue to severe squashing in a specimen is a lack of optical depth, but only major degrees of squashing can be detected by visual means.

The plot of width against length for valid species of *Strongyloides* (Fig.5:11) indicated that the published values for *S.tumefaciens* fell well outside the general trend for the genus. A new regression programme confirmed this by identifying *S.tumefaciens* as the species with the worst fit to the regression equation (Table 5:3). Substitution of the correct value for width gives a slightly changed equation and places *S.tumefaciens* closer to the regression line (Fig.5:11).

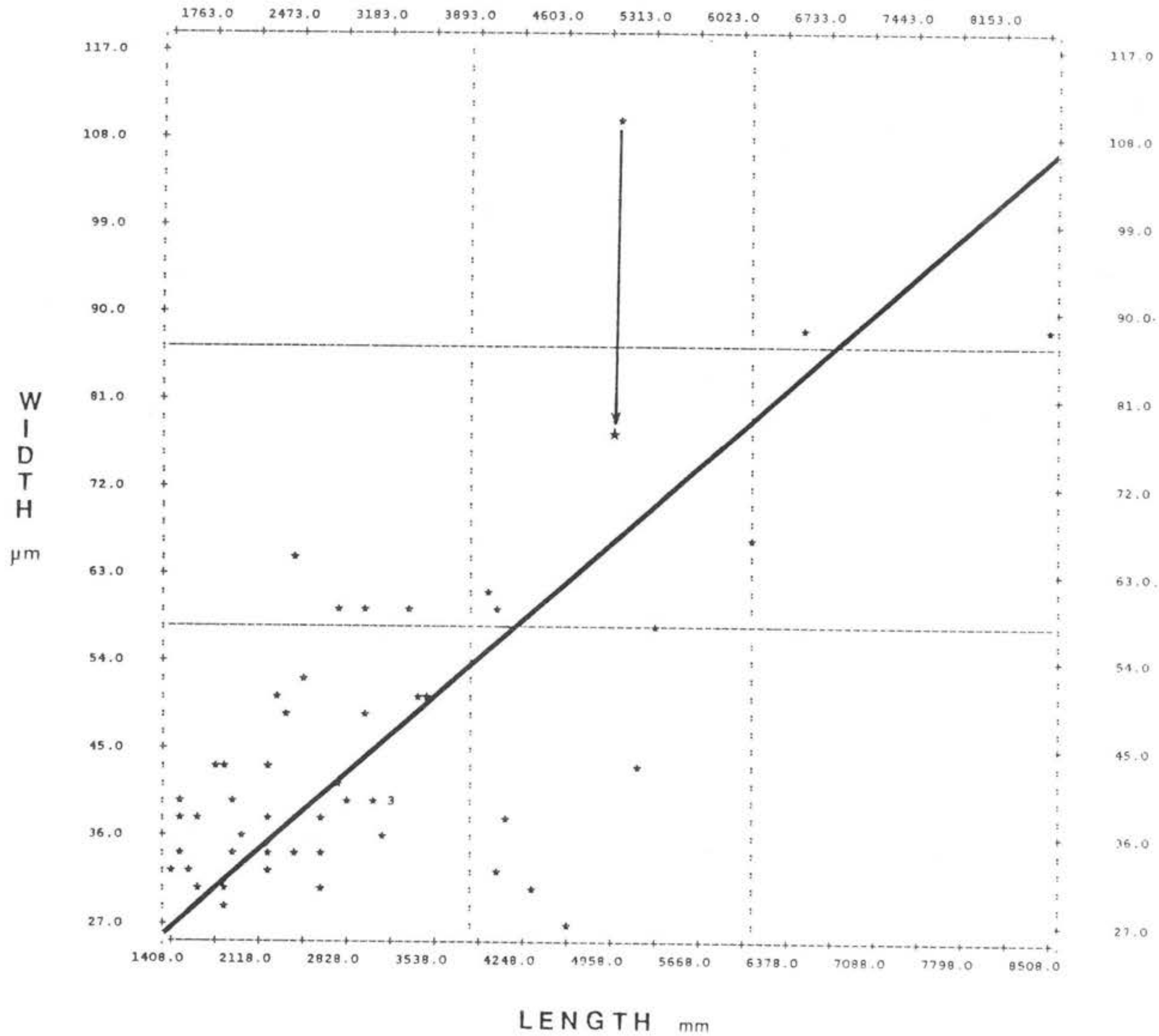


FIG.5:11. Regression of width on length for parasitic females. Data from literature. Note change in value for *Strongyloides tumefaciens* when corrected for squashing (arrow).

TABLE 5:3. Species with worst-fit for the regression of width on length.

ID	SPECIES	ZRESID
49	*S.tumefaciens*	3.92638
10	*S.chapini*	-2.35138
11	*S.cruzi*	1.91501
43	*S.sigmodontis*	-1.89102
39	*S.ratti* v. ondatrae	-1.55660
1	*S.agoutii*	-1.36038
16	*S.erschowi*	1.33648
41	*S.rostombekowi*	1.33242
26	*S.myopotami*	-1.30728
29	*S.oswaldi*	1.18094

5.3.2 Too Small.

A ZResidual of <2.0 is regarded as falling within two standard deviations of the regression line. *S.tumefaciens* had a ZResidual greater than two, while the next worst fit was for *S.chapini*, but in a negative direction (Table 5:3). *S.chapini* is atypically narrow, and is the species with the smallest width (Fig.5:11; Table 2:1). Two cotypes (USNMHC nos.24959) were examined and both had maximum diameters of 34.2µm. Sandground (1925) gave maximum width as 27.3µm. The value I obtained is closer to the generic average, but I am reluctant to substitute it since squashing of specimens may be responsible for this apparent increase in width.

Perusal of Table 5:3 reveals that the other species with negative ZResiduals are *S.sigmodontis* from the cotton rat, *S.ratti* v *ondatrae* from the musk rat, *S.agoutii* from the agouti and *S.myopotami* from the coypu rat. *S.chapini* was described from the capybara. All are parasites of American rodents. Specimens of *S.myopotami* (BMNH 1977.4661-4760) have been examined, and the width of 37µm agreed with those given by Little (1966a). These species may form a group, and *S.chapini* may not be so atypical as appeared on initial assessment.

Causes.

Processes which cause reduction in dimensions are fixation and immune damage (Moqbel and Denham, 1977; Moqbel and McLaren, 1980; Moqbel *et al*, 1980).

5.3.2.1 Shrinkage. –

Appearance.

Whereas wrinkling is a disruption of the smooth contour of the worm, shrinkage is a reduction in worm volume. Wrinkling can be one of its manifestations, but all wrinkled worms are not recessarily shrunken. A reliable morphological sign of shrinkage is collapse of the outer shell of the worm inwards, with moulding of the body wall onto the internal organs. Collapse is best seen in areas where the body wall is unsupported, e.g., the regions posterior to the base of the oesophagus, and anterior to the anterior reflection of ovary and in the tail. Moulding is seen best near the reflections of the ovaries where the body wall outlines the separate parts of the reproductive tract (Fig.5:12&13). In transverse section a shrunken worm is diminished in size and has lost its circular shape (Fig.5:17). Shrinkage can also be detected by measurement and statistical analysis (see Tables 5:1, 5:4, 5:5).

Causes.

Fixation.

70% alcohol causes considerable shrinkage, while 10% BN formalin causes less (Table 5:1).

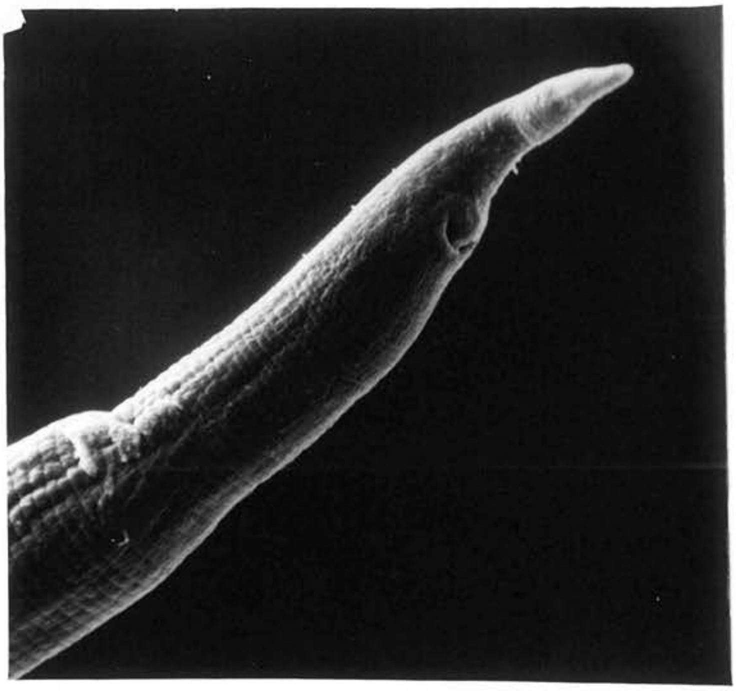


FIG.5:12. Tail of parasitic female of *Strongyloides* sp from stomach of agile wallaby. Collapse of body wall onto posterior reflection of ovary can be seen. Bles' fixative. SEM.

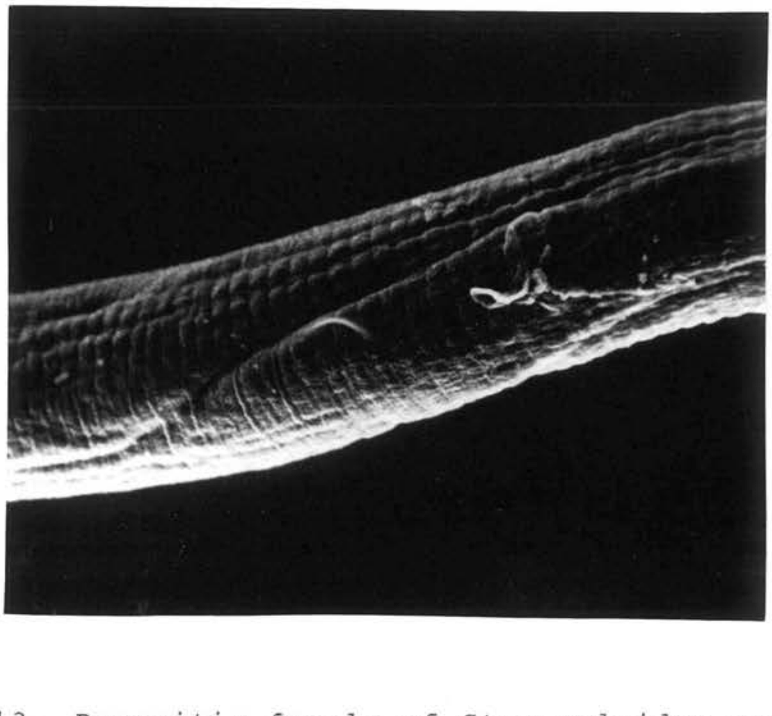


FIG.5:13. Parasitic female of *Strongyloides* sp from stomach of agile wallaby. Body wall outlines the ovaries. Collapse due to Bles' fixative. SEM.

Immunity.

Shrinkage was a major feature in *S.ratti* during rejection by lab rats (Moqbel and Denham, 1977; Moqbel and McLaren, 1980; Moqbel *et al*, 1980). An experimental infection of lab rats with *S.ratti* (see Chap.4.3.2.1) was used to confirm this effect. Larval output per worm per hour decreased from 30.9 on day 6 to 0.48 on day 30, worms became smaller, eggs per worm decreased (Table 5:4), and worms were found more posteriorly in the small intestine (Fig.5:14). These effects are typical of the response of *S.ratti* to host immunity (Moqbel and Denham, 1977). Wrinkling of cuticle was observed, but morphological changes of shrinkage are subtle. Comparative measurement and transverse section are means by which shrinkage can be detected.

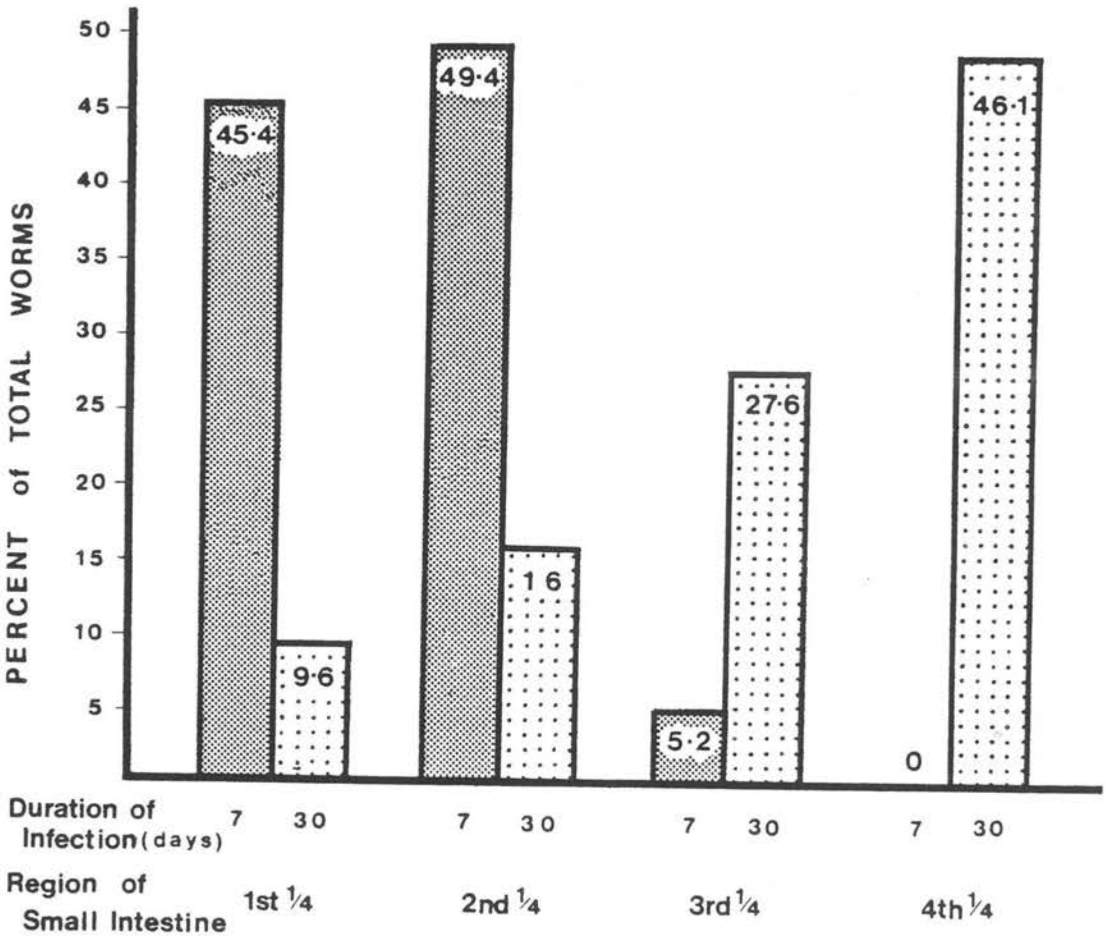


FIG. 5:14. Change in position of *Strongyloides ratti* in small intestine of rats in response to development of host immunity (see Chap.4.3.2.1).

TABLE 5:4. Changes in dimensions and proportions of *S.ratti* due to immune response of host.
(Experiment in Chap.4.3.2.1; non-immune = day 9 p.i.; immune = day 29 p.i.)

PARAMETER	NON-IMMUNE	IMMUNE (from ant 1/4 s.int)	(from post 1/4 s.int)
n	10	8	10
length (μm)	2817.9±189.8	1933.6±114.5	2164.5±59.9
change	-	-31.4%	-23.2%
width (μm)	44.0±1.5	34.6±1.1	36.9±1.0
change	-	-21.4%	-16.1%
oes (μm)	773.8±56.8	801.0±27.6	788.0±41.2
change	-	+3.5%	+1.8%
oes/length (%)	26.1±2.7	41.6±3.0	36.4±2.5
change	-	+59.4%	+39.5%
tail (μm)	48.6±5.7	45.3±3.5	45.9±3.4
change	-	-6.8%	-5.6%
tail/length (%)	1.73±0.19	2.35±0.18	2.72±1.83
change	-	+35.8%	+57.2%
M-V	1788.9±149.0	1291.5±96.4	1509.9±40.8
change	-	-27.8%	-15.6%
M-V/length (%)	63.4±1.7	66.7±1.6	69.8±2.1
change	-	+5.2%	+10.1%
eggs/worm	8.7±3.5	0.4±0.7	3.3±2.4
change	-	-95.4%	-62.1%

TABLE 5:5. Dimensions of *S.westeri* from foals: A. normal; B. rejected by immune response.

PARAMETER	**FOAL A**	**FOAL B**	**REDUCTION (%)**
Length (μ)	9506.0±1069.7	6567.4±1081.1	30.9
Max.width (μ)	81.3±7.9	73.4±4.6	9.7
Oes.length (μ)	1263.7±81.9	1158.1±86.1	8.4
M-V (μ)	5841.1±670.4	4221.5±636.0	27.7
Tail (μ)	129.0±16.3	114.5±14.0	11.3
Oes/length (%)	13.40±1.29	17.93±2.14	+33.8
M-V/length (%)	61.45±1.56	64.39±1.36	+4.8
Tail/length (%)	1.37±0.18	1.75±0.25	+27.7
Eggs/worm	59.4±14.7	26.8±9.7	54.9
Ant.uterus length(μ)	1288.6±224.9	644.2±123.4	50.0
Post.uterus length(μ)	1163.9±148.4	785.3±219.3	32.5

The effects on the parasite of host immunity in natural infections have not been described. A foal, aged two months, naturally infected with *S.westeri*, was found to have died from a paralytic ileus secondary to a rejection phenomenon. Heavy lymphocyte and plasma cell infiltration into the lamina propria of the duodenum was present, with focal haemorrhage and oedema, and marked villous atrophy (Fig.5:15). Examination of fixed gut under the dissecting microscope and by SEM confirmed the villous atrophy, showed the degree to vary from totally atrophic in one area to moderately atrophic in another even on the microscopic level, and revealed that many of the parasites were only partially embedded in the mucosa (Fig.5:16).

FIG.5:15. Duodenum of foal naturally infected with *Strongyloides westeri*, showing marked villous atrophy, oedema and focal haemorrhage with mononuclear infiltrate. H & E X 160.

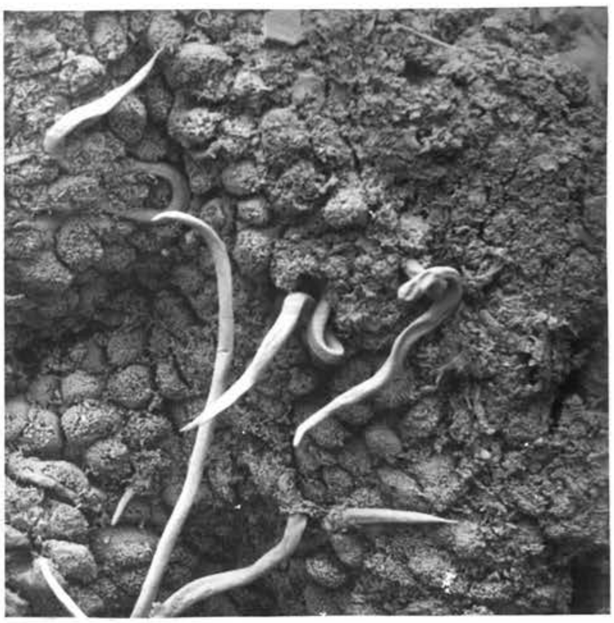


FIG.5:16. Duodenum of foal naturally infected with *Strongyloides westeri*. Villous atrophy is marked, parasites are only partly embedded in mucosa. SEM.

IgG was deposited onto the cuticle of the parasites and onto the brush borders of their intestines (Fig.5:17). IgA was also present in plasma cells and on the mucosal border of epithelial cells, but was not visible on or in the worms themselves. The majority of plasma cells in the lamina propria stained for IgG. IgM was not examined.

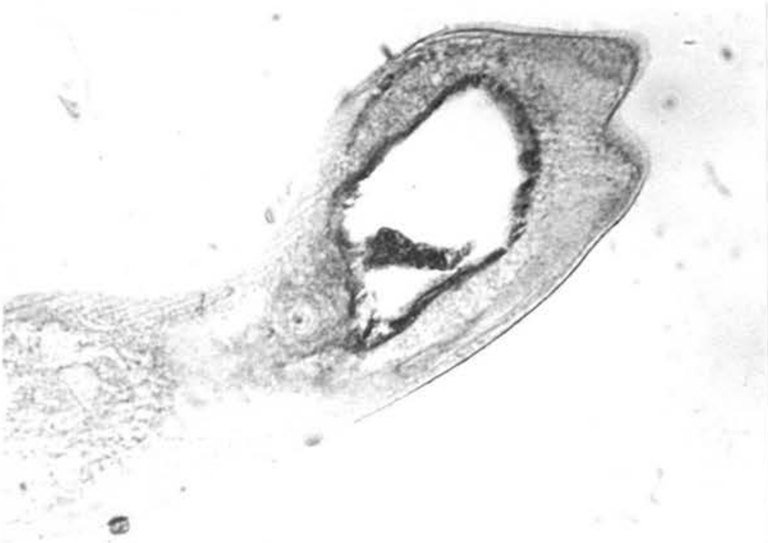


FIG.5:17. Parasitic female of *Strongyloides westeri* in small intestine of foal. The body is collapsed and lining of parasite gut stains positive for IgG. IgG Immunoperoxidase with haematoxylin X 320.

The parasitic females were wrinkled and shrunken and were smaller than specimens obtained from hosts not showing an immune response (Table 5:5). Several specimens were found which showed signs of autolysis, notably cuticular splitting, anterior prolapse and degeneration of the reproductive tract. Since the specimens had been fixed within 10min of death, too rapidly for host post mortem effects to cause autolysis, it is probable the worms had died in situ, and then undergone degenerative changes.

The host had evidently mounted both a cell-mediated and an humoral immunological response against the parasite. As shown by the effects on the parasites, and their displacement from their normal location in the mucosal layer, this attack was successful. The immune response, however, had extensively damaged the small intestine and led to the demise of the host.

S.westeri is normlly acquired at a young age by the transmammary route (Lyons *et al*, 1973) and is usually rejected by 24 weeks of age (Russell, 1948). *S.westeri* is rarely pathogenic (Drudge, 1972), but can occasionally cause disease and death. Surprisingly, there are no reports on the pathology of natural mortality in the horse, although the pathology associated with *S.westeri* in donkeys has been described (Pandey and Rai, 1960). The effects of the immune response of the host on the parasitic female are summarised in Table 5:6.

TABLE 5:6. Effects of host immunity on the morphology of the parasitic female.

CUTICLE
Wrinkling

GUT
Luminal border of intestine thicker and more refractile

REPRODUCTIVE TRACT
Numbers of eggs in uteri decrease

BODY
Shrinkage

EXTRANEOUS MATERIAL
Precipitates on mouth
Precipitates on cuticle

5.4 SHAPE.

5.4.1 Conformation.

The easiest specimen to examine is one that is straight. Calculation of dimensions is more difficult in coiled specimens, and occasionally some important morphological details may be obscured at cross-over points. The shape adopted by the live parasitic female after removal from the mucosa and placement in saline is dependent on the species of *Strongyloides*. *S.ratti*, for example, an inhabitant of the small intestine of the rat tends to coil, while *Strongyloides* sp. from the stomach of macropods rarely does so. The former lives in the base of the crypts, twisting around villi in mucosal tunnels, while the latter lives in the flatter, mucosal layer of the macropod stomach (Winter, 1958; Speare et al, 1982, 1983). The physical nature of the microenvironment in which different species live may influence their coiling tendencies in vitro.

The temperature of the fixative influences the straightness of worms fixed when alive. Those species with little tendency to coil, can be fixed with good result in formalin at a temperature of 50°C. *S.ratti*, however, needs a much higher temperature. Table 5:7 and Fig.5:18 show the effect of temperature of the fixative on the degree of coiling in *S.ratti*.

In a situation where no other specimens were available, "unusable" specimens of *S.ratti* could be utilized. The tendency to coil is much less than that shown by trichostrongyles, but nonetheless, the ideal is a specimen which is straight.

TABLE 5:7. Effect of temperature of fixative on the shape of *S.ratti*. (for definition of terms see Chap.4.3.3).

CRITERION	TEMPERATURE		
	60°C	75°C	90°C
No. of turns per worm	2.29±1.04	1.36±1.21	1.1±0.91
% of loose turns	10.9	20.0	72.7
% of tight turns	89.1	80.0	27.3
% of worms usable	8.0	36.4	70.0

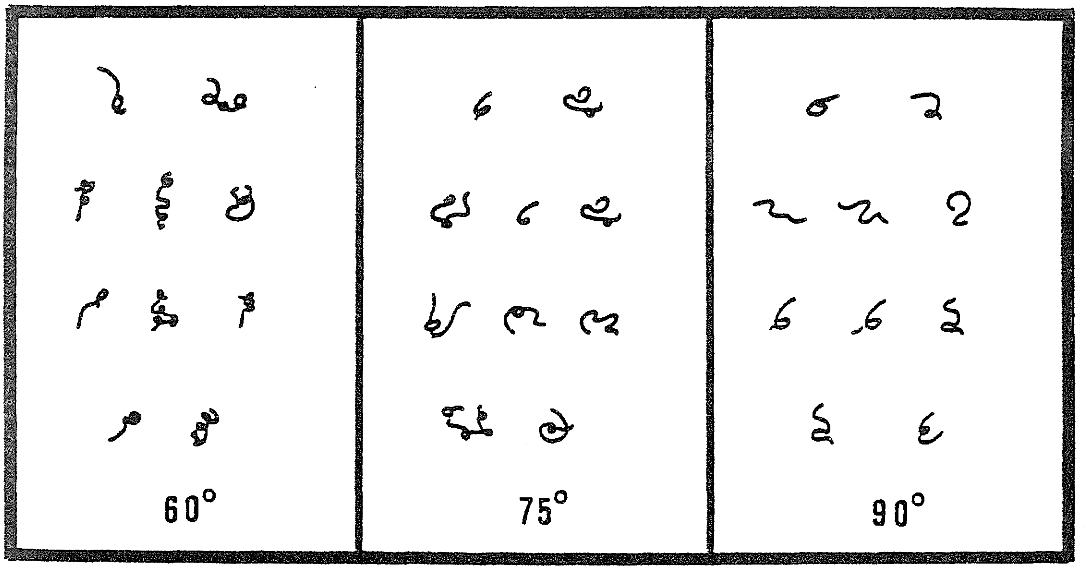


FIG.5:18. Effect of temperature of fixative on the conformation of the parasitic female of *Strongyloides ratti* (Experiment Chap.4.3.3)

5.5 EXTRANEOUS MATERIAL.

5.5.1 Bacteria.

Appearance.

Bacteria have been seen only on the cuticle. They appear as small refractile bodies, usually rod-shaped but occasionally coccoid, frequently clustered. Colley (1970) using TEM noted bacteria in the lumen of the intestine of the parasitic female of *S.myopotami*. The taxonomic significance of the bacteria is two fold. Firstly, if present in large numbers they can obcure cuticular details; eg., perivulval papillae and secondly, they can be confused with papillae.

5.5.2 Immune Precipitates.

Appearance.

Moqbel and McLaren (1980) described deposition of IgG on the cuticle of *S.ratti* during rejection by the host. The immunoglobulin appears as an amorphous, refractile mass in the buccal capsule, projecting anteriorly when present in large amounts (see Moqbel and McLaren, 1980; Fig.3). If extensive this material can obscure the stomal shape in the *en face* view (Fig.5:19). In lesser amounts the outline of the stoma appears blurred with the light microscope, while on SEM aggregates of amorphous material can be seen in and around the mouth and on the cuticle (Fig.2:2). Immunoglobulin on the cuticle is rarely seen by light microscopy, but can be detected by fluorescein labelled anti-globulin (Moqbel and McLaren, 1980) or peroxidase tagged anti-globulin (Fig.5:17).
The antibody class involved in the immune response of the foal described under 5.3.2.2 was IgG, while IgA appeared not to participate. IgG_{2a} was reported as the antibody with greatest affinity for the cuticle of the infective larvae of *S.ratti* (Murrell and Graham, 1982). The morphological effects on the parasitic

female of host immune response are given in Table 5:6.

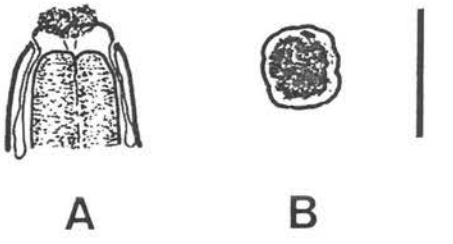


FIG.5:19. Amorphous material (probably immunoglobulin) obscuring the stomal shape of *Strongyloides* sp from large intestine of green tree frog. Specimens from this naturally infected frog were smaller with fewer eggs per worm. A. Dorso-ventral view; B. *en face* view. Scale line = 10µm.

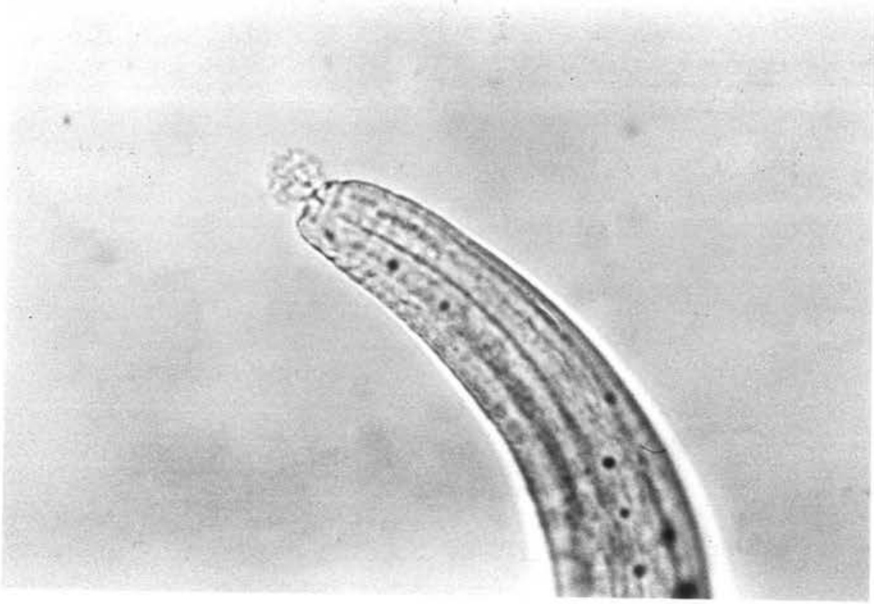


FIG.5:20. Material on head of parasitic female of *Strongyloides ratti* from small intestine of rat experimentally infected for 29 days. This is typical of immune precipitates.

5.5.3 Pigment.

Appearance.

When alive the parasitic female is colourless and transparent, and the internal organs are clearly visible. The taxonomic "ideal" retains these qualities. Most specimens are colourless, particularly if fixed while still alive. Only the occasional specimen is opaque or has morphological details obscured by pigment. The most common pigment encountered is tan in colour, and uniformly distributed through the body of the worm. Its taxonomic significance, apart from being an artifact per se, is that the internal organs, particularly the reproductive tract are difficult to see clearly. The paratypes of *S.robustus* (USNMHC 44911) are such a dark brown in colour, that the details of the buccal capsule are obscured.

Causes.

Anthelmintic Therapy.

A cat naturally infected with *S.felis* was treated with thiabendazole at 25mg/kg and killed six hours later. No worms were recovered from the small intestine, but dead parasitic females were found in the contents of the large intestine. These were uniformly tan in colour. The pigment was possibly bile absorbed by the worms killed by the anthelmintic.

Other causes have not been identified.

5.5.4 Sheaths.

Ransom (1911) introduced the concept of cuticular shedding based on specimens from the small intestine of a prong horned antelope, *Antilocapra americana*, which died at Washington in 1892. He proposed that this species had an unusual method of egg laying in which eggs were deposited under a cuticular sheath (Fig.5:9).

Ransom thought this sheath was formed by successive moults of the cuticle, and eggs and sheath were shed by the worm to enable the eggs to gain the lumen of the bowel. This phenomenon was not reported in the literature, although Brumpt (1910) had noted the occurrance of strings of eggs in the faeces of sheep. Ransom had not seen it previously in any other specimens of *Strongyloides*. He considered that the formation of cuticular sheaths indicated the specimens belonged to a new taxon, for which he proposed the name *S.ovocinctus*. Ransom (1911), however, had fears that this phenomenon may have been artifactual. Without its cuticular sheath and enclosed eggs, *S.ovocinctus* varied in only minor details from *S.papillosus*. Sandground (1925) considered *S.ovocinctus* to be a junior synonym of *S.papillosus*. Ransom's cuticular sheath was dismissed.

Sheaths encircling fixed specimens of *Strongyloides* are commonplace. They appear to be of two types. The most obvious consists of host mucosal epithelial cells. Cell outlines can be seen together with nuclei. This sheath often extends at least half the body diameter on either side of the encircled worms and can have several layers of epithelial cells (Fig.5:21). It rarely extends

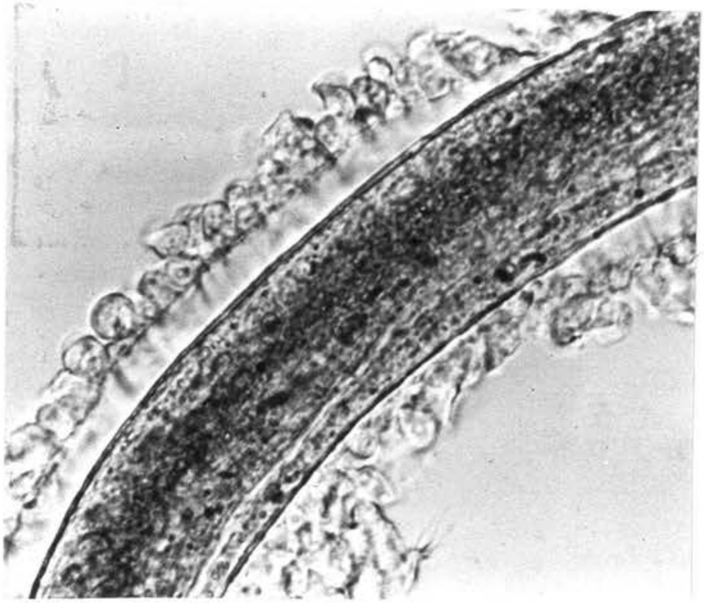


FIG.5:21. Cellular sheath around parasitic female of *Strongyloides ratti* from small intestine of rat 6hr after death of host.

the complete length of the worm, usually enclosing less than 25% of body length, and is frequently divided into several separate sections. This sheath is related to the trait of the parasitic female of threading its way through the mucosal cell layer. When the epithelial layer sloughs, cells adjacent to the worm, forming part of the wall of the tunnel, persist as an encircling sleeve.

The other sheath is more subtle. It is closely applied to the worm and is thus inside the cellular sheath. It lacks obvious features and appears as a fine membrane. Although it is difficult to see by light microscopy, it can be seen in transverse sections of tunnels as a fine eosinophilic membrane lying between the parasitic female and the tunnel wall. In whole specimens it either can be seen as a fine, featureless membrane close to the cuticle, or gives the impression of a veil obscuring the cuticular features. Where parasitic females emerge from the mucosal layer, SEM shows this fine membrane to be present (Fig.5:21). The sheath lacks striations and

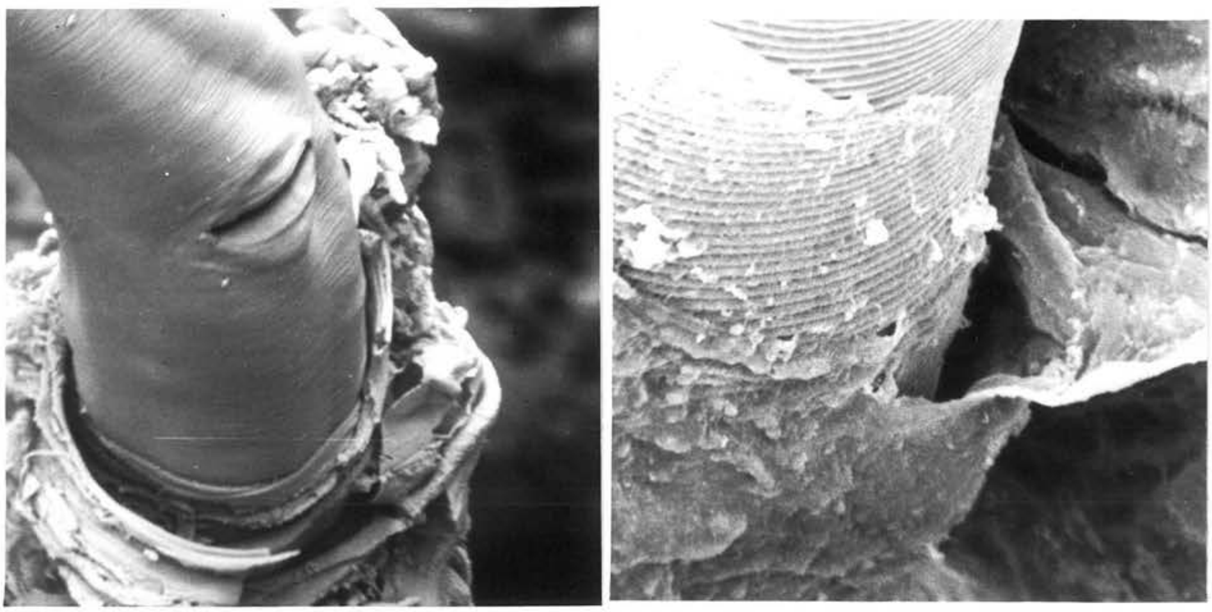


FIG.5:21. Fine inner sheath around parasitic female : A.*Strongyloides westeri* at point of emergence from mucosa of small intestine of foal; B. *Strongyloides* sp. at point of emergence from mucosa of stomach of agile wallaby. Delicate inner membrane is closely applied to worm while thicker outer membrane is separated from it. SEM.

looks more like a host product than that of the parasite. It does not appear to be derived from the cuticle. A study by Dawkins et al, (1983) showed *S.ratti* to lie between intestinal cells. The fine inner membrane, therefore, may be formed from the lateral walls of adjacent mucosal cells, and the outer cellular membrane from the remainder of the in contact epithelial cells together with variable numbers of cells adjacent to these. This theory assumes that the cells forming the tunnel may rupture their walls at right angles to the wall lining the tunnel, thereby allowing the inner and outer sheaths to separate. The fact that fine sheaths occur more commonly than cellular sheaths is consistent with the theory.

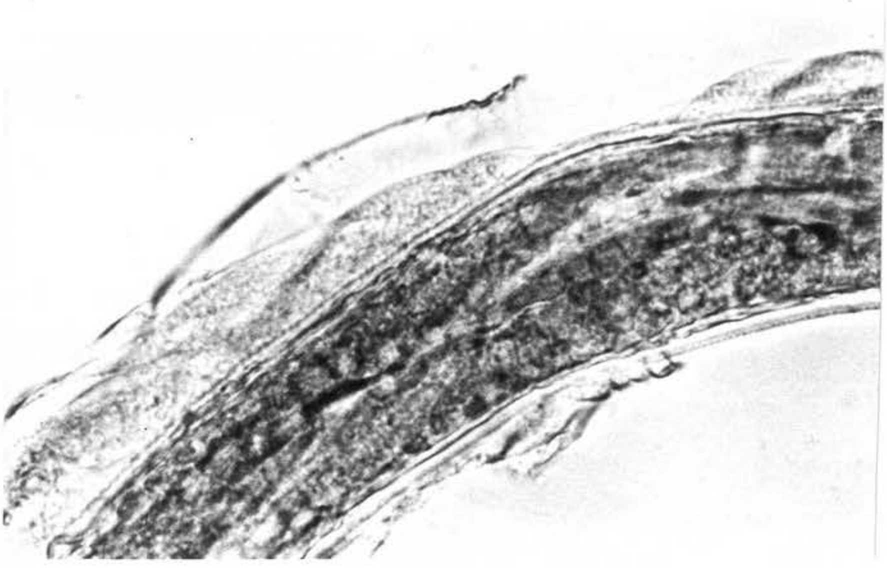


FIG.5:22. Advanced cuticular splitting with fragmentation plus sheath formation. Paratype of *Strongyloides ovocinctus*.

The specimens of *S.ovocinctus* (USNHC nos. 14647) examined were all enclosed in sheaths as Ransom (1911) had described. The specimens also showed advanced autolysis, with swelling, splitting and separation of the outer cuticular layers from the inner layers. (Fig.5:22 Ransom (1911) failed to appreciate that two processes were ocurring in his specimens. He noted the sheaths surrounding the worms and the splitting of the cuticle and assumed they were related, the latter giving rise to the former. The sheaths, however, were derived from the mucosal cell layer while the cuticular splitting was due to autolysis. Sheath formation is not, therefore, a feature of specific weight. It is a function of the biology of the parasitic female, and of ante and postmortem factors.

causes.

Sheaths are formed when, at the time of collection, parts of the mucosal tunnel remain encircling the parasitic female. Sheaths are seen on worms collected alive by dissection from the mucosa of recemtly dead hosts; but the frequency and extent of sheath formation is increased as the mucosa undergoes post-mortem sloughing. Sheaths can also be formed by mucosal sloughing occurring prior to death. Mucosal exfoliation was a feature of the response of the foal discussed in 5.3.3. The parasitic females of *S.westeri* were only partly embedded in the mucosa, and many had typical sheaths (Fig.5:23), complete with enclosed eggs. The small intestine from this foal had been fixed within 10 min of the animal being killed, so the effect was an ante-mortem one. Extensive sheaths on a particular specimen should alert one to be aware of autolytic or immune changes in the parasite.

FIG.2:23. Cellular sheath with entrapped eggs encircling parasitic female of *Strongyloides westeri*. The parasite was only partly embedded in mucosa of small intestine and host was mounting a marked immune response. SEM.

5.6 FREE-LIVING ADULTS.

5.6.1 Death.

Death of free-living stages is not uncommon. In all stages, including larvae, it can be recognised in fixed specimens by loss of definition of organs, granularity of the cuticle and other organs, wrinkling, and fragmentation of the specimen. Cuticular splitting as occurs in the parasitic female is not seen. Bacterial numbers on the surface are increased. It is of little importance taxonomically, since the specimens are readily recognised as degenerate. Its main significance is that in such specimens some of the finer features, e.g., caudal papillae, are hard to identify. In the male, spicules and gubernaculum remain unchanged even in badly degenerate specimens.

Lesser degrees of degenerative changes can be seen in the free-living stages just prior to their death in culture.

5.6.2 Bacterial Attack.

Bacteria can often be seen adhering to the surface of all stages, both parasitic and free-living, but are more common on the latter. They appear as refractile rods or cocci on the cuticular surface. In most free-living adults they can be seen in small numbers, scattered over the surface of the worm. Occasionally, they occur in dense colonies on the cuticle. These can obscure details of internal organs, and in the male make identification of caudal papillae almost impossible. Bacteria present in smaller numbers can be confused with caudal papillae. Caudal papillae can be distinguished by the minute dome of cuticle which surrounds the refractile nerve ending, and in addition the fine nerve fibre can be seen passing through the cuticle and hypodermis to the papillae.

5.6.3 Temperature of Culture.

Premvati (1958) obtained faeces from rhesus monkeys, *Macaca mulatta*, naturally infected with *S.fuelleborni*, cultured them at temperatures ranging from 15°C to 37°C, and noted changes in the morphology of the free-living adults. She particularly examined the morphology of the oesophagus and the post-vulval reduction in body diameter. The latter feature was a character of specific weight for *S.fuelleborni*. At 25°C morphology was typical, while at temperatures above and below 25°C, the maximum body width, the degree of post-vulval narrowing, and the number of eggs in utero decreased, while oesophageal length increased. The lips of the vulva were more salient at 25°C. The length of the infective larva was greatest at 25°C. The free-living male was not examined. Premvati concluded (p628):

> "An examination of these free-living females developing at different temperatures would lead an observer to consider them as belonging to different species."

The major effect of Premvati's study was to cast doubt on the validity of post-vulval narrowing as an important criterion in the free-living female. This feature has been described in three species, *S.fuelleborni*, *S.cebus* (Little, 1966a) and *S.felis* (Goodey, 1926; Speare and Tinsley, 1986). Several other species have a slight reduction in body diameter, but not the typical waist-like appearance of *S.fuelleborni*. Little (1966a) in his redescriptions of *S.fuelleborni* and *S.cebus* did not investigate the problem. It became less important after Little's study since he showed that the free-living males were of greater use than the females for distinguishing between the species. Thus, the question was avoided. Little (1966a) did, however, note variability in the degree of post-vulval narrowing in *S.fuelleborni* and *S.cebus*.

Experiments were performed (see Chapter 4.3.6) to investigate the effect of temperature on the morphology of the free-living stages; in particular, to determine if free-living females of species with a post-vulval narrowing could be modified, and to determine whether temperature had any effect on the free-living male. As a source of *S.fuelleborni* was not available, Premvati's experiments could not be repeated. *S.felis* was used since it has a similar post-vulval narrowing and rotation of the vulva posteriorly.

Free-living females cultured at 22°C and 32°C had a characteristic post-vulval constriction (Fig.5:24), but this was less marked at 22°C. The proportions of the four regions of the oesophagus were the same (Table 5:8). The free-living males showed no significant change in morphology. Free-living adults were uncommon at 32°C and very reluctant to grow at 15°C, as the direct cycle predominated at the former temperature and death of larvae occurred at the latter temperature. A single fertile free-living female obtained after culture at 15°C showed a characteristic post-vulval narrowing and vulval rotation, but unfortunately was lost prior to drawing and measuring.

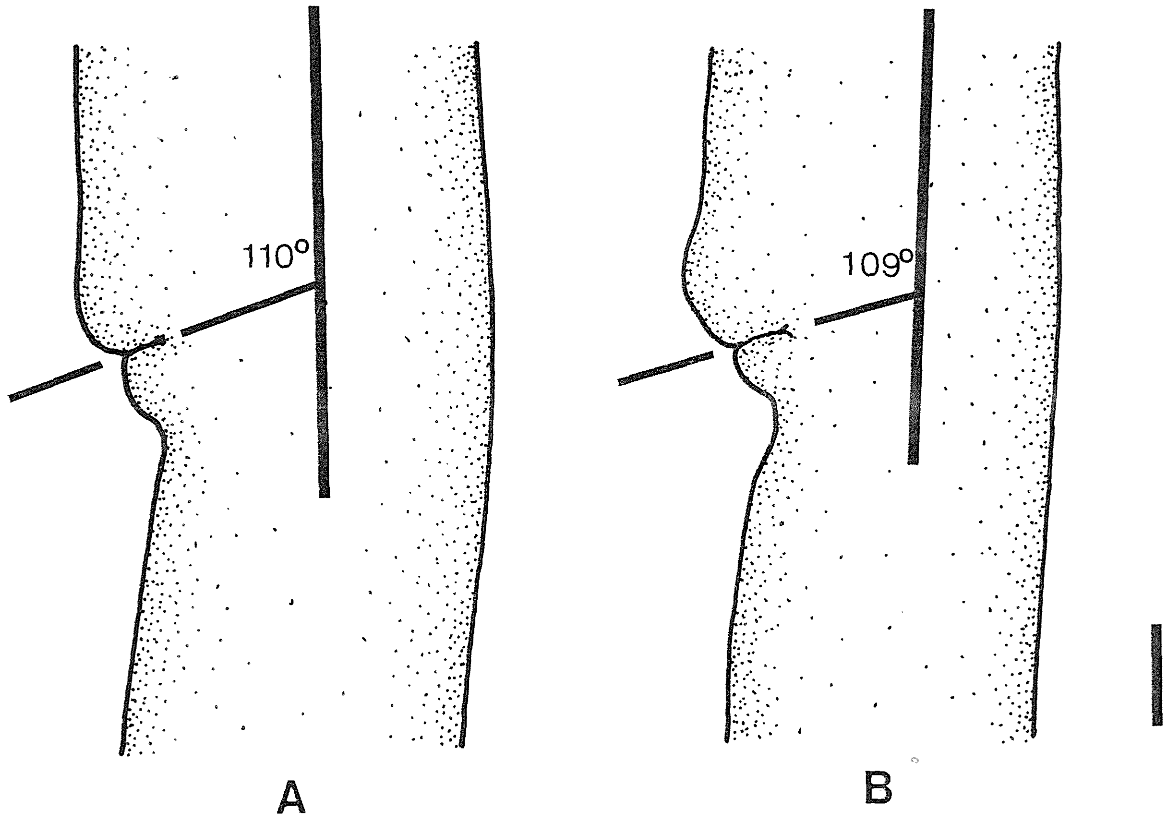


FIG.2:24. Vulval region of free-living female of *Strongyloides felis* : A. Temperature of culture 22^{0}C for 5 days; B. Temperature of culture 32^{0}C for 3 days. Scale line = 20μm.

Premvati's findings with *S.fuelleborni* had by extrapolation to other species cast doubt on the value of the post-vulval constriction in all free-living females. The finding that temperature at which free-living adults are cultured does not necessarily affect morphology suggests that the morphology may for some species be independent of external influences. This will allow descriptions of species to be made with more confidence, rather than having the uncertainty that the anatomy seen may be a product of the temperature at which the worms were grown.

TABLE 5:8A. Dimensions of *Strongyloides felis* free-living females cultured at 22°C and 32°C.

FEATURE	**22°C**	**32°C**
length	1338.0±57.0	1187.9±58.6
	(1275–1430)	(1094–1251)
max.width	83.0±5.4	72.3±5.6
	(75.0–93.8)	(66.7–83.4)
width post to vulva	68.0±3.6	54.6±4.2
	(62.5–75.0)	(50.0–62.5)
% reduction	17.5±2.3	24.5±2.9
	(13.9–20.0)	(18.8–29.4)
oes	160.7±4.0	178.0±6.0
	(156.4–168.9)	(168.9–189.7)
oes/length %	12.0±0.5	15.0±0.6
	(11.1–12.6)	(14.0–15.8)
tail	100.7±3.9	109.0±6.5
	(93.8–106.3)	(104.2–120.9)
tail/length %	7.53±0.20	9.18±0.32
	(7.14–7.85)	(8.68–9.67)
M-V	700.0±27.9	615.0±39.2
	(646.3–746.3)	(550.4–665.0)
M-V/length %	52.3±0.6	51.7±0.9
	(50.8–53.3)	(50.3–53.3)
vulval rotation	114.2±7.0	110.6±6.5
	(100–125)	(100–117)

TABLE 5:8B. Oesophageal regions of free-living female of *Strongyloides felis* cultured at 22°C and 32°C.
(% = region of oes / length of oes X 100)

REGION	22°C	32°C
corpus 1 μm	11.5±1.1	11.5±1.1
(%)	7.4±0.6	6.7±0.7
corpus 2 μm	82.8±2.0	90.3±3.8
(%)	53.9±1.3	52.8±1.0
isthmus μm	32.9±1.3	40.0±1.3
(%)	21.4±0.8	24.4±0.7
bulb μm	26.5±1.4	29.2±1.9
(%)	17.2±0.8	17.1±0.9

5.6.4 Age of Culture.

The only point of any taxonomic significance in older cultures is that as the free-living females age, the rate of egg production slows and hatching can occur in utero (Fig.5:25). Mackerras (1959) described this process in *S.thylacis*. It is of biological, not of taxonomic, importance and indicates a culture in which free-living adults are becoming effete.

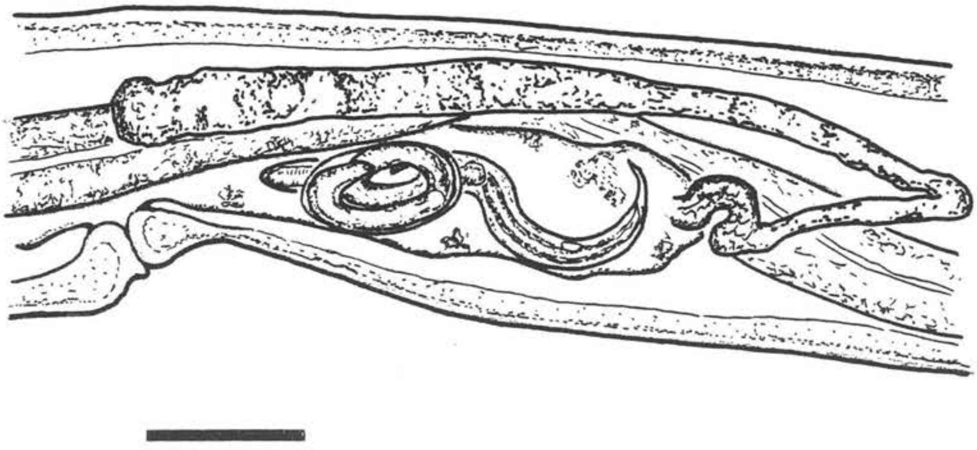


FIG.5:25. Effete free-living female of *Strongyloides felis* cultured for 100hr at 37 C. Note wasted ovaries, poor fucundity and larva in utero. Scale line = 50μm.

5.6.5 Contamination of Cultures.

Cultures can become contaminated by free-living rhabditoids even when faeces are collected directly from the rectum. Kreis and Faust (1933) described two species of Rhabditis found living on the skin of the perianal region of dogs and monkeys, these species being responsible for contamination even if faeces were collected directly into sterile containers. Contamination is likely if faeces are collected off the ground or floor (Speare *et al*, 1982; Speare and Tinsley, 1986). The general morphology of all *Strongyloides* is as described in Chapter 2. If worms are found in culture with different morphologies they are not *Strongyloides*. The taxonomic consequences of contamination of cultures are usually minor apart from loss of a useful diagnostic tool. An unusually disasterous and far-reaching consequence is shown by the effect of a paper by Kouri *et al* (1936). These workers reported on the maintenance in continuous culture of the free-living stages of *S.stercoralis*. This report is probably the basis for the oft-quoted but never substantiated "fact" that the free-living adults of *Strongyloides* can live indefinately outside the host. A critical examination of this paper reveals a change in morphology of the parasite as culture continued, with the final form evolving towards that of the more primitive rhabditoids. Illustrations were given (Plates XI-XIV) which clearly showed male and female rhabditoids. These worms were not *Strongyloides*, but free-living contaminants. Kouri *et al* (1936) were reporting not an amazing biological trait of *S.stercoralis*, but merely that their cultures were contaminated. Unfortunately, the idea was adopted by many text books, in spite of evidence to the contary (Kreis, 1932), and the fact that no subsequent worker was able to establish a continuous culture.

5.6.6 Pigmentation.

A dense brown pigment was occasionally seen in specimens held for prolonged periods; e.g., 20 years. This pigment was uniformly distributed and could not be removed by dehydration into glycerol or Owen's technique. In affected specimens it was usually so dense as to prevent observation of the details of the tail of the male. All affected specimens were stored in 70% alcohol with 5% glycerol, but many other specimens in different bottles containing 70% alcohol and 5% glycerol were non-pigmented.

5.7 SUMMARY.

This chapter has examined artifacts liable to cause confusion or errors in interpretation of morphological features and so cause problems with taxonomy. The cuticle and reproductive tract of the parasitic female are organs in which the most significant artifacts can occur. Degeneration, particularly after death of the host, immune responses of the host, and techniques of fixation are the major causes of artifactual changes in the parasitic female.

Artifacts are of less importance in the free-living adults. Bacteria in the culture medium can cause cuticular changes, and temperature of culture can effect the morphology of some species, although the significant features in others are not changed.

An awareness of the range of artifacts that can occur in the different stages will prevent mistakes such have been made in the past (e.g., *S.herodiae* and its "deep buccal capsule"; *S.ovocinctus* and its cuticular shedding; *S.turkmenica* and its inflated cuticle). Parasitic females when first examined should always be assessed for the signs of autolysis and the effects of the immune response of the host. If no evidence of these are found the taxonomic criteria can be determined. If signs of degeneration or immune damage are seen, taxonomic criteria can still be determined, but interpretation can be modified in the light of the artifacts present.

CHAPTER 6

CRITERIA FOR THE DIFFERENTIATION OF SPECIES

6.1 INTRODUCTION

Criteria for the separation of species need to be:

1. Unique to a particular species; or if not unique per se, to form a unique combination.
2. Reliable; that is, to be always present in the particular species.
3. Detectable; that is, able to be determined.

In the present state of knowledge of speciation in *Strongyloides*, criteria must of necessity be morphological. Biochemical and immunological differences between species may exist, but so little work has been done on these aspects, that in practice, these techniques would not be useful without a comprehensive study of the genus.

Little's (1966a) criteria for species differentiation superceeded all previous ones. He examined seven previously named species (Little 1966a) and described seven new ones (Little 1966b);

and in so doing showed the criteria worked for these 14 species. He did not, however, explain how to use the criteria for identifying unknown specimens, and failed to emphasise in the free-living male which were the most useful features for separating species.

How should one determine whether criteria are useful for species differentiation? The first point must be that they allow distinct taxa to be separated; uniqueness. In the practical sense, this is judged by their ability to separate what seem to be closely related species, species which show morphological similarities. Reliability, the second point, is determined in practice by looking within particular species for the ability to find the same criterion in different specimens of the same taxon; or if not found to be the same in a particular specimen, to be able to know why the particular criterion is different in those particular specimens. In a reliable character this difference from the norm will be due to factors external to the worm and not related to its identity. The final point, detectability, is assessed by the ease and confidence with which an experienced observer can identify the criterion.

The features proposed as useful for differentiation of the adult stages will be considered in turn, then other aspects thought to be of use will be examined. The assessment will be based on information from the literature and from my own studies. An attempt will be made to designate useful criteria as either major or minor, the former defined as a character which can be used as a primary tool for dividing species or specimens into categories, while minor criteria come into play only in separating species in those categories.

6.2 PARASITIC FEMALE

6.2.1 Stomal Shape.

Little (1966a) was the first to emphasise the importance of the shape of the stoma in the *en face* view. A few authors previously had noted this feature in their specimens (Kreis, 1932; Basir, 1950; Tarczynski, 1956), but had failed to note its usefulness in distinguishing between species. Little considered it one of the key features in speciation. In terms of uniqueness, it is an extremely useful criterion, as some species can be identified on this feature alone (Table 6:1).

Stomal shapes can be divided into four types: simple, angular, complex, and with oesophogeal teeth (Fig.6:1). A simple stoma is defined as a shape which has no angles; e.g., round, oval or dumbell. An angular stoma is angular; square, rectangular, hexagonal, badge-shaped. A complex stoma is multichambered, with compartments leading off from a central chamber. A stoma with oesophageal teeth has projections passing forward from the anterior end of the oesophagus to the level of the stomal verge.

Artifacts can affect the shape of the stoma. The extreme manifestation of autolysis is anterior prolapse (see Chapter 5.2.1.3). These marked changes make it impossible to determine stomal shape. Lesser degrees of autolytic change may modify the stoma, but in many species the head is one of the last regions of the cuticle to be affected. The edges of the stoma in specimens showing degenerative changes elsewhere are often unclear and not precisely defined. Precipitates of immunoglobulins on the stoma may blur the outline, making it difficult to determine, or they may form a refractile oral plug which obstructs the *en face* view. A reliable clue to a stoma that has been deformed by external forces is lack of

TABLE 6:1. Key features of fully described parasitic females.

SPECIES	STOMAL SHAPE	CIRCUMORAL LOBES	OVARY TYPE	TAIL SHAPE	STAGE in FAECES	REFERENCE
S.ardeae	hexagonal	2	spiral ant.	bluntly rounded	unknown	Little 1966b
S.cati	dumbell with oes.teeth	6	spiral both	bluntly rounded	eggs	Rogers 1939 Arizono et al 1976
S.cebus	modified X	0	spiral both	narrowly tapered	eggs	Little 1966b
S.dasypodis	open-badge closed-Y	6	dir.recurr.	narrowly tapered	larvae	Little 1966b
S.elephantis	ornate	?	dir.recurr.	narrowly tapered	unknown	Greve 1969
S.eryxi	oval	4	spiral both	narrowly tapered	eggs	this thesis
S.felis	rectangular	6	dir.recurr.	narrowly tapered	larvae	this thesis
S.fuelleborni	modified X	0	spiral both	blunt	eggs	Little 1966a
S.gulae	oval	2	spiral ant.	pointed	eggs	Little 1966b
S.lutrae	X-shape	8	spiral ant.	pointed	eggs	Little 1966b
S.myopotami	ornate, 8 chambered	2	dir.recurr.	narrowly tapered	eggs	Little 1966a
S.papillosus	X-shaped	6	spiral both	bluntly rounded	eggs	Basir 1950; this thesis
S.pavonis	hexagonal	6	spiral both	narrowly tapered	larvae	Sakamoto & Yamashita 1970
S.physali	oval with concave sides	6	spiral ant.	pointed	eggs	Little 1966b
S.procyonis	hexagonal	6	dir.recurr.	narrowly tapered	larvae	Little 1966b
S.ratti	badge	6	dir.recurrent	narrowly tapered	eggs and larvae	Little 1966a
S.serpentis	oval	2	spiral ant.	pointed	eggs	Little 1966b
S.spiralis	oval	6	spiral both	blunt	eggs	Grabda-Kazubska 1978
S.stercoralis	hexagonal	6	dir.recurr.	narrowly tapered	larvae	Little 1966a
S.suis	dumbell with oes.teeth	8	spiral both	pointed	eggs	this thesis
S.turkmenica	hexagonal	6	spiral ant.	narrowly tapered	unknown	Barus et al 1978
S.venezuelensis	ornate, 8 pointed	8	spiral both	short conical	eggs	Little 1966a
S.westeri	dumbell with oes.teeth	8	spiral both	narrowly tapered	eggs	this thesis

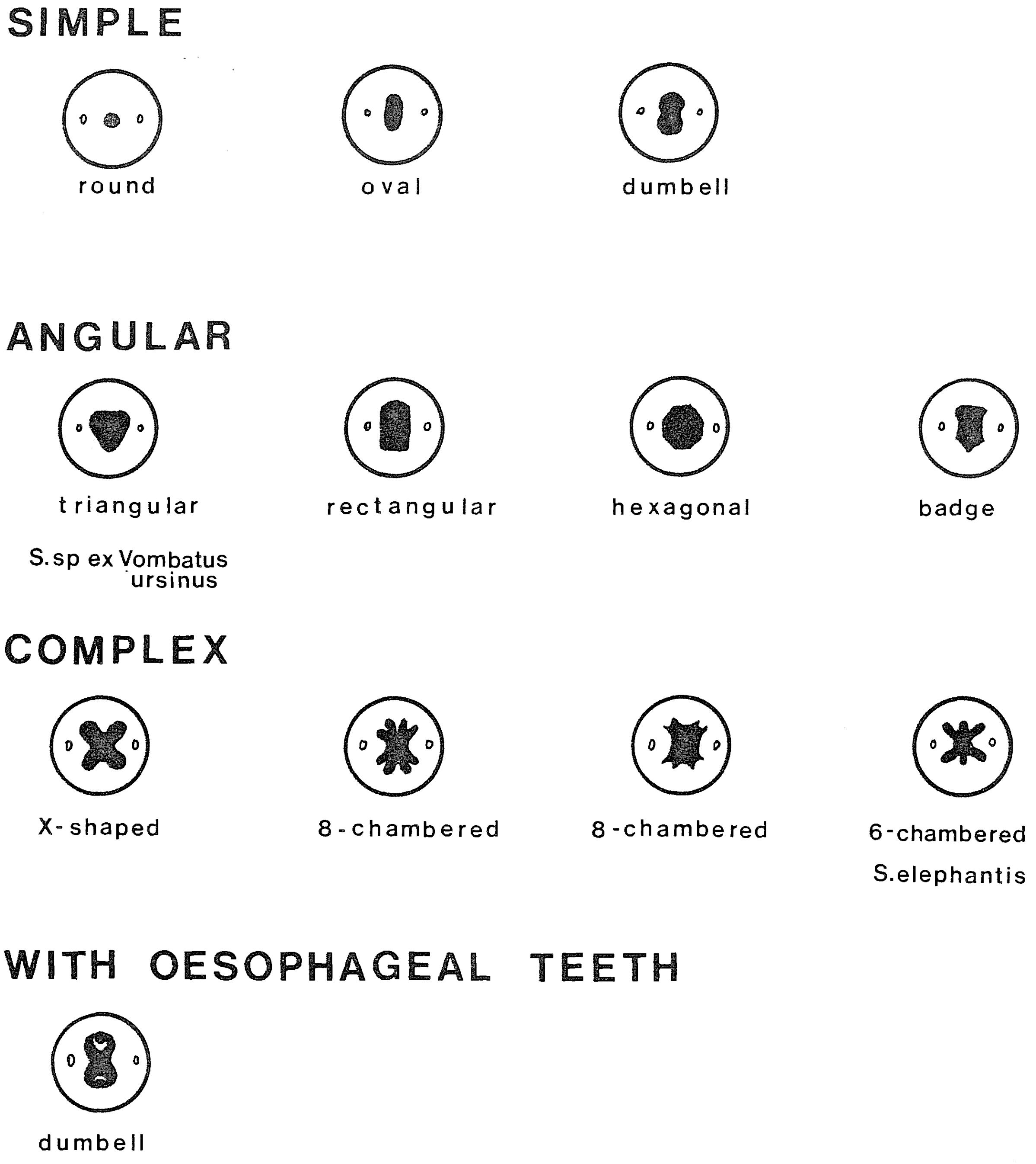


FIG.6:1. Types of stoma of parasitic female. *En face* view. Species with particular shapes listed in Table 6:1 or as indicated in Fig.6:2 or this Fig.

bilateral symmetry. Many artifactual changes affecting the stoma can be anticipated by recognition of their existence prior to examination of the apical view.

The size of the stoma within particular species varies from one specimen to another, often in the same host. This is of no concern if the stomal shape is constant. Most simple and geometric stoma have the same shape irrespective of the size of the stoma (Fig.6:2A). More complex stoma, however, sometimes change shape with change in size (Fig.6:2B). This is due to differences in the proportional reduction in size of different dimensions of the stoma.

In a stoma which maintains the same shape, all dimensions are reduced to the same degree. Little (1966a) hinted at this concept, but did not describe or explain it. Without definition, Little used the terms "open" and "closed" stoma. It appears he meant these terms to refer to the extremes of the range of stomal shapes shown by a particular species. An "open stoma" is one with the largest dimensions, while a "closed stoma" is one with the smallest. The factors affecting stomal size in particular specimens are unknown; they may be intrinsic or external to the worm. The open stoma is one which is most characteristic of a species. The closed stoma is also characteristic, but since it is compressed and smaller, the subtleies of shape possible are limited and not as useful as in the open stoma. In describing or identifying specimens, it is essential therefore to examine a number of *en face* views, determine the range of shapes and their relative sizes, and note the extremes of this range; the "open" and "closed" forms. "Closed" stoma are less common.

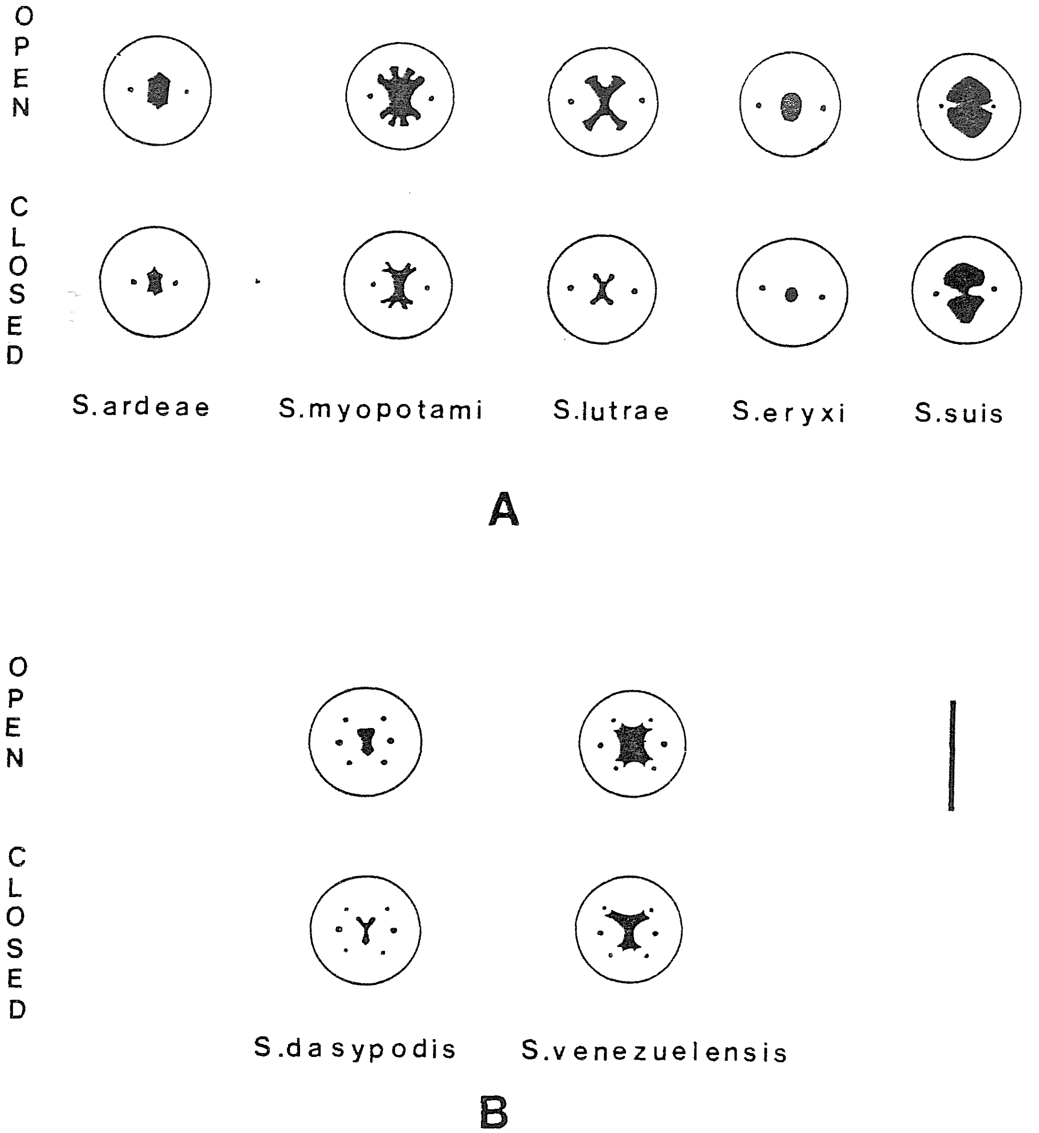


FIG.6:2. Variation in stomal shape within species :
A. open and closed stoma with no change in shape;
B. open and closed stoma with change in shape.
En face view.

The shape of the stoma is a reliable criterion. Greve (1968) in his description of *S.elephantis* criticised use of the stomal shape on the basis of its "plasticity" (p498). He implied stomal shape was an unreliable criterion, but did not elaborate. Two paratypes of *S.elephantis* (USNMHC 70980) were examined. They showed minimal degenerative change, but shrinkage was marked, with the cuticle greatly wrinkled and collapsed around the internal organs. The specimens had been fixed in 10% formalin (Greve, 1968 p498), and were permanently mounted on slides. The mounting medium was not stated by Greve (1968) or noted on the slides themselves. The mounting process may have caused excessive shrinkage. If a similar process was used to prepare *en face* views, deformation of the head would be expected, leading to variation in the stomal shape for different specimens. "Plastic" means capable of maintaining a new shape once a deforming force has been removed. Greve's stoma were, indeed "plastic", but due to his techniques and not to an intrinsic characteristic of the stoma of *Strongyloides*. His criticism of the reliability of the criterion is therefore unjustified.

The head of the parasitic female is small. *S.westeri*, the largest species, has a head about 20μm across, with a stoma about 11μm in diameter. One of the smallest stoma, e.g. the oval stoma of *S.eryxi* collected from the snake, *Elaphe carinata*, (Sprent Colln. 1271/PF4485-C-N) measured 2μm by 1.5μm. Consequently, ease of detection of stomal shape may be a problem. Scanning electron microscopy may help in some cases to clarify stomal shape, but deformation caused by the techniques involved lessen one's confidence in use of SEM alone.

The techniques of making *en face* preparations (see Chap.4.2.3.3) are mastered with practice and should not pose a major obstacle. With an experienced parasitologist the stomal shape can be consistently determined.

In all respects, therefore, uniqueness, reliability and detectability, the shape of the stoma of the parasitic female is a useful criterion.

6.2.2 CIRCUMORAL LOBULATION.

The circumoral elevation is frequently divided into small lobes, whose number is characteristic of the particular species (Little 1966a, 1966b; Arizono et al, 1976). The number of lobes present are determined from lateral and dorso-ventral views of the head (Fig.6:3). The lobes are always paired, none, two, four, six and eight have been seen. Two lobes are usually broad lateral lobes; specimens with four lobes were not seen by Little and have broad lobes in lateral, ventral and dorsal positions; with six lobes they occur in lateral, subventral and subdorsal positions; while the additionl pair with eight lobes is found ventrally and dorsally. In some species the lobes are easily seen, while in others they are not so prominent and one feels less confident in their enumeration. In species with prominent lobes and using good specimens lobulation is reliable and fairly easily determined if both views of the head can be obtained. In theory they could be a useful character for differentiation, but one would use them only after other criteria had been unable to separate the species. In practice the number of lobes in the circumoral lobulation has not been used as a major criterion for distinguishing between species.

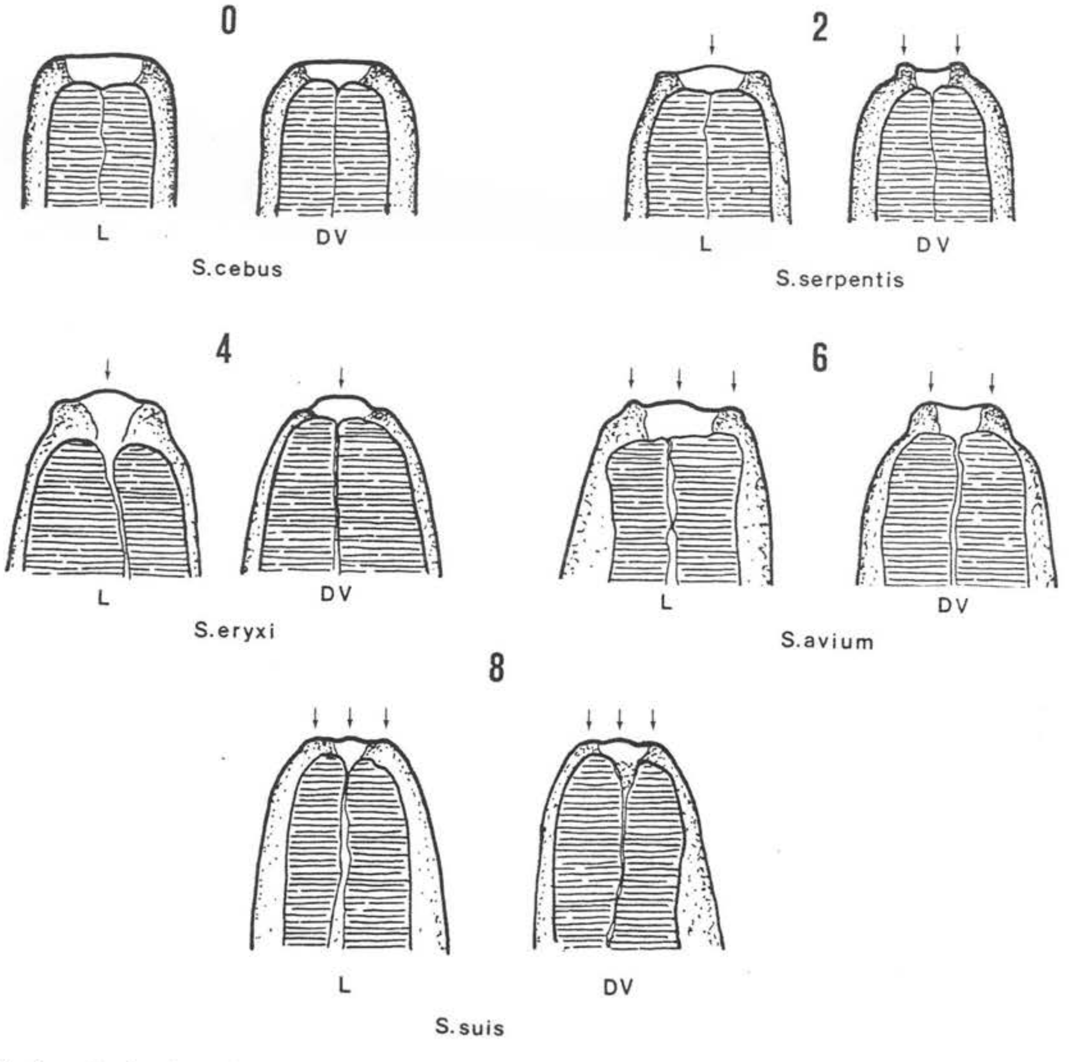


FIG.6:3. Lobulation of circumoral elevation of parasitic female. Arrows indicate position of lobes; numbers indicate number of lobes.
L = lateral view; DV = dorso-ventral view.

6.2.3 Type of Ovary.

The ovary in the parasitic female either forms a spiral with the intestine or it does not. The degree of spiraling is usually greater in the anterior ovary than the posterior, although Cameron and Reesal (1951) reported otherwise for *S.agoutii*. Sandground (1925) first suggested ovary type as a useful criterion for speciation. Litttle (1966a,b) confirmed this, and proposed it as a key feature.

It is not a feature with a high degree of uniqueness. There are only two options, spiral or directly recurrent. The degree of spiraling is of use in distinguishing between some species. *S.eryxi*, from snakes, usually has two anterior and one posterior coil (Singh, 1954), while similar species from snakes, *S.gulae* and *S.serpentis* have a single anterior coil only (Little, 1966a). It is easily detectable, except in specimens which are badly degenerated (Chap.5.2.2.1) or heavily pigmented (Chap.5.5.3). The reliability of the feature is good. One must be alert to the fact that the parasitic female in a species with spiralled ovaries may become mature before the ovary has begun to spiral (see Chap.5.2.2.2).

S.agoutii is one species in which spiralling has been noted to be variable (Griffiths, 1940; Cameron and Rheesal, 1951). Griffiths (1940) noted no constancy in the type of ovary in *S.agoutii* from the agouti, *Dasyprocta agouti*. Cameron and Reesal (1951) disagreed stating the species consistently had two coils posterior to the vulva and one anterior. They stated the variable ovary type noted by Griffiths was due to his use of specimens from experimentally infected guinea pigs, although Griffiths (1940) appeared to be using specimens only from agouti. The type of ovary in *S.agoutii* is, therefore, unresolved. It seems to be a special case and should not be taken to weaken the reliability of the criterion for other species.

Another species in which the ovary type was originally reported as variable was *S.ratti*. Sandground (1925) noted five out of 40 of his specimens had "sinuous" ovaries, while the remainder had "hairpin bend" ovaries. Early workers often used "sinuous" to refer to spiral ovaries. Plate IX Fig.B from Sandground (1925) shows a sinuous course for the ovaries, but if the geometery of the spiral is borne in mind spiral ovaries can be construed from the

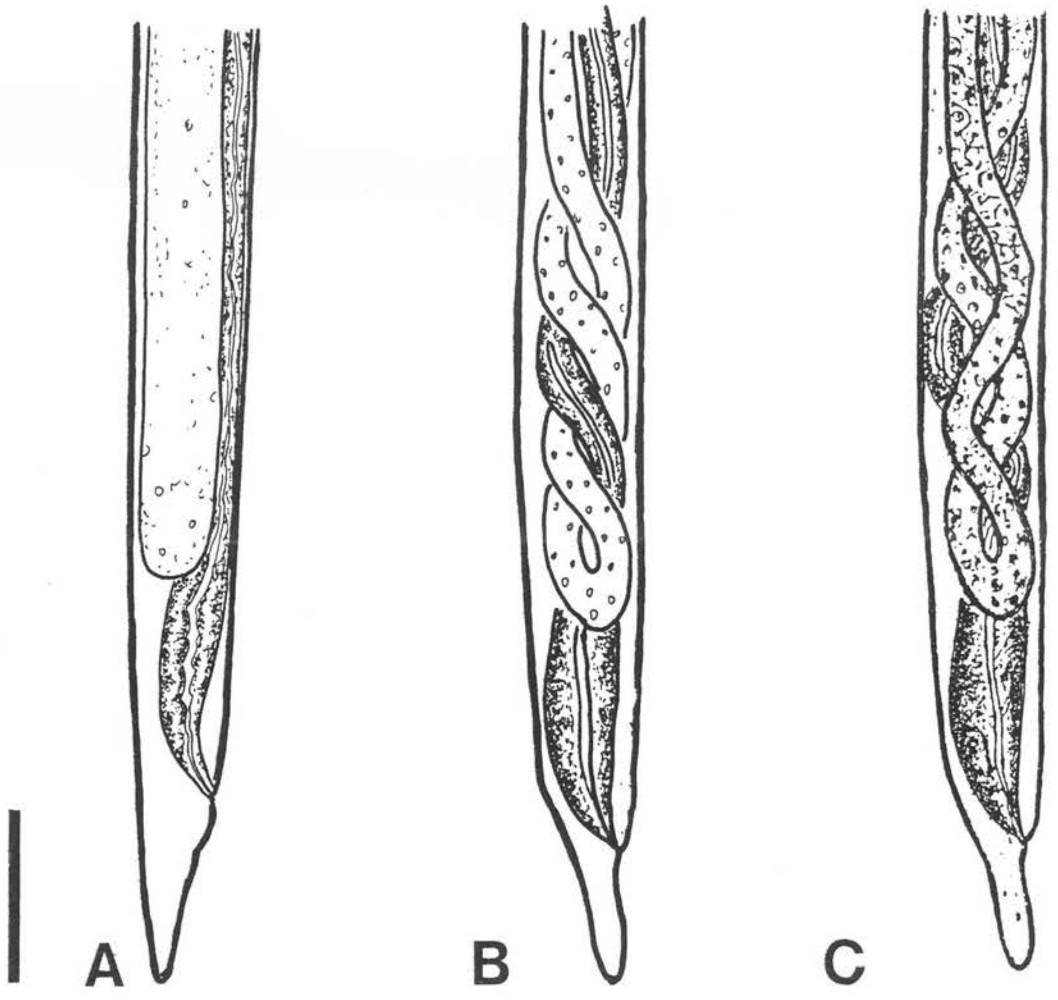


FIG.6:4. Types of ovary of parasitic female : A. directly recurrent - *Strongyloides ratti*; B. spiral - *Strongyloides venezuelensis*; C. "sinuous" ovary of "*Strongyloides ratti*" from Sandground (1925 Plate IX Fig.B) was probably spiral ovary of *Strongyloides venezuelensis*. Scale line = 50µm.

illustration (Fig.6:4). Since Sandground's original report, spiral ovaries have not been seen in *S.ratti*. The most likely explanation is that Sandground (1925) had a mixed population of *S.ratti* and *S.venezuelensis*. Both species are similar in size and proportions (Little, 1966a), but *S.venezuelensis* has spiral ovaries and *S.ratti* directly recurrent ones. Both species can exist experimentally in the same host (Wertheim, 1970). Concurrent natural infections are not uncommon (Little, 1961; Wertheim and Lengy, 1964). Sandground (1925) collected his rats, *Rattus norvegicus*, from rubbish dumps in Baltimore. Little frequented New Orleans refuse tips where he found

Rattus norvegicus infected with both species. It is highly probable therefore, that Sandground's "*S.ratti*" included specimens of both *S.ratti* and *S.venezuelensis*. His observations on variation in ovary type of "*Sratti*" are therefore not valid, although his general conclusion that ovary type was a useful criterion is correct.

The type of ovary in the parasitic female is an easily detectable, useful criterion of low specificity, and in most species of high reliability.

6.2.4 Shape of the Tail.

Sandground (1925) dismissed this character as a means of distinguishing between species. He found the shape of the tail to show too much variation to be of use (see Sandground, 1925, p.81, Plate VIII). Goodey (1926) stated tail shape was an important feature for distinguishing between *S.felis* and *S.stercoralis*, the former having a finely tapered, often pointed tail, while the latter was narrowly tapered but never as acutely as *S.felis*. Swartz and Alicata (1930) used the shape of the tail to separate the parasitic females of *S.papillosus* and *S.suis* (syn.*S.ransomi*). They found the range of shapes shown by each did not overlap. Cram (1936) also considered the shape of the tail to be a significant character in the identification of species in birds. Little (1966a) noted *S.cebus* had a more tapered and sharper tail than *S.fuelleborni*.

The main features of the tail which seems to be of importance are the degree of taper and the nature of the tip, whether it is bluntly rounded or narrowly tapered. Sandground's (1925) observation that tail shape is variable is accurate (Fig.6:5). Sandground examined the tails of seven species. One, *S.ovocinctus*

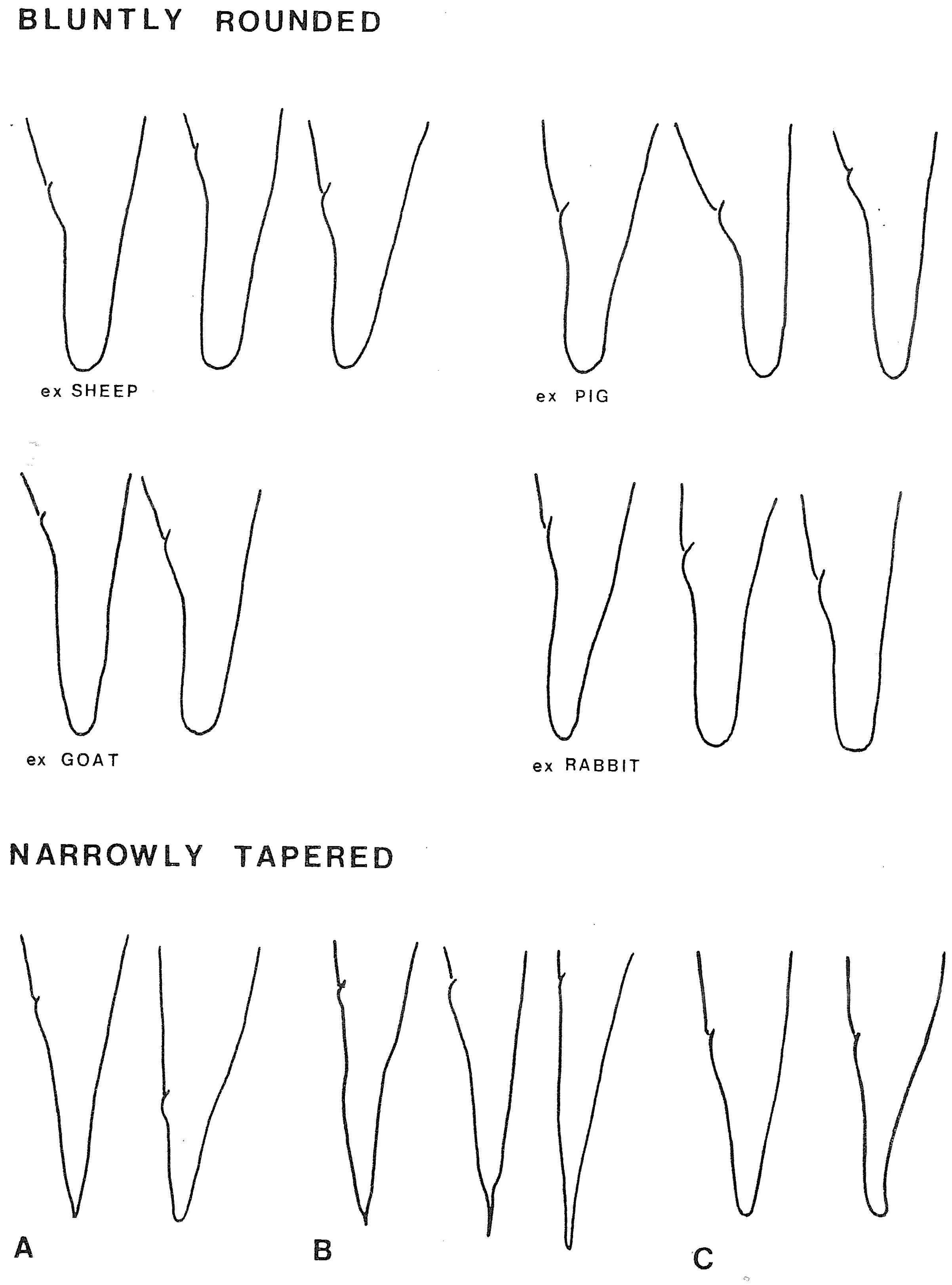


FIG. 6:5. Categories of tails of parasitic females: Bluntly rounded - *Strongyloides papillosus* from various hosts as indicated; Narrowly tapered - A. *Strongyloides suis* from pig; B. *Strongyloides felis* from cat; C. *Strongyloides stercoralis* from human. Lateral views.

was a synonym of the other, *S.papillosus*. Five of the remaining six species had the same type of tail, bluntly rounded, while the sixth *S.stercoralis* has a narrowly tapered tail with a truncated tip, giving a bluntly rounded appearance. Consequently, there was no difference in this feature between the seven species examined and Sandground found tail shape to be of no use. Tail shape, however, although showing an intraspecies variation, does show a limited range of variation. *S.papillosus* never has a tapered tip; it is always bluntly rounded. *S.felis* consistently is finely tapered often pointed, while *S.stercoralis* is not. This is useful in differentiating the latter two species (Goodey, 1926; Speare and Tinsley, 1986).

The shape of the tail can be used for distinguishing between particular species. It is a character of limited uniqueness, since only two main options, narrowly tapered-pointed or bluntly tapered-rounded, are possible, although the first category can refer to species with narrow, but blunt tips. Detectability is good. Reliability is a problem. The range of shapes shown by a species has to be considered. The criterion is a minor one, but in particular instances a useful one in practice since it is easily determined. *S.felis* and *S.stercoralis* have both been reported from cats (Chandler 1925a,b; Levine, 1968; Froes, 1976; Speare and Tinsley, 1986). The parasitic females are similar in many respects, but they can be quickly distinguished by the shape of the tail. The identification can then be confirmed by determination of the shape of the stoma, a more time consuming task.

6.2.5 Excretory System.

The parasitic female has an excretory pore situated on the ventral midline just posterior to the level of the nerve ring. A sacciform canal passes posteriorly to join a common chamber, associated with a renette cell, from which bilateral canals run anteriorly and posteriorly in the lateral chords (Little 1966a). Little (1966a) suggested differences in the morphology of the system may prove to be of use in species differentiation. The major problem with this criterion is detectability. The excretory system is difficult to study and can be seen clearly in less than 10% of specimens. In the practical sense, therefore, it is not a suitable feature.

6.2.6 Transverse Striations.

All parasitic females have transverse striations. Hung and Höeppli (1923) used the presence of transverse striations as an argument to justify their proposal that *S.simiae* was a new species, distinct from *S.fuelleborni* and *S.cebus*. They had no specimens of the latter two species to examine, but assumed from the descriptions in the literature that both species lacked transverse striations. The ease with which transverse striations are detected varies with the species, but with care striations can be seen in all.

The presence or absence of striations is of no use in species identification (Sandground, 1925).

6.3 FREE-LIVING MALE.

6.3.1 Spicule.

The ways in which spicules of different species vary are difficult to express in terms which can be understood exactly by all workers. Little (1966a&b) was the first to attempt a comparison of spicules. He described the general morphological features of the spicule and modifications due to specific identity. He failed to emphasize which features were important in species differentiation.

6.3.1.1 Type of Tip. -

A key feature is the nature of the tip or ventral end of the spicule. There are four types (Fig.6:6) : Sharply pointed, blunt, hooked, and pointed with lateral projections. The last category can be identified in lateral view by a refractile area at the base of the pointed tip and recognition that a projection passes laterally into optical planes other than that of the tip. Little (1966a&b) described the sharply pointed and hooked tips, but omitted Mackerras's (1959) report of a blunt tip in *S.thylacis*.

The nature of the tip is consistent and easily determined. Most species have sharply pointed spicules. Species from Australian marsupials and a new species from the domestic fowl have blunt tips. A hooked tip is found in *S.serpentis* from north American snakes and a species from Australian snakes. The more elaborate sharply pointed tip with lateral projections has been seen only in a species from New Guinea cuscuses, *Phalanger spp*.

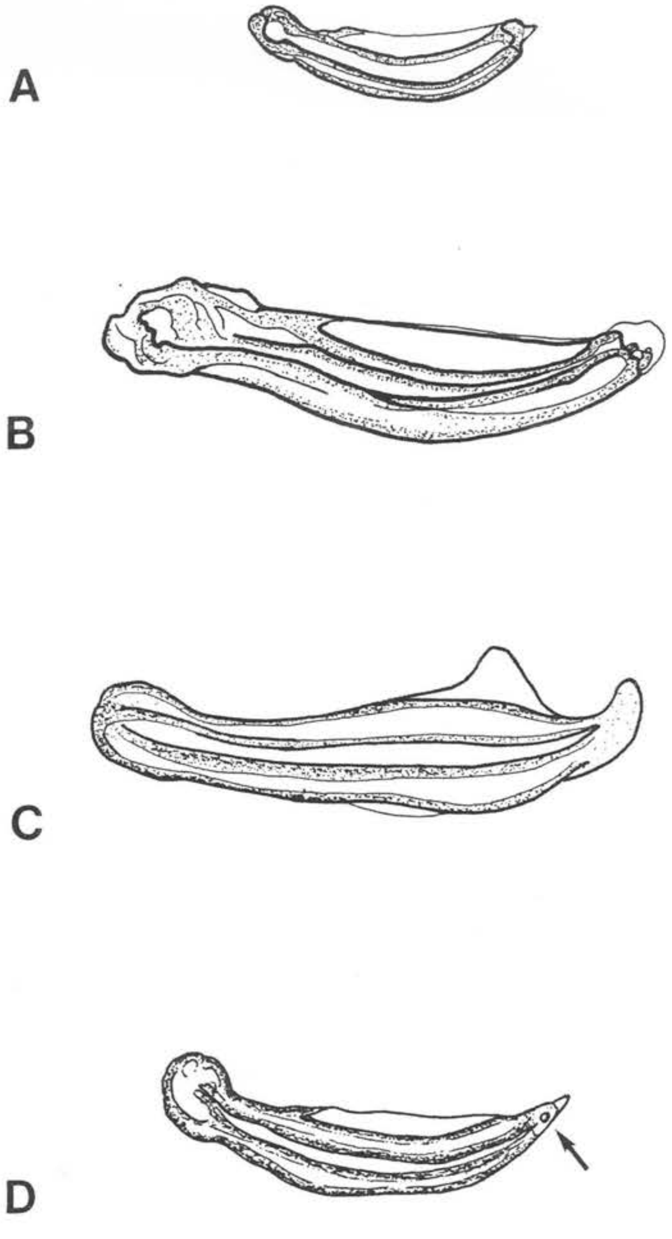
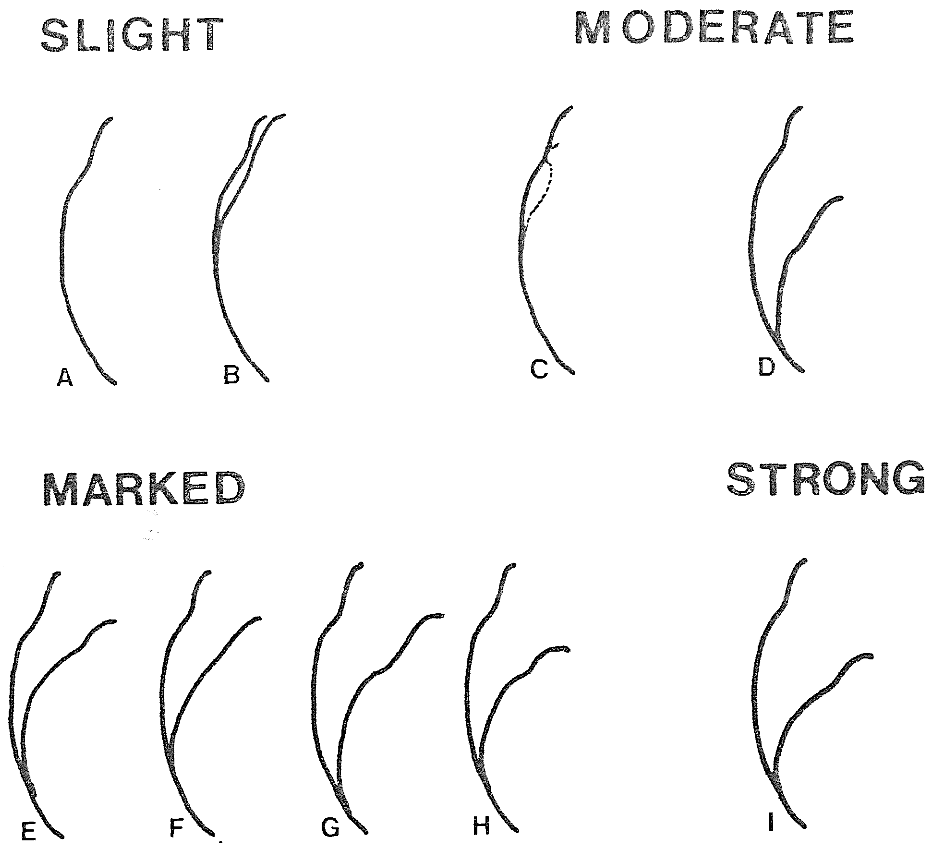


FIG.6:6. Categories of tips of spicule: A. pointed - *Strongyloides* sp from green tree frog, *Litoria caerulea;* B. blunt - *Strongyloides* sp from spectacled hare wallaby, *Lagorchestes conspicillatus;* C. hooked - *Strongyloides serpentis;* D. pointed with lateral projections - *Strongyloides* sp from cuscus, *Phalanger vestitus*. Arrow marks position of projection. Lateral views. Scale line = 10µm.

6.3.1.2 Curvature. -

The degree of curvature of the spicule is a character which is useful but difficult to quantitate. The curvature refers to the shape in lateral view of the dorsal edge of the spicule. Little (1966a) used the term "bowed" to refer to this, with the semiquantitative modifiers "slightly", "moderately", "markedly". The spicules of *S.serpentis* are unusual since they are straight with a dorsal bulge at the junction of the middle and ventral thirds. Fig.6:7 is made up of tracings from Little (1966a&b) of the curvature of the spicules of 12 species of *Strongyloides*. The general shape of the curves are similar, apart from that of *S.serpentis*. Quantification of degree of curvature is made difficult by differences in the form of particular species at particular points in the curve e.g., a bulge may occur earlier in the curve in one species than in another. Spicules of different sizes are difficult to compare and for meaningful comparison all should be brought to the same size. When this is done (Fig.6:8) it can be seen that the curves are very close. The curves of the dorsal halves of the "markedly bowed" spicule of *S.fuelleborni* and the "slightly bowed" spicule of *S.stercoralis* (Little 1966a) are, for example, separated only by about 20°; *S.dasypodis* classed as "moderately bowed" has the same curve as *S.stercoralis*, which is "slightly bowed".

Since intraobserver variation in classification is obviously a problem, interobserver variation would be expected to be greater. The degree of curvature of the spicule is, therefore, not a good criterion in terms of uniqueness, since the majority of spicules are the same. If one introduces spicules not examined by Little, one can separate the markedly curved spicule of *S.westeri* from that of



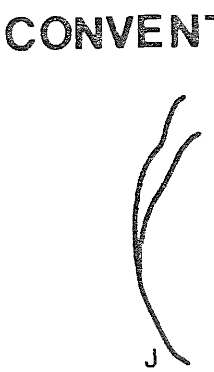


Fig. 6:7. Curvature of spicules with pointed tips: classification according to Little (1966a). Line of dorsal border is compared with that of *Strongyloides stercoralis*. A. *Strongyloides stercoralis*; B. *Strongyloides procyonis*; C. *Strongyloides dasypodis*; D. *Strongyloides physali*; E. *Strongyloides fuelleborni*; F. *Strongyloides lutrae*; G. *Strongyloides cebus*; H. *Strongyloides venezuelensis*; I. *Strongyloides myopotami*; J. *Strongyloides gulae*

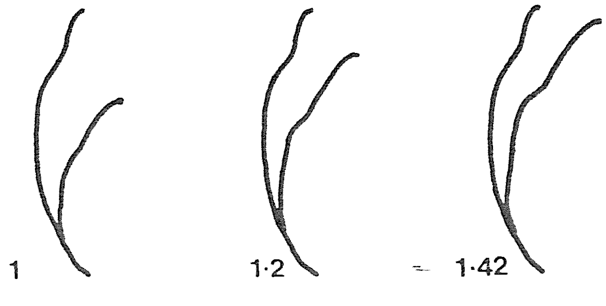


Fig. 6:8. Comparison of curvatures at different magnifications for spicules of different sizes. *Strongyloides stercoralis* to left, *Strongyloides physali* to right; numbers indicate magnification factor for *Strongyloides physali*

S.stercoralis since they are at the extreme ends of a fairly narrow spectrum, but the separation of the species in between these extremes can not be done with confidence using this criterion.

Curvature of the spicule is therefore a useful criterion of low uniqueness, ranging from the "not curved" spicules of *S.serpentis*, to the "markedly" curved spicules of *S.westeri*, with the majority of spicules being in the "slight-moderately" curved category. Comparison between spicules in this latter group is not of use, since their curvatures are essentially the same.

6.3.1.3 Ventral Membrane. -

Two features of the ventral membrane are of importance in species differentiation; the shape of the ventral border, and the prominence of the membrane. The ventral border is most usefully classified into convex, straight and concave (Fig.6:10). The "straight" category includes membranes with slight degrees of deviation from a central line. Most species fall into this category. "Convex" membranes are obviously so e.g. those of *S. cebus*; while the "concave" category refers to those which are obviously concave e.g. *S.westeri*. An indication that a membrane should be classed as "straight" is hesitancy on the part of the observer into which category it belongs. Only the obvious instances are otherwise classified.

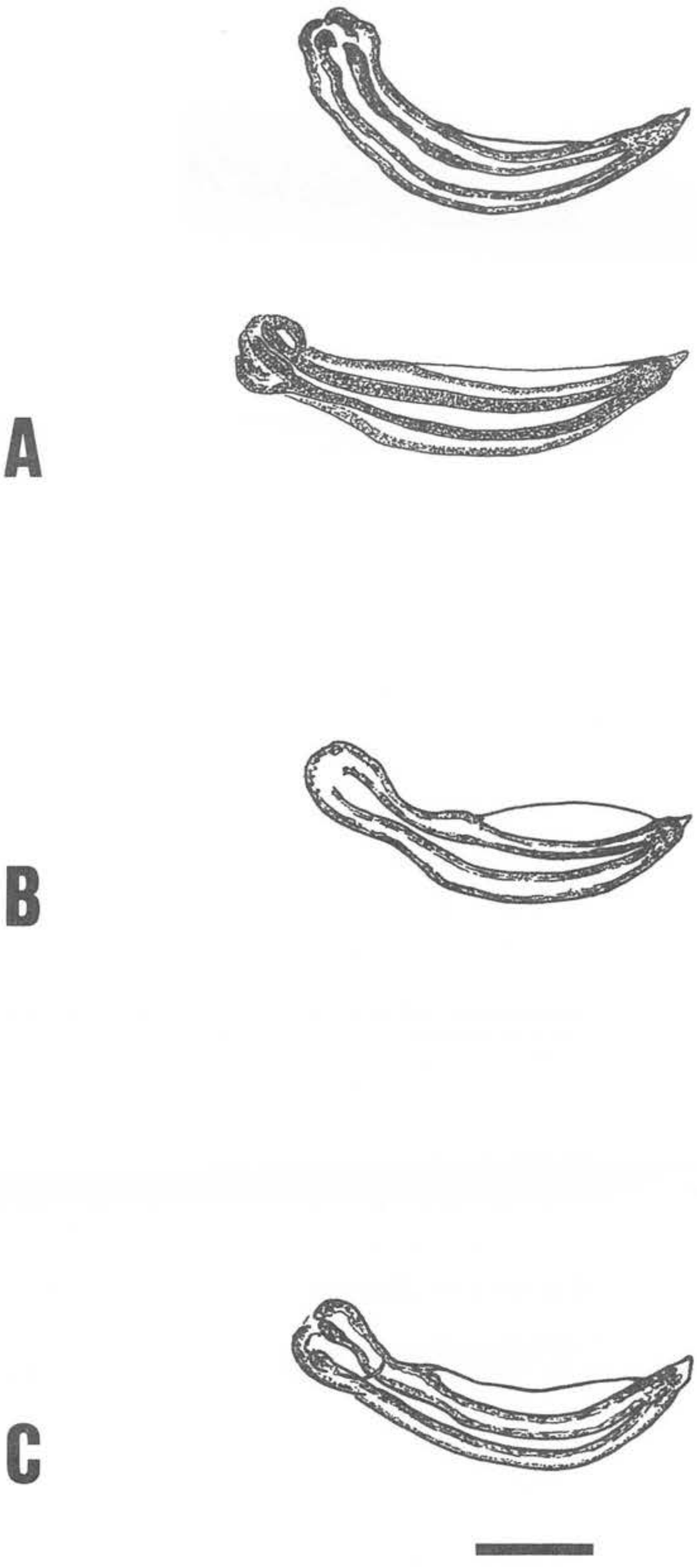


FIG.6:10. Categories of ventral membranes as determined by shape of ventral border: A. Straight; top - *Strongyloides westeri*, bottom - *Strongyloides stercoralis*; B. convex - *Strongyloides cebus* (from Little, 1966a); C. concave - *Strongyloides papillosus*. Scale line = 10μm.

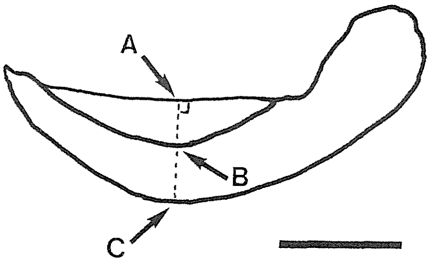


FIG.6:11. Technique for calculating prominence of ventral membrane : prominence = AB/AC %. Spicule of Kanabea *Strongyloides*. Scale = 10µm.

The prominence of the ventral membrane is also useful. Little (1966a&b) used the terms "prominent", "not prominent", "inconspicuous" and "narrow". The terms were not defined and "narrow" and "inconspicuous" were used interchangeably. A quantitative measure of the prominence of the ventral membrane can be obtained by drawing a line from the ventral border of the membrane at its widest point perpendicular to the membrane or its tangent across the spicule (Fig.6:11). The distance from this midpoint to the point of intersection of the line with the dorsal border of the membrane divided by the distance from the midpoint to the point of intersection with the dorsal border of the spicule is expressed as a percentage (Table 6:2). Narrow or inconspicuous membranes are less than 20%. There is good agreement with Little's description except for *S.gulae* which has a ratio of 29.8% and was classed as "not prominent".

The ventral membrane is a reliable criterion, but detectability is variable. It cannot be clearly seen in all specimens, but in good specimens can be detected in about 40%.

The most common combination of features is a slightly-moderately curved spicule, with a sharply pointed tip and a prominent ventral membrane with a straight edge. Spicule shape

TABLE 6:2. Features of spicules of free-living males.

SPECIES	TYPE of TIP	PROMINENCE of MEMBRANE Qualitative	Quantitative (%)	TYPE of EDGE	CURVATURE
S.cati	pointed	prominent	40.0	straight	sl-moderate
S.cebus	pointed	prominent	32.0	convex	sl-moderate
S.dasypodis	pointed	prominent	29.4	straight	sl-moderate
S.felis	pointed	inconspicuous	25.0	straight	sl-moderate
S.fuelleborni	pointed	prominent	29.1	straight	sl-moderate
S.gulae	pointed	prominent	29.8	straight	sl-moderate
S.lutrae	pointed	prominent	35.0	straight	sl-moderate
S.myopotami	pointed	prominent	40.0	straight	sl-moderate
S.papillosus	pointed	prominent	35.0	concave	marked[3]
S.physali	pointed	prominent	37.5	straight	sl-moderate
S.procyonis	pointed	inconspicuous	16.0	straight	sl-moderate
S.stercoralis	pointed	inconspicuous	17.6	straight	sl-moderate
S.suis	pointed	prominent	36.3	straight	sl-moderate
S.venezuelensis	pointed	prominent	38.2	straight	sl-moderate
S.westeri	pointed	inconspicuous	15.0	straight	marked[3]
Kanabea *Strongyloides*	pointed	prominent	36.5	straight	sl-moderate
S.serpentis	hooked	prominent	35.0	convex	straight[1]

1. Little (1966a,b) 2. Rogers (1939) 3. this thesis

therefore, is a useful criterion, and in some species the combination of the three major features will be unique, e.g. *S.cebus*. Table 6:2 lists the key features of spicules of fully described species.

6.3.2 Gubernaculum.

The shape of the gubernaculum in all species of *Strongyloides*, with one exception, *S.serpentis*, is fairly uniform (Fig.6:12). There are differences between species, but these are difficult to express and communicate. The features of the posterior half of the ventral border should not be used since this lies between the spicules and is hidden by them in many cases. The same applies to the ventral corner of the posterior pole, leaving the anterior pole, the dorsal border and dorsal aspects of the posterior pole to be considered. The shape of the wings in lateral view varies somewhat depending on which optical place is used for assessment. The dorsal border is always convex except in *S.serpentis*, which has a straight border. The dorsal pole seems to show slight differences between species in terms of prominence. There is however, intraspecific variation in the dorsal pole, some are rounded while others are almost pointed.

It is difficult to precisely define the limits of a particular species. This latter aspect becomes obvious when one tries to distinguish between the gubernacula of closely related species such as *S.stercoralis*, *S.procyonis* and *S.felis*. The gubernacula look slightly different, but not different enough to be able to confidently identify one or other of the species from the gubernaculum alone.

The percentage of width of gubernaculum to length was examined

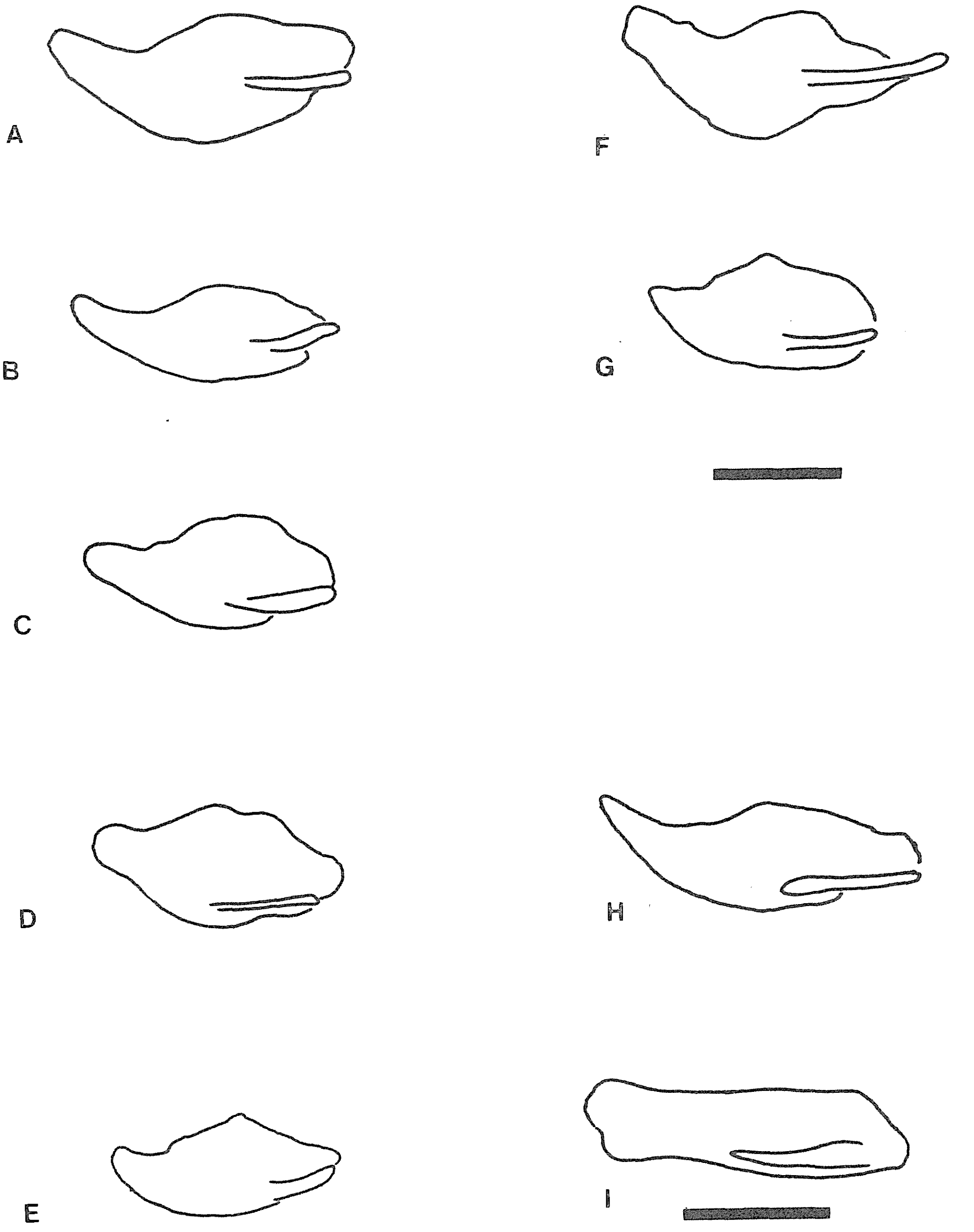


FIG. 6:12.
Gubernacula of free-living males:
A. *Strongyloides stercoralis;* B. *Strongyloides felis;*
C. *Strongyloides fuelleborni;* D. *Strongyloides suis;*
E. *Strongyloides papillosus;* F. *Strongyloides westeri;*
G. *Strongyloides venezuelensis;* H. *Strongyloides gulae;*
I. *Strongyloides serpentis.* Scale lines = 10µm;
larger scale refers to H & I.

(Table 6:3). Most species fall between 30 and 45%. Values useful in separating the ends of the spectrum from the greater number of species are less than 30% and greater than 50%.

The shape of the gubernaculum is, therefore, useful in separating out some species, but will not distinguish between the majority.

6.3.3 Caudal Papillae.

The positions of caudal papillae (Fig.2:15) can be used for speciation (Little, 1966a&b). Their positions are referred to key points; e.g., the subventral preanal papilla to the preanal organ, the postanal papillae to the cloaca and each other. The positions of the adanal papillae to the cloaca and the position of the lateral papilla seem to be of little value. The triad of subventral preanal and adanal papillae are of value in terms of their positions in the longitudinal plane.

The subventral preanal and its relationship to the preanal organ can be used (Fig.6:13). The papilla may be found anterior, as in *S.serpentis*, level with as in *S.papillosus*, or posterior as in most species. The distance of the subventral postanal from the cloaca is not a useful trait, but the distance between subventral postanal and subdorsal postanal can be used to separate some species. The distance of the preanal organ from the cloaca can be used to distinguish between some species e.g. *S.felis* and *S.stercoralis*.

A very useful feature is the longitudinal allignment of the subventral preanal and the two adanal papillae. Most species have these three papillae in the same longitudinal line, so that when one

TABLE 6:3. Features of the gubernacula of free-living males.

SPECIES	LENGTH (μm)	WIDTH (μm)	W/L (%)	DORSAL BORDER	REFERENCE
S.cati	24.5	10.0	40.8	straight	Rogers (1939)
S.cebus	23.3	8.3	35.7	curved	Little (1966a)
S.dasypodis	24.9	8.3	33.5	curved	Little (1966b)
S.felis	24.5	9.1	37.1	curved	this thesis
S.fuelleborni	23.3	7.5	32.2	curved	Little (1966a)
S.gulae	20.0	7.9	39.6	curved	Little (1966b)
S.lutrae	19.2	8.7	45.6	curved	Little (1966b)
S.myopotami	19.2	10.8	56.3	curved	Little (1966a)
S.papillosus	19.4	8.6	44.3	curved	this thesis
S.physali	15.0	5.4	36.0	curved	Little (1966b)
S.procyonis	24.2	9.2	38.0	curved	Little (1966b)
S.serpentis	16.7	4.6	27.5	straight	Little (1966b)
S.stercoralis	23.3	7.5	32.2	curved	Little (1966a)
S.suis	20.3	10.3	50.8	curved	this thesis
S.venezuelensis	15.8	7.1	44.7	curved	Little (1966a)
S.westeri	26.4	10.8	40.9	curved	this thesis

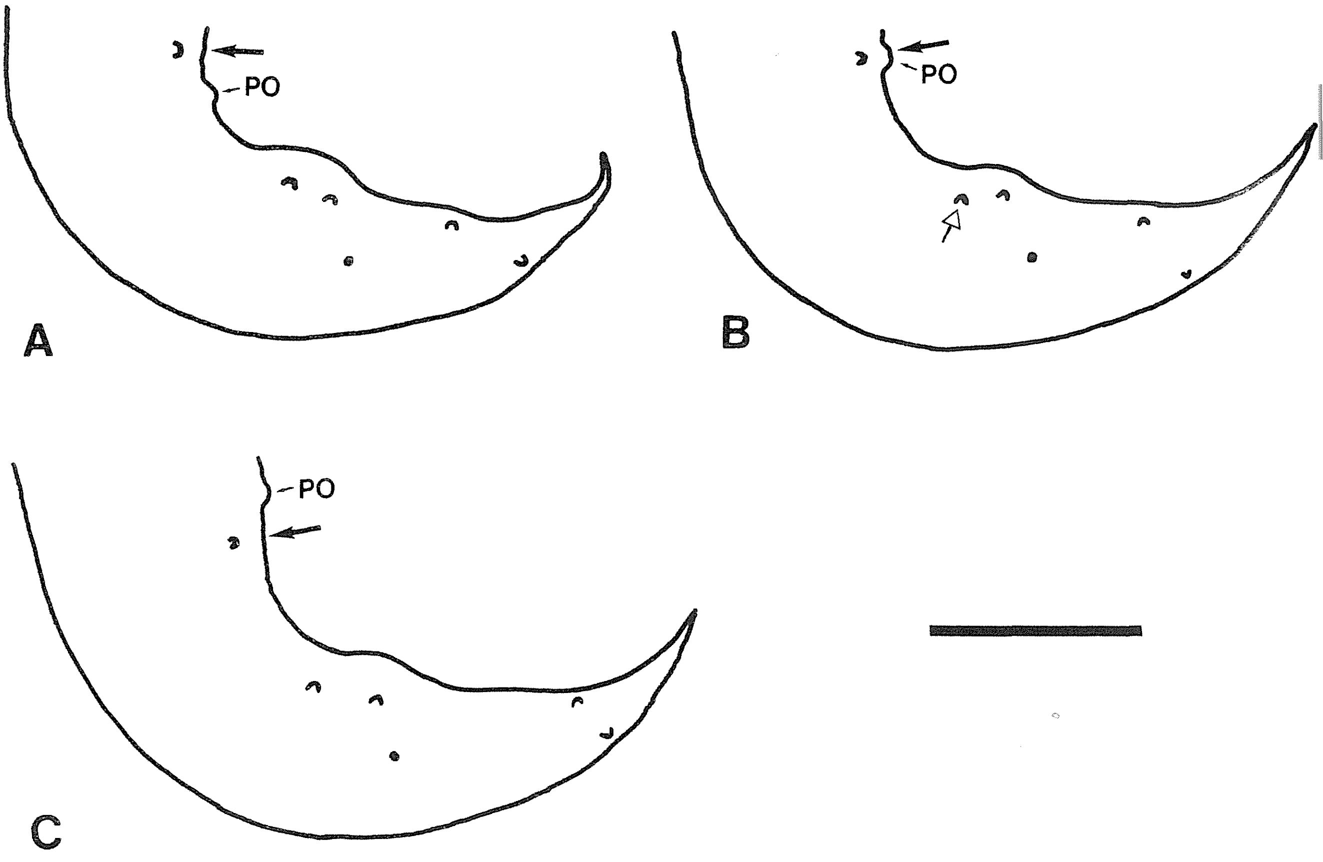


FIG.6:13. Positions of Subventral preanal papillae in relation to preanal organ: A. anterior to - *Strongyloides serpentis*; B. level with - *Strongyloides papillosus*; C. posterior to - *Strongyloides stercoralis*. Solid arrows mark positions of SPA; open arrow indicates dorsal displacement of AD1 from line of SPA, AD1 & AD2. Scale line = 30 μm.

is in focus in an optical plane so are the other two. In *S.westeri* the posterior adanal papillae is more ventrally placed, i.e., closer to the cloaca, and consequently not in the same optical plane as the other two, while with *S.fuelleborni*, *S.papillosus*, *S.suis*, *S.venezuelensis* and the *Strongyloides* from PNG the anterior adanal papillae is dorsally displaced from the line of the subventral preanal and the posterior adanal papillae.

The reliabilities of the positions of caudal papillae are good, being least for the relationship of the postanal pair. The subventral preanal papilla varies to a moderate extent in any species. Consequently, if, for example, in a particular species, it is level with the preanal organ, in some specimens it will be found exactly level; in others it will be slightly anterior; while in others it will be just posterior, but always close to the preanal organ.

The relationships of the caudal papillae are major criteria. The greatest emphasis is placed on the longitudinal allignment of the subventral preanal and the two adanals, with the position of the subventral preanal with respect to the preanal organ, the separation of the two postanals, and finally the distance of the preanal organ from the cloaca also being useful features.

6.3.4 Pericloacal Bulge.

The free-living male of *S.gulae* has the cloaca on a prominent ventral expansion (Fig.6:14). This is unique, and is a useful feature for differentiating this species from others (Little, 1966b).

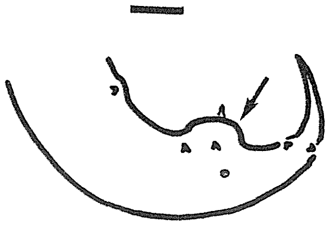


FIG.6:14. Pericloacal bulge of free-living male of *Strongyloides gulae* (from Little, 1966a). Scale = 20µm.

6.4 FREE-LIVING FEMALE

Uniformity of morphology is the norm for the free-living female. Only two features are of use in distinguishing between species, and both are in the region of the vulva.

6.4.1 Post-Vulval Narrowing.

Some species have a uniform body diameter, anterior to as well as posterior to the vulva. Others show a reduction immediately posterior to the vulva (Fig.6:15). Of this latter group, two species, *S.fuelleborni* and *S.felis* have females with a marked reduction in diameter, while in others, e.g. *S.stercoralis*, the narrowing is present but is less. These latter species have reductions of over 15% in diameter, while the change in diameter in species with a lesser degree of narrowing is usually less than 10%. The main criticism of this character has been on the basis of reliability.

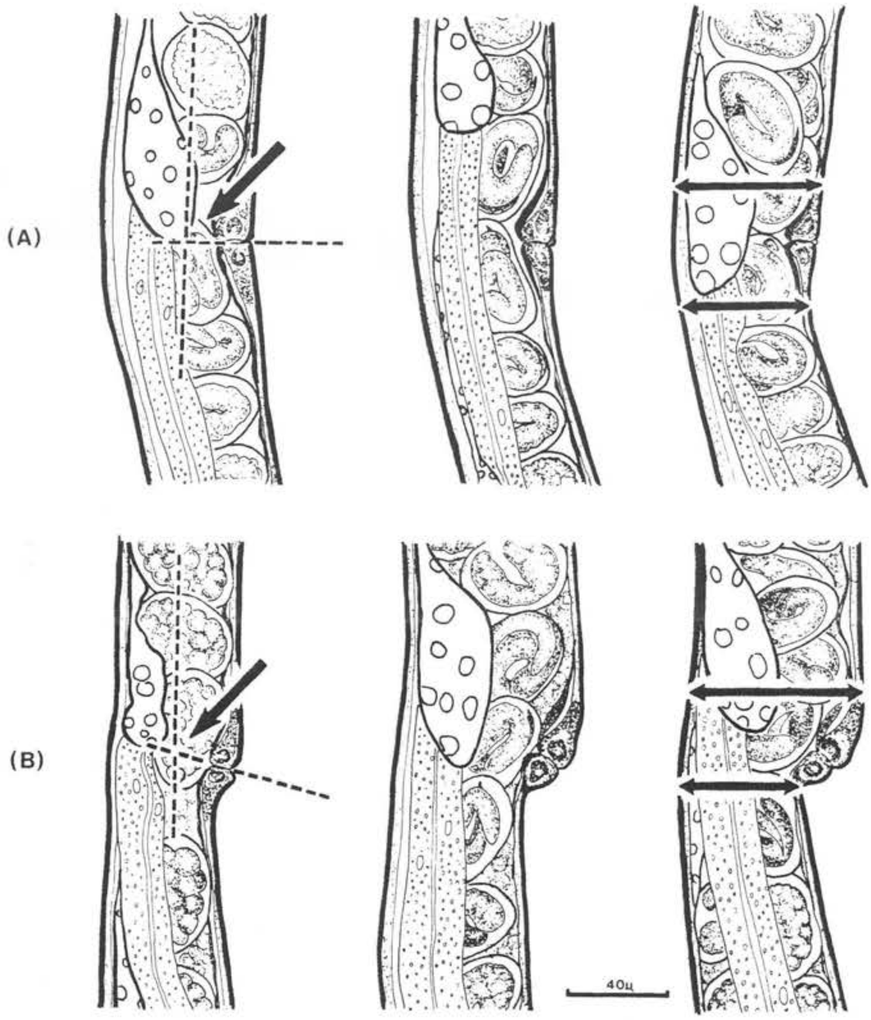


FIG.6:15. Postvulval narrowing and posterior rotation of the vulva in free-living female. Extent of narrowing is calculated by measuring across points before and after vulva as shown by double-headed arrows. Angle of vagina with longitudinal axis of anterior half of body is measured as shown. A. *Strongyloides stercoralis*; B. *Strongyloides fuelleborni*.

Premvati (1958) demonstrated that in *S.fuelleborni* the post-vulval narrowing was capable of variation in response to the external environment. In my own studies on *S.felis* the character was not affected significantly by temperature as had been *S.fuelleborni*. It is a major criterion with very good reliability in the case of *S.felis*, but perhaps less so for *S.fuelleborni*. It is easily determined.

6.4.2 Rotation of the Vulva.

In lateral view the angle formed by the vulval slit or the very short vagina with the long axis of the anterior half of the body (Fig.6:15) is a useful feature for differentiation. In most species the angle is 90 to 100°, but in *S.fuelleborni* and *S.felis* it is over 100°. The vulva has the appearance of being rotated in the posterior direction. This was a consistent feature in all *S.felis* (approximately 250) and in the 30 *S.fuelleborni* examined. Posterior rotation of the vulva was not seen in specimens of any other species. It is independent of the post-vulval constriction, and is a major criterion.

6.5 DIMENSIONS AND PROPORTIONS.

Many authors have relied heavily on measurements and proportions of various stages of *Strongyloides* to differentiate species due to a superficial assessment of morphological features. Those species descriptions in which mensuration has played a major role have been mainly generic, with occasionally no key feature relevent to that species being presented (Travassos, 1930a,b; Mirza and Narayan, 1935; Pereira, 1935; Chandler, 1941; Perez Vigueras, 1942; Kurtieva, 1953). Table 6:4 lists the dimensions and proportions that have been used as significant for species diagnosis. An assessment of their reliability is presented as well as a comment on their usefulness or significance.

Some features can be rejected on the grounds of poor reliability. The variation in specimens from the same source, e.g.,

TABLE 6:4. Dimensions and proportions used in literature to differentiate species of *Strongyloides* and assessment of reliability and usefulness.

PARASITIC FEMALE	RELIABILITY	COMMENT
Body length	average	major criterion
Maximum width	average	minor criterion
Oes.length	average	minor criterion
Tail length	average	minor criterion
Mouth-vulva	average	generic character
Vulva-tail	average	generic character
ARO-post.oes	poor	too variable
PRO-anus	poor	too variable
No.of eggs in utero	poor	variable
Egg size	good	minor criterion
Oes./body length %	good	minor criterion
M-V/body length %	good	generic character
Tail/body length %	good	minor criterion
FREE-LIVING ADULTS		
Body length	average	minor criterion
Oes.length	average	minor criterion
Tail length	average	minor criterion
Oes./length %	average	minor criterion
Tail/length %	average	minor criterion
FREE-LIVING MALE		
Spicule length	good	minor criterion
Spicule length / body length %	good	minor criterion
FREE-LIVING FEMALE		
M-V	average	generic character
M-V/length %	good	generic character
INFECTIVE LARVAE		
Body length	average	minor criterion

an individual host or the same faecal culture, can be assessed by calculation of the coefficient of variation (CV), where CV = mean / S.D. %. A reliable feature has a CV of 10% or less. ARO-oes and PRO-anus often have CV greater than 10%. In some species so do distances from the distal ends of the ovaries to the vulva, while in other species this feature has a good reliability. When populations from different sources are compared the CV of these features increase markedly. ARO-oes and PRO-anus have been used as a significant criterion in species from birds (Travassos, 1930a&b; Perez Vigueras, 1942; Kurtieva, 1953; Boyd, 1966&67). The variation is so great however, that they are unreliable.

6.5.1 Body Length.

The only measurable feature which is a major criterion is the body length of the parasitic female (Table 6:4). It is useful to place parasitic females into three categories: small, medium and large, where small = less than 2.0mm, medium = 2.0 to 5.0mm, and large = greater than 5.0mm (Table 6:5). The limits of the categories are not rigid, but are approximate only, those species with their means close to the border of one category and with a significant portion of their range in the other, are placed in the category in which their mean falls.

TABLE 6:5. Classification of parasitic females by size.

SMALL		
S.akbari	*S.minimum*	
S.amphibiophilus	*S.pereiri*	
S.ardeae	*S.physali*	
S.bufonis	*S.quiscali*	
S.carinii	*S.spiralis*	
S.darevskyi	*S.turkmenica*	
MEDIUM		
S.avium	*S.herodiae*	*S.ratti* v.ondatrae
S.cati	**S.lutrae*	*S.rostombekowi*
S.cebus	*S.martis*	*S.serpentis*
S.chapini	*S.mustelorum*	*S.sigmodontis*
S.cruzi	*S.myopotami*	*S.stercoralis*
S.cubaensis	*S.nasua*	*S.stercoralis* v.vulpi
**S.dasypodis*	*S.ophidae*	*S.suis*
S.elephantis	*S.oswaldi*	*S.thylacis*
S.eryxi	*S.pavonis*	*S.tumefaciens*
S.felis	*S.procyonis*	*S.venezuelensis*
S.fuelleborni	*S.putorii*	
S.gulae	*S.ratti*	
LARGE		
**S.agoutii*	**S.robustus*	
S.erschowi	*S.westeri*	
**S.papillosus*		

(Small = body length < 2.0mm; medium = body length between 2.0 and 5.0mm; large = body length > 5.0mm. * = about half of range in other category but mean in category indicated.)

Body length has been used in some species descriptions as the only specific character. *Strongyloides akbari* was described as the small est species (Mirza and Narayan, 1935); *S.ratti v. ondatrae* was reported to look like *S.ratti* but to be larger and more slender (Chandler, 1941); while *S.robustus* was "larger than *S.ratti*" (Chandler, 1942). In all cases, the descriptions were inadequate, key taxonomic features being absent. The use of body length as the only major feature for differentiating species of *Strongyloides* is usually an indication of incompetence on the part of the parasitologist concerned, and should serve to alert one to the fact that the species description is inadequate or that the identification is of dubious accuracy.

An excellent example of this is *S.akbari*. This species was described from the shrew, *Crocidura coerulea*, a Soricidae (although the common name of the host was given as "musk rat"). Mirza and Narayan (1935) gave it the distinction of being the smallest species of *Strongyloides*, with a body length of 1408.5μm. The only other record of *S.akbari* (Srivistava, 1964), used body length as the only criteria to identify as *S.akbari* a specimen from a new host, the honey badger, *Mellivora indica*, a Mustelidae. Although his specimen measured 1530μm, Srivastava apparently ignored the existence of *S.carinii* and *S.minimum* whose body lengths were smaller than his specimen. If body length was Srivistava's major criteria, the latter two species were closer to his specimen than *S.akbari*. The record of *S.akbari* in *M.indica* is unfounded.

Another example of the misuse of body length in the identification of specimens is a report of *S.westeri* in pigs by Miyamoto (1929). In the small intestine of pigs from Taiwan he found some parasitic females with lengths of 9mm. These values are outside the normal range of *S.suis* (syn.*S.papillosus*), which he also recovered, but were similar to those of *S.westeri*, previously reported only from Equidae. Using size as the only criterion, Miyamoto tentatively identified the specimens as *S.westeri*. Georgi (1984), in a review of strongyloidiasis, listed *S.westeri* as occurring in pigs, but failed to cite the original source, which was in fact Galliard (1951) (Georgi, pers.comm. 1985). Miyamoto (1929) was the only original record found. Three attempts by me to experimentally infect pigs with *S.westeri* were unsuccessful. Thus the host record is unfounded.

The variation of body length within species can be great. Body length can be influenced by forces outside the genetics of the parasite. The immune response of the host has been shown to reduce body size (see Chap.5.3.3). The species of the host also has an effect on body length. A strain of *S.papillosus* originally collected from a goat was used to infect a lamb, a rabbit and a piglet.

TABLE 6:6. Effect of species of host on dimensions of parasitic female of *Strongyloides papillosus*.
(Experiment Chap.4.3.5)

PARAMETER	GOAT	SHEEP	PIG	RABBIT
length	5401.5±792.2	5709.8±321.9	4789.8±352.7	3979.9±406.1
(μm)	(4251-6871)	(5162-6231)	(4363-5281)	(3425-4751)
width	61.1±5.0	62.3±2.1	51.3±3.1	48.6±3.1
(μm)	(52.1-66.7)	(52.1-64.6)	(45.9-56.3)	(43.8-54.2)
oes	952.1±47.3	864.3±94.2	802.4±44.6	906.4±91.9
(μm)	(896-1017)	(615-952)	(740-867)	(763-1032)
M-V	3189.6±435.7	3527.9±204.3	3093.3±205.8	2580.4±249.7
(μm)	(2704-4088)	(3160-3846)	(2829-3425)	(2270-2783)
tail	59.6±8.8	63.0±7.5	53.0±5.8	58.4±4.6
(μm)	(50.0-73.0)	(50.0-75.0)	(47.9-66.7)	(50.0-66.7)
oes/length	17.9±2.0	15.1±1.4	16.8±1.0	23.0±3.0
(%)	(14.8-21.1)	(11.9-16.5)	(15.5-18.2)	(16.1-26.0)
M-V/length	59.2±2.1	61.8±1.1	64.6±1.9	64.9±1.6
(%)	(56.9-63.6)	(60.7-63.4)	(61.5-67.6)	(62.3-66.7)
tail/length	1.13±0.17	1.10±0.09	1.11±0.12	1.47±0.08
(%)	(0.81-1.32)	(0.97-1.2)	(0.92-1.28)	(1.40-1.59)
eggs/worm	14.3±2.1	28.6±2.6	13.6±3.7	4.1±2.7
	(11-17)	(24-32)	(8-19)	(0-8)
egg size				
length	53.6±3.7	53.6±2.3	53.8±2.6	51.5±1.9
(μm)	(45.9-58.4)	(50.0-56.3)	(51.2-56.3)	(47.9-54.2)
width	33.4±1.0	30.0±2.1	31.8±2.3	29.8±1.5
(μm)	(31.3-35.4)	(27.1-33.4)	(28.2-33.3)	(29.2-33.4)
prepatent period (days)	-	13-16	11-14	11-14

Morphology was not affected by the species of host, but dimensions varied both in absolute and relative terms (Table 6:6). The effect on body length was not so great, however, as to place *S.papillosus* into a different category. This would have been a problem if its average length was near the lower limit of its category.

6.5.2 Body Width.

Body width has rarely been used for speciation. Chandler (1941) stated *S.ratti* v.*ondatrae* was "more slender" than *S.ratti*. In absolute terms this is not correct, both have average maximum diameters of 33 and 34μm respectively (Table 2:1). The width/length percentage is, however, 0.82% for *S.ratti* v.*ondatrae* and 1.43% for *S.ratti*, making the width to length less for the former, and causing the "slender" appearance. The large body diameter of *S.tumefaciens* has already been mentioned (Chap.5.3.1.1). This was an artifact due to squashing of specimens.

Apart from the examples given above body width has not been used as a taxonomic criteria. It shows a significant correlation with body length (R 0.580, R^2 0.336, sig.<0.001). It would therefore be expected to be of no more value than body length.

6.5.3 Width-Length Percent.

There is no correlation between length and width/length % (R -0.0356, R^2 0.00127, sig.0.402). This means the width/length % values are a function of the species, not of the genus, as for example is M-V/length % (see Chap.2.2.1.2). In theory width/length % combined with total length could be of use in distinguishing between particular species. It would be a minor criterion. In practice no example of its use in this way is available.

6.5.4 Use of Measurable Features.

Measurable features are used in practice as a way of distinguishing between specimens which cannot be separated on morphological grounds. The morphological assessment is made initially and carries more weight. Examples of use of measurable features in this way are provided by Little (1966b). The first example was to separate two species of *Strongyloides* found as concurrent infections in snakes. The parasitic females were morphologically similar, both were in the medium size category, but the differences in their body lengths were significant. Other features which differed were the tail/length % and length of the egg of the parasitic female. Unfortunately, the differences were not expressed statistically. These two species, *S.gulae* and *S.serpentis*, were subsequently found to have quite distinct free-living males, thus confirming the value of mensuration in this case as a taxonomic tool (Little, 1966b).

The second case was use of dimensions and proportions to separate two morphological identical species, *S.procyonis* and *S.stercoralis*. Statistically different values in the parasitic females were body length, maximum width, oesophageal length, width/length % and oes/length %. In the free-living male body length, oesophageal length, tail length, spicule length, oes/length %, tail/length % and spicule/length % were statistically different, while in the free-living female body length, oesophageal length and oes/length % were significant. Biological evidence supported Little's conclusion that the two species were distinct. *S.procyonis*, found commonly in raccoons, produced only a transient infection in a human volunteer. Little (1966b) recorded the number of specimens on which the statistics were based, but failed to comment on how many sources the parasites came from and what the variation was between sources. This aspect needs to be investigated when statistical methods are used to separate species. Little's action in proposing a separate species from the raccoon was justified, but a more comprehensive statistically and biological study is required to confirm the separation.

The role of dimensions and proportions in the differentiation of species is a minor one. In practice mensuration can be used to separate morphologically similar species, but it could similarly be used to separate specimens of the same species derived from different sources. Before mensuration is used to demarcate a particular species, a comprehensive study using specimens of the species concerned derived from many sources is required. This has not been done for any of the species for which dimensions and proportions have been used as a final means of differentiation.

6.6 STAGE IN FAECES.

As there are only three options, eggs , larvae, or both, for this criterion, uniqueness is limited. It is a reliable criterion as long as freshly collected faeces are used. Most species with only eggs in faeces have the embryo in the morula or tadpole stage when passed and hatching may occur within 24hr depending on the temperature. Those with both eggs and larvae, usually have eggs with well developed larvae and hatching occurs within hours. Eggs containing a morula usually take at least 24hr to hatch. Those species with larvae in faeces usually have first-stage larvae, except for autoinfective larvae. Finding autoinfective larvae presently identifies the species as either *S.stercoralis* or *S.felis*, since these larvae have been found only in these species. Autoinfective larvae have not been reported previously for *S.felis*.

This is a major criterion with good reliablity. The literature contains three reports which indicate otherwise. In the original description of *S.fuelleborni* von Linstow (1905) stated only larvae were found in faeces. In the same paper he said *S.stercoralis* had only eggs. These were both errors; no further workers have confirmed his observations. Faust (1930) experimentally infected a spider monkey, *Ateles geoffroyi*, with a human strain of *Strongyloides*, presumable *S.stercoralis*, although few taxonomic details were given. After 27 days the monkey passed eggs in faeces for 2 weeks. No larvae, as would have been expected for *S.stercoralis*, were found in faeces. It is possible the monkey was already infected with *S.cebus*, found in South American non-human primates (Little 1966a), or that the human strain used for the infection was not *S.stercoralis*. Faust (1930) failed to make much of the discrepancy. Similarly Strong (1901b) claimed to have experimentally infected a "monkey" with *S.stercoralis*. He noted eggs in faeces, although also recording natural infections with *Strongyloides* in other wild "monkeys". Since Strong was working in the Philippines he may have been dealing with *Macaca irus*, but this is the only clue to the identity of the host. These experimental infections by both workers were not clearly described, and are open to the criticism that the monkeys may have been previously naturally infected by a *Strongyloides* which has eggs in faeces.

Since no convincing evidence to the contrary is available, the stage in the faeces is regarded as a reliable criterion. Development of the embryo or larvae must be arrested if faeces are not examined immediately. Hot 10% BNF is suitable for this. If this is not done, eggs may hatch. The stage in faeces may be hard to determine if parasite numbers are low; e.g., this criterion was not determined for *S.ardeae* since the intensity of infection was low. It is a major criterion.

6.7 SITE IN HOST.

The site of the parasitic female in the host is too variable to be of use as a major criterion. Individual species do tend to occupy specific niches, usually in a longitudinal direction down the gut, but a radial separation has also been documented for *S.ratti* and *S.venezuensis* (Wertheim, 1970). The site is subject to outside forces, and occasionally varies for no apparent reason. The host immune response has been shown to be responsible for a posterior migration in the small intestine for *S.ratti* in lab rats (Moqbel and Denham, 1977). Fig 5:14 illustrates this for *S.ratti*. Increase in parasite numbers leads to less prefered niches in the gut being occupied. In an experimental hyperinfective syndrome in white handed gibbons, *Hylobates lar*, parasitic females of *S.stercoralis* were found in stomach, small intestine and large intestine (de Pauli, 1974). In lighter infections *S.stercoralis* is found in the anterior small intestine. Variation in site for no apparent reason was documented by Cram (1936) for *S.avium*. Infective larvae cultured from domestic fowls with a natural infection in the small intestine, give rise to parasitic adults in the caecum only. I found a species of *Strongyloides* from the green tree frog, *Litoria caerulea*, usually in the large intestine, but occasionally in both natural and experimental infections an individual parasite was found in the small intestine. In unusual hosts parasitic females may be found outside the gut, e.g., guinea pigs infected experimentally with *S.ratti*, had mature females in the lungs (Sheldon and Otto, 1938).

Most species do occupy a prefered region of the gut of the host, but this is subject to variation. It is a useful feature, but, if faced with a parasite that fulfils the major morphological criteria of a particular species, but occupies a different site in the host, one should not decide against the identification on the basis of differences in location.

6.8 HOST.

Table 6:7 is a host-parasite list for *Strongyloides*. Hosts are arranged alphabetically by class, order (for all classes except Aves), and then by family and genus. The binomial name used for the host is that currently accepted as valid. This aspect posed significant problems with some groups, e.g. primates and rodents. The authorities consulted were for primates, the series of monographs by Hill (1957-1970) and for rodents Ellerman (1940).

Invalid synonyms for the host used by the authors reporting the parasite are given in parenthesis. The specific name used for the *Strongyloides* is that considered valid in Chapter 3. Parasite synonyms used by the authors are also given in parentheses. INF refers to the type of infection; N = naturally acquired, E+ = patent experimental infection, E- = unsuccessful experimental infection. AC is the accuracy of the record assessed by data given in the publication, or, if inadequate details were provided, by reference to other records for the same parasite and host. G = good (important taxonomic details given and consistent with diagnosis); M= mediocre (lacks some important taxonomic details, but consistent with diagnosis); P = poor (no taxonomic details or insignificant details given, but consistent with other records); D = dubious (no taxonomic details given, inconsistent with other records or experimental evidence); I = incorrect (taxonomic details differ from those of the species diagnosed). Assessment of accuracy is subjective to some extent, but will enable incorrect and dubious records to be treated as such.

Table 6:8 is a *Strongyloides* sp - host list. Both lists are not exhaustive, but the occurrence of a particular species of *Strongyloides* in a particular species of host is included at least once. When more than one particular *Strongyloides* - particular host record existed, the first record and the records most of use from the taxonomic viewpoint were included. For records of *Strongyloides* sp. usually the first and the most current were chosen.

Additional symbols used in Tables 6:7 and 6:8 are:

* = my own new record

– = paper not sighted

TABLE 6:7. Host - *Strongyloides* list.
(see text for key)

FAMILY	HOST BINOMIAL	COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
AMPHIBIA						
Bufonidae	*Bufo marinus*	cane toad	*S.sp*	E-	★	
Bufonidae	*Bufo melanostictus*	toad	*S.bufonis*	N	Rao&Singh 1968,1954	M
Bufonidae	*Bufo peltocephalus*	toad	*S.amphibiophilus*	N	Perez Vigueras 1942	M
Bufonidae	*Bufo valiceps*	Weigman's toad	*S.physali*	N	Little 1966b	G
Hylidae	*Litoria caerulea*	green tree frog	*S.sp*	N+	★	
Hylidae	*Litoria lesueurii* (*Hyla lesueuri*)	Lesueur's frog	*S.sp*	N	Ballantyne 1971	M
Hylidae	*Litoria rubella*	desert tree frog	*S.sp*	E+	★	
Leptodactylidae	*Adelotus brevis*	tusked frog	*S.sp*	N	Ballantyne 1971	P
Leptodactylidae	*Leptodactylus gracilis*	frog	*S.carinii*	N	Pereira 1935	M
Leptodactylidae	*Limnodynastes peronii* (*Limnodynastes peroni*)	brown-striped frog	*S.sp*	N	Ballantyne 1971	M
Leptodactylidae	*Platypectron ornatus*	ornate burrowing frog	*S.sp*	N	★	
Ranidae	*Rana clamantans*	frog	*S.sp*	N	Little 1966b	P
Ranidae	*Rana esculenta*	edible frog	*S.sp*	N	Vojthova&Moravec 1977	M
Ranidae	*Rana esculenta*	edible frog	*S.spiralis*	N	Grabda-Kazubska 1978	G
Ranidae	*Rana lessonae*	edible frog	*S.spiralis*	N	Grabda-Kazubska 1978	G
Ranidae	*Rana pipens*	frog	*S.sp*	N	Rau et al 1978	-
Ranidae	*Rana ribidunda*	frog	*S.spiralis*	N	★	
		frog	*S.stercoralis*	E-	Sandground 1925	P
		frog	*S.stercoralis*	E+	Tessier 1896	D
		frog	*S.stercoralis*	N	Alfieri 1908	D
REPTILIA - SAURIA						
Agamidae	*Physignathus cocincinus*	green iguana	*S.sp*	N	Maier 1980	P
Lacertidae	*Lacerta armenica*	lizard	*S.darevskyi*	N	Shapilo 1976	M
Lacertidae	*Lacerta rostombekovi*	lizard	*S.darevskyi*	N	Shapilo 1976	M
Lacertidae	*Lacerta rudis*	lizard	*S.darevskyi*	N	Shapilo 1976	M
Lacertidae	*Lacerta saxicola*	lizard	*S.darevskyi*	N	Shapilo 1973	M
Lacertidae	*Lacerta saxicola*	lizard	*S.darevskyi*	N	Shapilo 1976	M
Scincidae	*Eumeces laticeps*	greater five-lined skink	*S.sp*	N	Little 1966b	P
Scincidae	*Tiliqua gerrardi*	pink-tongued lizard	*S.sp*	N	Ballantyne 1971	M
Scincidae	*Tiliqua scincoides*	blue-tongued lizard	*S.sp*	N	Ballantyne 1971	M

FAMILY	HOST BINOMIAL	COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
- SERPENTES						
Boidae	*Chondropython viridis*	green python	*S.mirzai*	N	Wiesman&Greve 1982	M
Boidae	*Eryx jaculus*	snake	*S.sp*	N	Baylis 1923	P
Boidae	*Eryx johnii*	snake	*S.eryxi*	N	Singh 1954	M
Boidae	*Eryx johnii*	snake	*S.eryxi*	N	Shapilo 1973	M
Boidae	*Eryx tataricus*	snake	*S.eryxi*	N	Shapilo 1973	M
Boidae	*Liasus fuscus*	water python	*S.sp*	E+	☆	
Boidae	*Morelia spilotes*	carpet snake	*S.sp*	N	☆	
Boidae	*Python reticulatus*	reticulated python	*S.sp*	N	Holt et al 1979	P
Colubridae	*Amphiesma mairii*	keelback	*S.sp*	N	Ballantyne 1971	M
Colubridae	*Boiga dendrophila*	mangrove snake	*S.sp*	N	Schmidt&Kuntz 1972	P
Colubidae	*Boiga irregularis*	brown tree snake	*S.sp*	N	☆	
Colubridae	*Coluber constrictor flaviventris*	blue racer	*S.gulae*	N	Little 1966b	G
Colubridae	*Coluber constrictor flaviventris*	blue racer	*S.serpentis*	N	Little, 1966b	G
Colubridae	*Coronella austriaca*	smooth snake	*S.mirzai*	N	Shapilo 1973	M
Colubridae	*Demansia atra*	black whipsnake	*S.sp*	N	☆	
Colubridae	*Dendrelaphis punctulatus*	common tree snake	*S.sp*	N	☆	
Colubridae	*Elaphe obsoleta obsoleta*	yellow rat snake	*S.sp*	N	Holt et al 1979	P
Colubridae	*Elaphe obsoleta quadrivittata*	grey rat snake	*S.sp*	N	Holt et al 1979	P
Colubridae	*Heterodon platyrhinos platyrhinos*	common hog-nosed snake	*S.gulae*	N	Little 1966b	G
Colubridae	*Heterodon platyrhinos platyrhinos*	common hog-nosed snake	*S.serpentis*	N	Little 1966b	G
Colubridae	*Lampropeltis getulis*	speckled king snake	*S.sp*	N	Holt et al 1978	P
Colubridae	*Lampropeltis getulis holbrooki*	speckled king snake	*S.gulae*	N	Little 1966b	G
Colubridae	*Lampropeltis getulis holbrooki*	speckled king snake	*S.serpentis*	N	Little 1966b	G
Colubridae	*Natrix cyclopion cyclopion*	green water snake	*S.gulae*	N	Little 1966b	G
Colubridae	*Natrix cyclopion cyclopion*	green water snake	*S.serpentis*	N	Little 1966b	G
Colubridae	*Natrix natrix*	grass snake	*S.eryxi*	N	Shapilo 1973	M
Colubridae	*Natrix sipedon confluens*	Mississippi River water snake	*S.gulae*	N	Little 1966b	G
Colubridae	*Natrix sipedon confluens*	Mississippi River water snake	*S.serpentis*	N	Little 1966b	G

FAMILY	HOST BINOMIAL	HOST COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
Colubridae	*Natrix taxispilota rhombifera*	diamondback water snake	*S.gulae*	N	Little 1966b	G
Colubridae	*Natrix taxispilota rhombifera*	diamondback water snake	*S.serpentis*	N	Little 1966b	G
Colubridae	*Natrix taxispilota taxispilota*	brown water snake	*S.gulae*	N	Little 1966b	G
Colubridae	*Natrix taxispilota taxispilota*	brown water snake	*S.serpentis*	N	Little 1966b	G
Crotalidae	*Trimeresurus fravoviridis*	yellow spotted lance head snake	*S.sp*	N	Hori&Kaneko 1969	P
Elapidae	*Naja naja atra*	Indian cobra	*S.sp*	N	Schmidt&Kuntz 1972	P
Elapidae	*Pseudonaja textilis*	brown snake	*S.sp*	N+	☆	
Viperidae	*Arkistrodon contortrix contortrix*	southern copperhead	*S.gulae*	N	Little 1966b	G
Viperidae	*Arkistrodon contortrix contortrix*	southern copperhead	*S.serpentis*	N	Little 1966b	G
Viperidae	*Arkistrodon piscovorus leucostoma*	cotton mouth moccasin	*S.gulae*	N	Little 1966b	G
Viperidae	*Arkistrodon piscovorus leucostoma*	cotton mouth moccasin	*S.serpentis*	N	Little 1966b	G
AVES						
Anatidae	*Anas platyrhyncha domestica*	domestic duck	*S.avium*	E-	Cram 1929	M
Anatidae	*Anas platyrhyncha domestica*	domestic duck	*S.pavonis*	E-	Sakamoto&Yamashita 1970	G
Anatidae	*Anas platyrhyncha domestica*	duck	*S.sp*	E-	☆	
Anatidae	*Anas platyrhynchos fulvigula*	Florida duck	*S.sp*	N	Kinsella&Forrester 1972	P
Anatidae	*Dafila bahamensis*		*S.minimum*	N	Travassos 1930b	P
Anatidae	*Malacorhynchus membranaceous*	pink eared duck	*S.sp*	N	Harrigan 1981	P
Aramidae	*Aramus gnarauna pictus*	limpkin	*S.avium*	N	Barus 1969	-
Ardeidae	*Ardea herodias herodias*	great blue heron	*S.herodiae* (*S.ardeae*)	N	Boyd 1966	M
Ardeidae	*Ardea herodias herodias*	great blue heron	*S.herodiae*	N	Boyd 1967	M
Ardeidae	*Butorides virescens maculatus*	heron	*S.cubaensis*	N	Perez Vigueras 1942	M
Ardeidae	*Butorides virescens virescens*	eastern green heron	*S.ardeae*	N	Little 1966b	M
Ardeidae	*Nyctanassa violacea*	yellow crowned night heron	*S.ardeae*	N	Little 1966b	M
Columbidae	*Columba livia*	domestic pigeon	*S.pavonis*	E-	Sakamoto&Yamashita 1970	G
Columbidae	*Columba livia*	domestic pigeon	*S.sp*	E-	☆	
Cuculidae	*Centropus phasianinus*	pheasant coucal	*S.sp*	N	☆	

FAMILY	HOST BINOMIAL	COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
Gruidae	*Grus canadensis*	greater sandhill crane	*S.sp*	N	Forrester et al 1974	P
Icteridae	*Agelaius phoeniceus*	red-winged blackbird	*S.sp*	N	Little 1966b	P
Icteridae	*Quiscalus niger caribaeus*	?	*S.quiscali*	N	Barus 1968	M
Laridae	*Larus canus*	common gull	*S.turkmenica* (*S.turkmenicus*)	N	Barus et al 1978	M
Meleagrididae	*Meleagris gallapavo*	turkey	*S.avium*	E+	Cram 1931	M
Meleagrididae	*Meleagris gallopavo*	wild turkey	*S.avium*	N	Maxfield et al 1963	P
Meleagrididae	*Meleagris gallopavo osceola*	wild turkey	*S.sp*	N	How et al 1975	P
Meleagrididae	*Meleagris gallopavo silvestris*	wild turkey	*S.sp*	N	Prestwood 1968	P
Numididae	*Numida meleagridis galeata*	grey-breasted helmeted guinea fowl	*S.avium*	N	Fabiyi 1972	P
Phasianidae	*Colinus virginianus*	bob white quail	*S.avium*	N	Davidson et al 1980	P
Phasianidae	*Colinus virginianus*	bob white quail	*S.avium*	N	Cram 1929	P
Phasianidae	*Coturnix coturnix japonica*	Japanese quail	*S.pavonis*	E−	Sakamoto&Yamashita 1970	G
Phasianidae	*Gallus gallus*	domestic fowl	*S.avium*	N	Cram 1929	M
Phasianidae	*Gallus gallus* (*Gallus domesticus*)	domestic fowl	*S.oswaldi*	N	Travassos 1930a	M
Phasianidae	*Gallus gallus*	domestic fowl	*S.papillosus*	E−	Schwartz&Alicata 1930	P
Phasianidae	*Gallus gallus*	domestic fowl	*S.papillosus*	N	Krijgsman 1933	D
Phasianidae	*Gallus gallus*	domestic fowl	*S.pavonis*	E+	Sakamoto&Yamashita 1970	G
Phasianidae	*Gallus gallus*	domestic fowl	*S.pavonis*	E+	Sakamoto et al 1981	G
Phasianidae	*Gallus gallus*	domestic fowl	*S.suis* (*S.ransomi*)	E−	Schwartz&Alicata 1930	M
Phasianidae	*Gallus gallus*	domestic fowl	*S.sp*	N+	☆	
Phasianidae	*Pavo cristatus cristatus*	Indian peafowl	*S.pavonis*	E+	Sakamoto&Yamashita 1970	G
Phasianidae	*Pavo muticus*	green peacock	*S.pavonis*	N+	Sakamoto&Yamashita 1970	G
Pleocididae	*Paser montanus kaibatoi*	Japanese tree sparrow	*S.pavonis*	E−	Sakamoto&Yamashita 1970	G
Rallidae	*Fulica americana*	American coot	*S.avium*	N	Cram 1930	P
Rallidae	*Fulica americana*	American coot	*S.sp*	N	Kinsella 1973	P
Rallidae	*Fulica atra*	coot	*S.sp*	N	☆	
Rallidae	*Gallinula chloropus*	common gallinule	*S.avium*	N	Barus 1969	−
Rallidae	*Gallinula chloropus*	common gallinule	*S.sp*	N	Dollfus et al 1961	P
Rallidae	*Junco hyemalis hyemalis*	junco	*S.avium*	N	Cram 1930	P
Rallidae	*Porphyrio porphyrio*	swamphen	*S.sp*	N	☆	
Rallidae	*Porphyrula martinica*	purple gallinule	*S.sp*	N	Kinsella et al 1973	P
Rallidae	*Rallus aquaticus indicus*	eastern water rail	*S.avium*	N	Sakamoto&Sarashina 1968	I
Recurvirostridae	*Himantopus candidus*	stilt	*S.turkmenica*	N	Kurtieva 1953	M
Tetraonidae	*Bonasa umbellus*	ruffed grouse	*S.avium*	E+	Cram 1930	M
Tetraonidae	*Bonasa umbellus*	ruffed grouse	*S.sp*	N	Davidson et al 1977	P
Threskiornithidae	*Eudocimus albus*	white ibis	*S.sp*	N	Bush&Forrester 1976	P

FAMILY	HOST BINOMIAL	 COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
MAMMALIA - ARTIODACTYLA						
Antilocapridae	*Antilocapra americana*	prong-horned antelope	*S.papillosus* (*S.ovocinctus*)	N	Ransom 1911	M
Antilocapridae	*Antilocapra americana*	prong-horned antelope	*S.papillosus*	N	Sandground 1925	M
Bovidae	*Aepyceros melampus*	impala	*S.papillosus*	N	Round 1968	P
Bovidae	*Aepyceros melampus*	impala	*S.sp*	N	Horak 1980	P
Bovidae	*Ammotragus lervia*	Barbary sheep	*S.papillosus*	N	Tilc&Hanuskova 1976	P
Bovidae	*Antidorcas marsupialis*	springbok	*S.papillosus*	N	Ortlepp 1961	
Bovidae	*Antidorcas marsupialis*	springbok	*S.papillosus*	E+	Mönnig 1931	P
Bovidae	*Antidorcas marsupialis*	springbok	*S.sp*	N	Horak 1980	P
Bovidae	*Bos banteng*	banteng	*S.papillosus*	N	Adewinata 1955	P
Bovidae	*Bos sondaicus*	banteng	*S.papillosus*	N	Krijgsman 1933	
Bovidae	*Bos taurus*	domestic ox	*S.papillosus*	E+	Vegors&Porter 1950	P
Bovidae	*Bos taurus*	domestic ox	*S.papillosus*	N	Ransom 1911	M
Bovidae	*Bos taurus*	domestic ox	*S.papillosus* (*S.vituli*)	N	Brumpt 1921	P
Bovidae	*Bubalus bubalis*	domestic buffalo	*S.papillosus*	N	Chauhan 1978	P
Bovidae	*Bubalus bubalis*	domestic buffalo	*S.papillosus*	N	Chuahan et al 1973	P
Bovidae	*Capra aegagrus*	?	*S.papillosus*	N	Tilc&Hanuskova 1976	P
Bovidae	*Capra hircus*	domestic goat	*S.papillosus*	E+	Borah et al 1983	P
Bovidae	*Capra hircus*	domestic goat	*S.papillosus*	E+	Turner 1959	P
Bovidae	*Capra hircus*	domestic goat	*S.papillosus*	N	Ransom 1911	M
Bovidae	*Capra hircus*	domestic goat	*S.papillosus*	E+	Bezubik 1963	P
Bovidae	*Capra prisca camerun.*	?	*S.papillosus*	N	Tilc&Hanuskova 1976	P
Bovidae	*Capra sibirica*	Siberian ibex	*S.papillosus*	N	Tilc&Hanuskova 1976	P
Bovidae	*Connochaetes taurinus* (*Gorgon taurinus*)	blue wildebeest	*S.papillosus*	N	Horak 1980	P
Bovidae	*Connochaetes taurinus*	blue wildebeest	*S.sp*	N	Round 1968	P
Bovidae	*Damaliscus dorcas albifrons*	blesbok	*S.papillosus*	N	Mönnig 1931	P
Bovidae	*Damaliscus dorcas dorcas*	bontbok	*S.sp*	N	Verster et al 1975	P
Bovidae	*Gazella granti*	Grant's gazelle	*S.sp*	N	Eckert 1963	P
Bovidae	*Gazella subgutturosa*	gazelle	*S.sp*	N	Cherthova 1971	-
Bovidae	*Ovis aries*	domestic sheep	*S.papillosus*	E+	Woodhouse 1948	P
Bovidae	*Ovis aries*	domestic sheep	*S.papillosus*	N	Ransom 1911	M
Bovidae	*Ovis aries*	domestic sheep	*S.papillosus*	N	Basir 1950	G
Bovidae	*Ovis aries*	domestic sheep	*S.papillosus*	N	Wedl 1856	M
Bovidae	*Ovis musimon*	?	*S.papillosus*	N	Kotrly&Kotrla 1980	-

FAMILY	HOST BINOMIAL	COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
Camelidae	*Camelus bactrianus*	bactrian camel	*S.*sp	N	Silva et al 1973	P
Camelidae	*Camelus dromedarius*	dromedary	*S.*sp	N	Steward 1950	P
Camelidae	*Camelus dromedarius*	dromedary	*S.*sp	N	Enyehini 1972	P
Camelidae		camel (unspecified)	*S.*sp	N	Lim&Lee 1977	P
Camelidae	*Lama guanicoe*	lama	*S.*sp	N	Tilc&Hanuskova 1976	P
Camelidae	–	lama	*S.*sp	N	Lim&Lee 1977	P
Cervidae	*Alces alces*	moose	*S.papillosus*	N	Wetzl&Enigk 1937	–
Cervidae	Capreolus capreolus	roe deer	*S.papillosus*	N	Kotrlly&Kotrla 1980	–
Cervidae	*Cervus elephus*	red deer	*S.papillosus*	N	Kotrly&Kotrla 1980	–
Cervidae	*Darma darma*	fallow deer	*S.papillosus*	N	Barth&Matzke 1984	P
Cervidae	*Mazama simplicicornis*	Trinidad deer	*S.papillosus*	N	Cameron 1936	P
Cervidae	*Odocoileus hemionus*	mule deer	*S.*sp	N	Reed et al 1976	P
Cervidae	*Odocoileus virginianus*	white tailed deer	*S.papillosus*	N	Forrester et al 1974	M
Cervidae	*Odocoileus virginianus*	white tailed deer	*S.*sp	N	Glazener&Knowlton 1967	P
Cervidae	*Sikkon nippon*	Japanese deer	*S.papillosus*	N	Kotrly&Kotrla 1980	–
Cervidae		deer (unspecified)	*S.*sp	N	Lim&Lee 1977	P
Giraffidae	*Giraffa camelopardalis*	giraffe	*S.*sp	N	Frank et al 1963	P
Giraffidae	*Okapia johnstoni*	okapi	*S.papillosus*	N	Smits&Jacobi 1965	P
Giraffidae	*Okapia johnstoni*	okapi	*S.*sp	N	Wetzel&Fortmeyer 1964	P
Hippopotamidae	*Hippopotamus amphibius*	hippopotamus	*S.*sp	N	Round 1968	P
Suidae	*Sus scrofa*	domestic pig	*S.felis*	E–	☆	
Suidae	*Sus scrofa*	domestic pig	*S.papillosus*	E+	☆	
Suidae	*Sus scrofa*	domestic pig	*S.*sp	N	Lutz 1885	P
Suidae	*Sus scrofa*	domestic pig	*S.stercoralis*	E+	Lukshina et al 1971	P
Suidae	*Sus scrofa*	domestic pig	*S.suis* (*S.longus*)	N	von Linstow 1905	P
Suidae	*Sus scrofa*	domestic pig	*S.suis* (*S.ransomi*)	N	Schwartz&Alicata 1930	M
Suidae	*Sus scrofa*	domestic pig	*S.suis*	N	Tarczynski 1956	M
Suidae	*Sus scrofa*	domestic pig	*S.westeri*	N	Miyamoto 1929	D
Suidae	*Sus scrofa*	domestic pig	*S.westeri*	E–	☆	
Tragulidae	*Tragulus javanicus*	Malayan chevrotain	*S.papillosus*	N	Jaros et al 1966	P

FAMILY	HOST BINOMIAL	COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
- CARNIVORA						
Canidae	*Canis aureus*	oriental jackal	*S.sp*	N	Rodononya 1966	P
Canidae	*Canis familiaris*	dog	*S.canis*	N	Brumpt 1922	P
Canidae	*Canis familiaris*	dog	*S.cati* (*S.planiceps*)	E+	Horie et al 1981	G
Canidae	*Canis familiaris*	dog	*S.cati* (*S.planiceps*)	E+	Fukase et al 1985	M
Canidae	*Canis familiaris*	dog	*S.cati* (*S.planiceps*)	N	Horie et al 1980	G
Canidae	*Canis familiaris*	dog	*S.cati* (*S.planiceps*)	N+	Arizono et al 1976	G
Canidae	*Canis familiaris*	dog	*S.eryxi* (*S.mirzai*)	E-	Singh 1954	M
Canidae	*Canis familiaris*	dog	*S.felis*	N-	☆	
Canidae	*Canis familiaris*	dog	*S.fuelleborni*	E+	Sandground 1925	M
Canidae	*Canis familiaris*	dog	*S.procyonis*	E+	Little 1966a	G
Canidae	*Canis familiaris*	dog	*S.simiae*	E	Azevedo&Meira 1947	-
Canidae	*Canis familiaris*	dog	*S.sp*	E+	Augustine 1940	P
Canidae	*Canis familiaris*	dog	*S.sp*	E+	Horie et al 1974	M
Canidae	*Canis familiaris*	dog	*S.sp*	N	Lucker 1942	M
Canidae	*Canis familiaris*	dog	*S.sp*	N	Whitney 1936	P
Canidae	*Canis familiaris*	dog	*S.sp*	N	Enyenihi 1972	P
Canidae	*Canis familiaris*	dog	*S.sp*	N	Chandler 1939	M
Canidae	*Canis familiaris*	dog	*S.sp*	N	Munro&Munro 1978	P
Canidae	*Canis familiaris*	dog	*S.sp*	N	Augustine&Davey 1939	M
Canidae	*Canis familiaris*	dog	*S.stercoralis*	E+	Fülleborn 1914	
Canidae	*Canis familiaris*	dog	*S.stercoralis*	E+	Horie et al 1980	G
Canidae	*Canis familiaris*	dog	*S.stercoralis*	E+	Dawkins&Grove 1982	G
Canidae	*Canis familiaris*	dog	*S.stercoralis*	N	Ware&Ware 1923	M
Canidae	*Canis familiaris*	dog	*S.stercoralis*	N	Georgi 1984	P
Canidae	*Canis familiaris*	dog	*S.stercoralis*	N	Worley 1964	P
Canidae	*Canis familiaris*	dog	*S.stercoralis*	N	Ohder&Hurni 1978	P
Canidae	*Canis familiaris*	dog	*S.stercoralis*	N+	Georgi&Sprinkle 1974	P
Canidae	*Canis familiaris*	dog	*S.suis* (*S.ransomi*)	E+	Kotlan&Vajda 1934	M
Canidae	*Nyctereutes procyonoides usuriensis*	raccoon dog	*S.ershowi*	N	Popova 1938	M
Canidae	*Nyctereutes procyonoides viverrinus*	raccoon dog	*S.cati* (*S.planiceps*)	N	Horie et al 1981	M
Canidae	*Nyctereutes procyonoides viverrinus*	raccoon dog	*S.cati*	N	Fukase et al 1985	M
Canidae	*Vulpes alopex*	fox	*S.stercoralis v.vulpi*	N	Mirza&Narayan 1935	P
Canidae	*Alopex lagopus* (*Vulpes lagopus*)	Artic fox	*S.vulpis*	N	Petrov 1940b	-
Canidae	*Vulpes vulpes*	red fox	*S.vulpis*	N	Petrov 1940b	-

FAMILY	HOST BINOMIAL	COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
Felidae	*Felis catus*	cat	*S.cati*	E+	Rogers 1939	M
Felidae	*Felis catus*	cat	*S.cati* (*S.planiceps*)	E+	Rogers 1943	M
Felidae	*Felis catus*	cat	*S.cati* (*S.planiceps*)	E+	Fukase et al 1985	M
Felidae	*Felis catus*	cat	*S.cati* (*S.planiceps*)	E+	Horie et al 1980	G
Felidae	*Felis catus*	cat	*S.cati* (*S.planiceps*)	N+	Horie et al 1981	G
Felidae	*Felis catus*	cat	*S.felis*	N	Chandler 1925a,b	M
Felidae	*Felis catus*	cat	*S.felis*	N+	Speare&Tinsley 1986	M
Felidae	*Felis catus*	cat	*S.fuelleborni*	E-	Sandground 1925	M
Felidae	*Felis catus*	cat	*S.papillosus*	E+	☆	
Felidae	*Felis catus*	cat	*S.sp*	N	Miyamoto&Katsumi 1980	P
Felidae	*Felis catus*	cat	*S.sp*	N	Sandosham 1952	P
Felidae	*Felis catus*	cat	*S.stercoralis*	E+	Sandground 1925	M
Felidae	*Felis catus*	cat	*S.stercoralis*	E+	Horie et al 1980	M
Felidae	*Felis catus*	cat	*S.stercoralis*	E+	Sandground 1928	?
Felidae	*Felis catus*	cat	*S.stercoralis*	N	Froes 1976	D
Felidae	*Felis catus*	cat	*S.suis* (*S.ransomi*)	E+	Kotlan&Vajda 1934	M
Felidae	*Felis catus*	cat	*S.suis*	E-	Schwartz&Alicata 1930	M
Felidae	*Felis catus*	cat	*S.tumefaciens*	N	Price&Dikmans 1941	M
Felidae	*Felis chaus*	Indian wild cat	*S.tumefaciens*	N	Dubey&Pande 1964	M
Felidae	*Felis planiceps*	rusty tiger cat	*S.cati*	N	Rogers 1939	M
Felidae	*Lynx rufus*	bobcat	*S.sp*	N	Little 1966b	P
Felidae	*Panthera leo*	lion	*S.sp*	N	Enyenihi 1972	P
Mustelidae	*Lutra lutra*	otter	*S.martis*	N	Shakmatova 1966	-
Mustelidae	*Lutra canadensis*	Canadian river otter	*S.lutrae*	N	Little 1966b	G
Mustelidae	*Martes martes*	?pine martin	*S.martis*	N	Shakmatova 1966	-
Mustelidae	*Martes zibellina*	sable	*S.martis*	N	Petrov 1940a	P
Mustelidae	*Meles meles*	badger	*S.sp*	N	Enyenihi 1972	P
Mustelidae	*Mellivora capensis* (*Mellivora indica*)	ratel	*S.akbari*	N	Srivastava 1964	D
Mustelidae	*Mephitis mephitis*	skunk	*S.papillosus*	N	Stiles&Baker 1935	D
Mustelidae	*Mephitis mephitis*	skunk	*S.sp*	N	Babero 1960	P
Mustelidae	*Mephitis mephitis*	skunk	*S.sp*	N	Little 1966b	P
Mustelidae	*Mustela ermina*	stoat	*S.martis*	N	Petrov 1940a	P
Mustelidae	*Mustela ermina*	stoat	*S.mustelorum*	N	Cameron&Parnell 1933	P
Mustelidae	*Mustela lutreola* (*Lutreola vison*)	mink	*S.papillosus*	N	Zimmerman 1959	P
Mustelidae	*Mustela lutreola*	mink	*S.sp*	N	Law&Kennedy 1932	P

FAMILY	HOST BINOMIAL	COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
Mustelidae	*Mustela nivalis*	weasel	*S.papillosus*	N	Stiles&Baker 1935	D
Mustelidae	*Mustela nivalis*	weasel	*S.sp*	N	Dollfus et al 1961	P
Mustelidae	*Mustela putorius* (*Putorius putorius*)	polecat	*S.putorii*	N	Morozov 1939	M
Mustelidae	*Mustela putorius*	polecat	*S.papillosus*	N	Stiles&Baker 1935	D
Mustelidae	*Mustela sibirica*	Japanese weasel	*S.cati* (*S.planiceps*)	N	Fukase et al 1985	M
Procyonidae	*Nasua narica* (*Nasua nasica panamensis*)	coati	*S.nasua*	N	Darling 1911	M
Procyonidae	*Nasua narica*	coati	*S.stercoralis*	E+	Sandground 1926	M
Procyonidae	*Procyon lotor*	raccoon	*S.procyonis*	N	Little 1966b	G
Procyonidae	*Procyon lotor*	raccoon	*S.sp*	N	Chandler&Melvin 1951	P
Procyonidae	*Procyon lotor*	raccoon	*S.stercoralis*	E+	Johnson 1962	P
Ursidae	*Ursus americanus*	black bear	*S.sp*	N	Crum et al 1978	P
- EDENTATA						
Dasypodidae	*Dasypus novemcinctus*	nine-banded armadillo	*S.dasypodis*	N	Little 1966b	G
Myrmecophagidae	*Tamadua longicaudata*	lesser ant eater	*S.sp*	N	Cameron 1939	P
- INSECTIVORA						
Erinaceidae	*Erinaceus europea*	European hedgehog	*S.rostombekovi*	N	Gamzemlidse 1941	M
Erinaceidae	*Erinaceus roumanicus*	hedgehog	*S.sp*	N	Lukasiak 1939	P
Soricidae	*Crocidura coerula*	white-toothed shrew (musk rat)	*S.akbari*	N	Mirza&Narayan 1935	M
Soricidae	*Sorex minutus*	pigmy shrew	*S.sp*	N	Cameron&Parnell 1933	P
Talpidae	*Talpa europaea*	European common mole	*S.sp*	N	Cameron&Parnell 1933	P
- LAGOMORPHA						
Leporidae	*Lepus ruficaudatus*	hare	*S.papillosus*	N	Mirza&Narayan 1935	P
Leporidae	*Oryctolagus cuniculus*	rabbit	*S.agoutii*	E-	Griffiths 1940	M
Leporidae	*Oryctolagus cuniculus*	rabbit	*S.papillosus* (*S.longus*)	E+	Ransom 1907a	M
Leporidae	*Oryctolagus cuniculus*	rabbit	*S.papillosus*	N	Hall 1916	P
Leporidae	*Oryctolagus cuniculus*	rabbit	*S.pavonis*	E-	Sakamoto&Yamashita 1970	G

FAMILY	HOST BINOMIAL	COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
Leporidae	*Oryctolagus cuniculus*	rabbit	*S.ratti*	E-	Sandground 1925	M
Leporidae	*Oryctolagus cuniculus*	rabbit	*S.sigmodontis*	E-	Melvin&Chandler 1950	M
Leporidae	*Oryctolagus cuniculus*	rabbit	*S.sp*	E-	Fleming et al 1979	P
Leporidae	*Oryctolagus cuniculus*	rabbit	*S.stercoralis*	E-	Grove&Dawkins 1982	M
Leporidae	*Oryctolagus cuniculus*	rabbit	*S.suis* (*S.ransomi*)	E+	Kotlan&Vadja 1934	M
Leporidae	*Oryctolagus cuniculus*	rabbit	*S.suis* (*S.ransomi*)	E+	Oshio 1956	M
Leporidae	*Oryctolagus cuniculus*	rabbit	*S.suis* (*S.ransomi*)	E-	Schwartz&Alicata 1930	M
Ochotonidae	*Ochotona princeps*	pika	*S.sp*	N	Grundman&Lombardi 1976	P
- MARSUPIALIA						
Didelphidae	*Didelphis aurita*	opossum	*S.sp*	N	Froes 1976	P
Didelphidae	*Didelphis virginiana*	American opossum	*S.sp*	N	Little 1966b	P
Didelphidae	*Didelphis virginiana*	American opossum	*S.sp*	N	Contacos 1954	P
Macropodidae	*Aepyprymnus rufescens*	rufous rat-kangaroo	*S.sp*	N	Speare et al 1982	P
Macropodidae		kangaroo	*S.sp*	N	Lim&Lee 1977	P
Macropodidae	*Lagorchestes conspicillatus*	spectacled hare-wallaby	*S.sp*	N	Speare et al 1982	P
Macropodidae	*Macropus agilis*	agile wallaby	*S.sp*	N	Speare et al 1983	P
Macropodidae	*Macropus agilis*	agile wallaby	*S.sp*	N	Speare et al 1982	P
Macropodidae	*Macropus antelopinus*	antelopine kangaroo	*S.sp*	N	Speare et al 1982	P
Macropodidae	*Macropus dorsalis*	black stripe wallaby	*S.sp*	N	Speare et al 1982	P
Macropodidae	*Macropus giganteus*	eastern grey kangaroo	*S.sp*	N	Speare et al 1982	P
Macropodidae	*Macropus parryi*	pretty face wallaby	*S.sp*	N+	Speare et al 1982	P
Macropodidae	*Macropus robustus*	eastern wallaroo	*S.sp*	N	Speare et al 1982	P
Macropodidae	*Macropus rufus*	red kangaroo	*S.sp*	N	Mackerras 1958	P
Macropodidae	*Onychogalea fraenata*	bridled nail-tail wallaby	*S.sp*	N	Speare et al 1982	P
Macropodidae	*Onychogalea unguifera*	northern nail-tail wallaby	*S.sp*	N	Speare et al 1982	P
Macropodidae	*Petrogale inornata*	unadorned rock wallaby	*S.sp*	N	Speare et al 1982	P
Macropodidae	*Thylogale stigmatica*	red legged padymelon	*S.sp*	N	Speare et al 1982	P
Macropodidae		kangaroo	*S.sp*	N	Winter 1958	P
Peramelidae	*Isoodon macrouris* (*Thylacis obesulus*)	short nosed bandicoot	*S.thylacis*	N-	Mackerras 1959	M
Phalangeridae	*Trichosurus vulpecula*	brush tailed possum	*S.sp*	N	Gordon&Summerville 1958	P
Pseudocheiridae	*Dactylopsila trivirgata*	striped possum	*S.sp*	N	Speare et al 1984	P
Pseudocheiridae	*Pseudocheirus herbertensis herbertensis*	Herbert River ringtail possum	*S.sp*	N	Speare et al 1984	P

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- PERISSODACTYLA						
Equidae	*Equus asinus* (*Asinus asinus*)	burro	*S.westeri*	N	Benbrook&Sloss 1962	P
Equidae	*Equus asinus*	donkey	*S.westeri*	N	Pande&Rai 1960	P
Equidae	*Equus burchelli*	common zebra	*S.sp*	N	Silva et al 1973	P
Equidae	*Equus caballus*	horse	*S.westeri*	N	Ihle 1917	M
Equidae	*Equus caballus*	horse	*S.westeri*	N	Schuurmans-Stekhoven 1930	M
Equidae	*Equus caballus*	horse	*S.westeri*	N+	Greer et al 1974	M
Equidae		zebra	*S.sp*	N	Eckert 1963	P
Rhinocerotidae	*Rhinoceros sondaicus*	Javan rhinoceros	*S.sp*	N	Palmieri et al 1980	P
- PRIMATA						
Cebidae	*Ateles geoffroyi*	black-handed spider monkey	*S.cebus*	N	Little 1966a	G
Cebidae	*Ateles geoffroyi*	black-handed spider monkey	*S.fuelleborni*	E+	Sandground 1925	M
Cebidae	*Ateles geoffroyi*	black-handed spider monkey	*S.fuelleborni*	N	Hayama&Nigi 1963	P
Cebidae	*Ateles geoffroyi*	black-handed spider monkey	*S.simiae*	E+	Beach 1936	P
Cebidae	*Ateles geoffroyi*	black-handed spider monkey	*S.sp*	N	Kreis 1932	M
Cebidae	*Ateles geoffroyi*	black-handed spider monkey	*S.sp*	E+	Faust 1930	P
Cebidae	*Ateles geoffroyi*	black-handed spider monkey	*S.sp*	N	Eckert 1963	P
Cebidae	*Ateles paniscus*	black spider-monkey	*S.fuelleborni*	N	Hayama&Nigi 1963	P
Cebidae	*Ateles paniscus*	black spider-monkey	*S.papillosus*	N	Krynicka et al 1979	D
Cebidae	*Ateles pentadactylus*	monkey	*S.sp*	N	Leger 1921	P
Cebidae	*Cebus apella*	tufted capuchin monkey	*S.sp*	N	Leger 1921	P
Cebidae	*Cebus apella*	tufted capuchin monkey	*S.sp*	N	Augustine 1940	P
Cebidae	*Cebus apella*	tufted capuchin monkey	*S.stercoralis*	N	Jaros et al 1966	P
Cebidae	*Cebus apella fatuellus* (*Cebus apella fatuella*)	Columbian capucin monkey	*S.cebus*	N	Little 1966a	G
Cebidae	*Cebus capucinus* (*Cebus hypoleucus*)	white-throated capucin monkey	*S.cebus*	N	Darling 1911	M
Cebidae	*Cebus capucinus*	white-throated capucin monkey	*S.simiae*	N	Beach 1936	P
Cebidae	*Cebus capucinus*	white-throated capucin monkey	*S.sp*	N	Noda 1962	M
Cebidae	*Cebus capucinus imitator*	Panamanian white-throated capucin monkey	*S.sp*	N	Faust 1930	P
Cebidae	*Cebus sp.*		*S.cebus*	E+	Darling 1911	M

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Cebidae	*Lagothrix lagotricha* (*Lagothrix lagotrica*)	Humboldt's woolly monkey	*S.cebus*	N	Little 1966a	G
Cebidae	*Lagothrix lagotricha* (*Lagothrix humboldti*)	Humboldt's woolly monkey	*S.papillosus*	N	Pillers&Southwell 1929	D
Cebidae	*Lagothrix lagotricha*	Humboldt's woolly monkey	*S.*sp	N	Noda 1962	M
Cebidae	*Saimiri orstedi orstedi*	red-backed squirrel monkey	*S.*sp	N	Faust 1930	P
Cebidae	*Saimiri sciurea*	common squirrel monkey	*S.cebus*	N	Little 1966a	G
Cebidae	*Saimiri sciurea*	common squirrel monkey	*S.*sp	N	Noda 1962	M
Cebidae		squirrel monkey	*S.*sp	N	Cullum&Hamilton 1965	P
Cercopithecidae	*Cercopithecus aethiops*	grivet	*S.*sp	N	Silva et al 1973	P
Cercopithecidae	*Cercopithecus aethiops*	grivet	*S.*sp	N	Reardon&Rininger 1968	P
Cercopithecidae	*Cercopithecus ascanius*	red-tailed guenon	*S.fuelleborni*	N	Hayama&Nigi 1963	P
Cercopithecidae	*Cercopithecus cephus*	moustached guenon	*S.fuelleborni*	N	Hayama&Nigi 1963	P
Cercopithecidae	*Cercopithecus diana*	diana monkey	*S.*sp	N	Eckert 1963	P
Cercopithecidae	*Cercopithecus mitis*	daidemed guenon	*S.fuelleborni*	N	Dollinger&Ruedi 1974	P
Cercopithecidae	*Cercopithecus mitis*	diademed guenon	*S.fuelleborni*	N	Hayama&Nigi 1963	P
Cercopithecidae	*Cercopithecus mona*	mona monkey	*S.papillosus*	N	Krynicka et al 1979	D
Cercopithecidae	*Cercopithecus pygerythus*	vervet monkey	*S.fuelleborni*	N	Blackie 1932	M
Cercopithecidae	*Cercopithecus pygerythus pygerethus* (*C.aethiops pyg.*)	vervet monkey	*S.*sp	N	Yamashiroya et al 1971	P
Cercopithecidae	*Cercopithecus sabaeus* (*Cercopithecus callitricus*)	green monkey	*S.fuelleborni*	N	Chung 1937	P
Cercopithecidae	*Cercopithecus sabaeus* (*Cercopithecus callitrichus*)	green monkey	*S.simiae*	N	Azevedo&Meira 1947	–
Cercopithecidae	*Cercopithecus* sp		*S.*sp	N	Weinberg&Romanovitch 1908	P
Cercopithecidae	*Colobus guereza* (*Colobus geraza*)	colobus	*S.*sp	N	Cooper&Holt 1975	P
Cercopithecidae	*Erythrocebus patas*	patas monkey	*S.papillosus*	N	Krynicka et al 1979	D
Cercopithecidae	*Erythrocebus patas*	patas monkey	*S.*sp	N	Noda 1962	M
Cercopithecidae	*Erythrocebus patas*	patas monkey	*S.stercoralis*	N	Cowper 1966	P
Cercopithecidae	*Erythrocebus patas*	patas monkey	*S.stercoralis*	N	Harper et al 1982	M
Cercopithecidae	*Macaca arctoides*	stump-tailed macaque	*S.*sp	N	Jesse et al 1970	P
Cercopithecidae	*Macaca arctoides*	stump-tailed macaque	*S.*sp	N	Wong&Conrad 1978	P
Cercopithecidae	*Macaca arctoides arctoides* (*Macaca speciosa*)	Indo-Chinese bear macaque	*S.fuelleborni*	N	Hansen et al 1969	P
Cercopithecidae	*Macaca cyclopis*	Taiwan macaque	*S.*sp	N	Jesse et al 1970	P
Cercopithecidae	*Macaca cyclopis*	Taiwan macaque	*S.*sp	N	Noda 1962	M
Cercopithecidae	*Macaca fuscata*	Japanese macaque	*S.fuelleborni*	N	Tanaka et al 1962	M
Cercopithecidae	*Macaca fuscata*	Japanese macaque	*S.*sp	N	Noda 1962	M

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Cercopithecidae	*Macaca irus* (*Macaca cynomolgus*)	crab-eating macaque	*S.fuelleborni*	N	Weinberg&Romanovitch 1908	P
Cercopithecidae	*Macaca irus* (*Macaca cynomolgus*)	crab-eating macaque	*S.stercoralis*	N	Brumpt 1913	P
Cercopithecidae	*Macaca irus* (*Macaca fascicularis*)	crab-eating macaque	*S.fuelleborni*	N	Wong&Conrad 1978	P
Cercopithecidae	*Macaca irus* (*Macaca fascicularis*)	crab-eating macaque	*S.fuelleborni*	N	Panaitescu&Potorac 1981	P
Cercopithecidae	*Macaca irus* (*Macaca fascicularis*)	crab-eating macaque	*S.sp*	N	Sano et al 1980	P
Cercopithecidae	*Macaca irus*	Java ape	*S.fuelleborni*	N	Tanaka et al 1962	M
Cercopithecidae	*Macaca irus*	Java ape	*S.fuelleborni*	N	Bisseru&Poopalachelvam 1968	P
Cercopithecidae	*Macaca irus*	Java ape	*S.sp*	N	Weinberg&Romanovitch 1908	P
Cercopithecidae	*Macaca irus philippinensis* (*Macaca philippensis*)	Philippine macaque	*S.sp*	N	Reardon&Rininger 1968	P
Cercopithecidae	*Macaca irus philippinensis* (*Macaca philippensis*)	Philippine macaque	*S.sp*	N	Habermann&Williams 1957	P
Cercopithecidae	*Macaca mulatta*	rhesus monkey	*S.cebus*	E+	Little 1966a	G
Cercopithecidae	*Macaca mulatta*	rhesus monkey	*S.fuelleborni*	N	Premvati 1958	M
Cercopithecidae	*Macaca mulatta*	rhesus monkey	*S.fuelleborni*	N	Little 1966a	G
Cercopithecidae	*Macaca mulatta*	rhesus monkey	*S.fuelleborni*	N	Sandground 1925	
Cercopithecidae	*Macaca mulatta*	rhesus monkey	*S.papillosus*	N	Poindexter 1942	D
Cercopithecidae	*Macaca mulatta*	rhesus monkey	*S.sp*	N	Weinberg&Romanovitch 1908	P
Cercopithecidae	*Macaca mulatta*	rhesus monkey	*S.sp*	N	Cullum&Campbell 1963	P
Cercopithecidae	*Macaca mulatta*	rhesus monkey	*S.sp*	N	Ford&Speltie 1973	P
Cercopithecidae	*Macaca mulatta*	rhesus monkey	*S.stercoralis*	N	Brumpt 1913	P
Cercopithecidae	*Macaca nemestrina*	pig-tailed macaque	*S.fuelleborni*	N	Wong&Conrad 1978	P
Cercopithecidae	*Macaca nemestrina*	pig-tailed macaque	*S.fuelleborni*	N	Jesse et al 1970	P
Cercopithecidae	*Macaca nemestrina*	pig-tailed macaque	*S.fuelleborni*	N	Weinberg&Romanovitch 1908	P
Cercopithecidae	*Macaca radiata*	bonnet macaque	*S.sp*	N	Wong&Conrad 1978	P
Cercopithecidae	*Macaca radiata*	bonnet macaque	*S.sp*	N	Reardon&Rininger 1968	P
Cercopithecidae	*Macaca sinica* (*Macaca sinicus*)	toque monkey	*S.sp*	N	Gonder 1907	P
Cercopithecidae	*Macaca sinica* (*Macaca sinicus*)	toque monkey	*S.sp*	N	Weinberg&Romanovitch 1908	P
Cercopithecidae	*Macaca sinica* (*Macaca sinicus*)	toque monkey	*S.stercoralis*	N	Brumpt 1913	P
Cercopithecidae	*Macaca* sp	macaque	*S.fuelleborni*	N	Sandground 1925	
Cercopithecidae	*Macaca* sp	macaque	*S.fuelleborni*	N+	Wallace et al 1948	P
Cercopithecidae	*Macaca* sp	macaque	*S.sp*	N	Höeppli 1927	P

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Cercopithecidae	*Macaca sylvanus* (*Macaca sylvana*)	Barbary ape	*S.sp*	N	Silva et al 1973	P
Cercopithecidae	*Mandrillus leucophaeus*	drill	*S.sp*	N	Noda 1962	M
Cercopithecidae	*Papio anubis*	anubis baboon	*S.sp*	N	Owen&Casillo 1973	P
Cercopithecidae	*Papio anubis*	anubis baboon	*S.sp*	N	Jesse et al 1970	P
Cercopithecidae	*Papio cyanocephalus* (*Cyanocephalus babuin*)	yellow baboon	*S.fuelleborni*	N	von Linstow 1905	M
Cercopithecidae	*Papio cyanocephalus*	yellow baboon	*S.fuelleborni*	N	Gretillat et al 1967	M
Cercopithecidae	*Papio cyanocephalus*	yellow baboon	*S.sp*	N	Reardon&Rininger 1968	P
Cercopithecidae	*Papio papio*	Guinea baboon	*S.fuelleborni*	N	Goodey 1926	M
Cercopithecidae	*Papio papio*	Guinea baboon	*S.simiae*	N	Azevedo&Meira 1947	-
Cercopithecidae	*Papio papio*	Guinea baboon	*S.sp*	N	Weinberg&Romanovitch 1908	P
Cercopithecidae	*Papio* sp	baboon	*S.sp*	N	Weinberg&Romanovitch 1908	P
Cercopithecidae	*Papio ursinus*	chacma baboon	*S.fuelleborni*	N	Goldsmid 1974	P
Cercopithecidae	*Papio ursinus*	chacma baboon	*S.sp*	N	McConnell et al 1974	P
Cercopithecidae	*Papio ursinus* (*Papio porcarius*)	chacma baboon	*S.fuelleborni*	N	Blackie 1932	M
Cercopithecidae	*Presbytis cristatus*	silvered leaf monkey	*S.fuelleborni*	N	Arambulo et al 1974	P
Cercopithecidae	*Presbytis cristatus*	silvered leaf monkey	*S.fuelleborni*	N	OwYang 1965	P
Cercopithecidae	*Presbytis cristatus*	silvered leaf monkey	*S.sp*	N	Palmieri et al 1977	P
Cercopithecidae		baboon (unspecified)	*S.fuelleborni*	N	Blackie 1932	P
Cercopithecidae		makaken	*S.simiae*	N	Hung&Höeppli 1923	P
Cercopithecidae		stump-tailed monkey	*S.sp*	N	Cullum&Hamilton 1965	P
Cercopithecidae			*S.sp*	N	Pandey 1978	P
Hapalidae	*Tamarin midas* (*Midas midas*)	red-handed tamarin	*S.sp*	N	Leger 1921	P
Hapalidae	*Sanguinus fusicollis*	brown-handed tamarin	*S.sp*	N	Cosgrove et al 1968	P
Homidae	*Homo sapiens*	man	*S.canis*	E-	Augustine 1940	P
Homidae	*Homo sapiens*	man	*S.cebus*	E-	Sandground 1925	M
Homidae	*Homo sapiens*	man	*S.fuelleborni*	N+	Blackie 1932	M
Homidae	*Homo sapiens*	man	*S.fuelleborni*	N+	Pampiglione&Ricciardi 1972	M
Homidae	*Homo sapiens*	man	*S.fuelleborni*-like	N	Kelly et al 1976	M
Homidae	*Homo sapiens*	man	*S.myopotami*	E-	Little 1965	P
Homidae	*Homo sapiens*	man	*S.myopotami*	N	Burks&Jung 1960	P
Homidae	*Homo sapiens*	man	*S.procyonis*	E+	Little 1966b;1965	G
Homidae	*Homo sapiens*	man	*S.simiae*	E-	Azevedo&Meira 1947	-
Homidae	*Homo sapiens*	man	*S.sp*	N	van der Hoeven&Rijpstra 1962	P
Homidae	*Homo sapiens*	man	*S.sp*	N	Brown&Girardeau 1977	P
Homidae	*Homo sapiens*	man	*S.sp* (ex PNG)	N	Kelly&Voge 1973	M

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Homidae	*Homo sapiens*	man	*S.stercoralis*	N	Bavay 1876	M
Homidae	*Homo sapiens*	man	*S.stercoralis*	N	Georgi&Sprinkle 1974	P
Homidae	*Homo sapiens*	man	*S.suis* (*S.ransomi*)	E+	Kotlan&Vajda 1934	M
Homidae	*Homo sapiens*	man	*S.suis* (*S.papillosus*)	E-	Tomita 1940	P
Hylobatidae	*Hylobates agilis*	agile gibbon	*S.stercoralis*	N	Hayama&Nigi 1963	P
Hylobatidae	*Hylobates concolor leucogenis*	black gibbon	*S.sp*	N	Urbain&Nouvel 1944	P
Hylobatidae	*Hylobates hoolock*	hoolock	*S.papillosus*	N	Chandler 1925b	D
Hylobatidae	*Hylobates lar*	white handed gibbon	*S.stercoralis*	N+	de Pauli 1974	M
Hylobatidae	*Hylobates lar*	white handed gibbon	*S.stercoralis*	N+	de Pauli&Johnsen 1978	M
Hylobatidae	*Hylobates moloch*	silver gibbon	*S.stercoralis*	N	Hayama&Nigi 1963	P
Hylobatidae	*Hylobates pileatus*	black breasted gibbon	*S.stercoralis*	N	Hayama&Nigi 1963	P
Lemuridae		lemur	*S.sp*	N	Weinberg&Romanovitch 1908	P
Pongidae	*Gorilla gorilla*	gorilla	*S.fuelleborni*	N	Jaros et al 1966	P
Pongidae	*Gorilla gorilla*	gorilla	*S.papillosus*	N	Krynicka et al 1979	D
Pongidae	*Gorilla gorilla*	gorilla	*S.sp*	N	Noda 1962	M
Pongidae	*Gorilla gorilla*	gorilla	*S.stercoralis*	N	Penner 1981	M
Pongidae	*Pan paniscus*	pigmy chimpanzee	*S.sp*	N	Hasegawa et al 1983	
Pongidae	*Pan troglodytes*	chimpanzee	*S.fuelleborni*	N	von Linstow 1905	M
Pongidae	*Pan troglodytes*	chimpanzee	*S.sp*	N	Blacklock&Adler 1922	P
Pongidae	*Pan troglodytes*	chimpanzee	*S.stercoralis*	N	Desportes 1945	M
Pongidae	*Pan troglodytes*	chimpanzee	*S.stercoralis*	N	Penner 1981	M
Pongidae	*Pongo pygmaeus*	orang utan	*S.fuelleborni*	N	☆	
Pongidae	*Pongo pygmaeus*	orang utan	*S.papillosus*	N	Krynicka et al 1979	D
Pongidae	*Pongo pygmaeus*	orang utan	*S.sp*	N	Uemera et al 1979	P
Pongidae	*Pongo pygmaeus*	orang utan	*S.sp*	N	Eckert 1963	P
Pongidae	*Pongo pygmaeus*	orang utan	*S.sp*	N	McClure et al 1973	P
Pongidae	*Pongo pygmaeus*	orang utan	*S.stercoralis*	N	Fox 1923	P
Pongidae	*Pongo pygmaeus*	orang utan	*S.stercoralis*	N	Swellengribel&Rijpstra 1965	P
Pongidae	*Pongo pygmaeus*	orang utan	*S.stercoralis*	N	Krynicka et al 1979	P
Pongidae	*Pongo pygmaeus*	orang utan	*S.stercoralis*	N	☆	

- PROBOSCOIDEA

Proboscidae	*Elephas indicus*	Indian elephant	*S.elephantis*	N	Greve 1969	G
Proboscidae		elephant	*S.sp*	N	Lim&Lee 1977	P

- RODENTIA

Caviidae	*Cavia porcellus*	guinea pig	*S.agoutii*	E+	Griffiths 1940	M
Caviidae	*Cavia porcellus*	guinea pig	*S.fuelleborni*	E-	Rego 1972	M
Caviidae	*Cavia porcellus*	guinea pig	*S.papillosus*	E+	Brumpt 1921	P
Caviidae	*Cavia porcellus*	guinea pig	*S.papillosus*	E-	Bezubik 1961	P
Caviidae	*Cavia porcellus*	guinea pig	*S.papillosus*	E-	Schwartz&Alicata 1930	P

FAMILY	HOST BINOMIAL	COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
Caviidae	*Cavia porcellus*	guinea pig	*S.ratti*	E+	Sheldon&Otto 1938	P
Caviidae	*Cavia porcellus*	guinea pig	*S.ratti*	E-	Sandground 1925	M
Caviidae	*Cavia porcellus*	guinea pig	*S.sigmodontis*	E-	Melvin&Chandler 1950	M
Caviidae	*Cavia porcellus*	guinea pig	*S.simiae*	E-	Avezedo&Meira 1947	-
Caviidae	*Cavia porcellus*	guinea pig	*S.sp*	N	Krediet 1921	-
Caviidae	*Cavia porcellus*	guinea pig	*S.stercoralis*	E-	Dawkins&Grove 1982	P
Caviidae	*Cavia porcellus*	guinea pig	*S.suis* (*S.ransomi*)	E-	Oshio 1956	P
Caviidae	*Cavia porcellus*	guinea pig	*S.suis*	E-	Schwartz&Alicata 1930	M
Caviidae	*Hydrochoerus hydrochaeris* (*Hydrochoerus hydrochoera*)	capybara	*S.chapini*	N	Sandground 1925	P
Dasyproctidae	*Dasyprocta agouti*	golden rumped agouti	*S.agoutii*	N	Griffiths 1940	M
Dasyproctidae	*Dasyprocta agouti*	golden rumped agouti	*S.agoutii*	N	Cameron&Reesal 1951	M
Muridae	*Acomys cahirinus*	spiny desert mouse	*S.ratti*	E-	Wertheim 1959	P
Muridae	*Apodemis agrarius*	long-tailed field-mouse	*S.ratti*	N	Schmidt 1962	-
Muridae	*Apodemis flavicollis*	yellow-necked field-mouse	*S.ratti*	N	Schmidt 1962	-
Muridae	*Apodemis sylvaticus*	wood-mouse	*S.ratti*	N	Roman 1964b	P
Muridae	*Arvicanthus niloticus*	mouse	*S.sp*	N	Paperna et al 1970	P
Muridae	*Bandicoota indica*	bandicoot rat	*S.ratti*	N	Sinniah 1979	P
Muridae	*Clethrionomys glareolus*	bank vole	*S.ratti*	N	Roman 1964a	P
Muridae	*Mastomys natalensis*	multimammate rat	*S.sp*	N	Paperna et al 1970	P
Muridae	*Meriones tristrami*	gerbil	*S.ratti*	E+	Wertheim 1959	P
Muridae	*Mesocricetus auratus*	golden hamster	*S.papillosus*	E-	Bezubik 1961	P
Muridae	*Mesocricetus auratus*	golden hamster	*S.ratti*	E+	Wertheim 1959	P
Muridae	*Mesocricetus auratus*	golden hamster	*S.sigmodontis*	E-	Melvin&Chandler 1950	M
Muridae	*Micromys minutus*	?	*S.ratti*	N	Schmidt 1962	-
Muridae	*Microtus agrestris*	?	*S.ratti*	N	Roman 1964a	P
Muridae	*Microtus arvelis*	?	*S.ratti*	N	Roman 1964a	P
Muridae	*Microtus guentheri*	?	*S.ratti*	E+	Wertheim 1959	P
Muridae	*Mus musculus*	house mouse	*S.cati* (*S.planiceps*)	E-	Horie et al 1974	M
Muridae	*Mus musculus*	house mouse	*S.fuelleborni*	E-	Rego 1972	M
Muridae	*Mus musculus*	house mouse	*S.papillosus*	E-	Worley&Barrett 1964	P
Muridae	*Mus musculus*	house mouse	*S.pavonis*	E-	Sakamoto&Yamashita 1970	G
Muridae	*Mus musculus*	house mouse	*S.ratti*	E+	Brackett&Bliznick 1949	P
Muridae	*Mus musculus*	house mouse	*S.ratti*	E+	Sheldon 1937	M
Muridae	*Mus musculus*	house mouse	*S.ratti*	E-	Sandground 1925	M
Muridae	*Mus musculus*	house mouse	*S.ratti*	N	Prokopic&del Valle 1966	P
Muridae	*Mus musculus*	house mouse	*S.sigmodontis*	E-	Melvin&Chandler 1950	M
Muridae	*Mus musculus*	house mouse	*S.sp*	E-	Fleming et al 1979	M
Muridae	*Mus musculus*	house mouse	*S.stercoralis*	E+	Horie et al 1974	M
Muridae	*Mus musculus*	house mouse	*S.suis* (*S.ransomi*)	E-	Oshio 1956	P
Muridae	*Mus musculus*	house mouse	*S.thylacis*	E-	Mackerras 1959	M

FAMILY	HOST BINOMIAL	COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
Muridae	*Ondatra zibethica* (*Ondatra zibethicus*)	rice rat	*S.ratti* v.*ondatrae*	N	Chandler 1941	M
Muridae	*Ondatra zibethica* (*Ondatra zibethicus*)	rice rat	*S.sp*	N	Marval 1978	P
Muridae	*Rattus annandalai*	rat	*S.ratti*	N	Sinniah 1979	P
Muridae	*Rattus argentiventer*	rat	*S.ratti*	N	Sinniah 1979	P
Muridae	*Rattus exulans*	rat	*S.ratti*	N	Sinniah 1979	P
Muridae	*Rattus exulans*	rat	*S.sp*	N	Yap Loy Fong et al 1977	P
Muridae	*Rattus fuscipes*	bush rat	*S.ratti*	N	Ballantyne 1971	M
Muridae	*Rattus fuscipes*	bush rat	*S.venezuelensis*	N	☆	
Muridae	*Rattus norvegicus*	brown rat	*S.fuelleborni*	E−	Sandground 1925	M
Muridae	*Rattus norvegicus*	brown rat	*S.myopotami*	E+	Enigk 1952	
Muridae	*Rattus norvegicus*	brown rat	*S.papillosus*	E−	Sandground 1925	M
Muridae	*Rattus norvegicus*	brown rat	*S.papillosus*	N	Hall 1916	D
Muridae	*Rattus norvegicus*	brown rat	*S.pavonis*	E−	Sakamoto&Yamashita 1970	G
Muridae	*Rattus norvegicus*	rat	*S.ratti*	N	Sandground 1925	M
Muridae	*Rattus norvegicus*	brown rat	*S.ratti*	N+	Little 1966a	G
Muridae	*Rattus norvegicus*	brown rat	*S.sigmodontis*	E−	Melvin&Chandler 1950	M
Muridae	*Rattus norvegicus*	brown rat	*S.sp*	E−	Fleming et al 1979	M
Muridae	*Rattus norvegicus*	brown rat	*S.stercoralis*	E−	Dawkins&Grove 1982	P
Muridae	*Rattus norvegicus*	brown rat	*S.suis* (*S.ransomi*)	E−	Schwartz&Alicata 1930	M
Muridae	*Rattus norvegicus*	brown rat	*S.venezuelensis*	N	Wertheim&Lengy 1964	M
Muridae	*Rattus norvegicus*	brown rat	*S.venezuelensis*	N+	Little 1966a	G
Muridae	*Rattus norvegicus*	brown rat	*S.venezuelensis*	N+	Wertheim 1970	M
Muridae	*Rattus rattus*	black rat	*S.ratti*	N	Chu Tsio-chih 1937	–
Muridae	*Rattus rattus*	black rat	*S.ratti*	N	Dollfus et al 1961	P
Muridae	*Rattus rattus*	black rat	*S.ratti*	E+	☆	
Muridae	*Rattus rattus*	black rat	*S.venezuelensis*	N	Ballantyne 1971	M
Muridae	*Rattus rattus alexandrinus*	rat	*S.ratti*	N	Ash 1962	P
Muridae	*Rattus rattus alexandrinus*	rat	*S.ratti*	N+	Tanabe 1938	P
Muridae	*Rattus rattus diardii*	rat	*S.ratti*	N	Seng et al 1979	P
Muridae	*Rattus rattus diardii*	rat	*S.ratti*	N	Sinniah 1979	P
Muridae	*Rattus sabanus*	rat	*S.ratti*	N	Sinniah 1979	P
Muridae	*Rattus tiomanicus*	rat	*S.ratti*	N	Sinniah 1979	P
Muridae	*Uromys caudimaculatus*	giant tailed white rat	*S.sp*	N	☆	
Muridae	*Zyzomys argurus*	common rock rat	*S.sp*	N	☆	
Muridae	*Zyzomys woodwardi*	large rock rat	*S.sp*	N	☆	
Muridae		gerbil	*S.papillosus*	E−	Ryan 1976	–
Muridae		gerbil	*S.sp*	E+	Marval 1978	P
Muridae		meadow mouse	*S.papillosus*	E−	Worley&Barrett 1964	P
Muridae		white footed mouse	*S.papillosus*	E−	Worley&Barrett 1964	P

FAMILY	HOST BINOMIAL	COMMON NAME	STRONGYLOIDES SPECIES	INF	REFERENCE	AC
Muscardinidae	*Eliomys quercinus*	garden doormouse	*S.ratti*	E+	Roman et al 1970	P
Sciuridae	*Sciurus carolinensis*	grey squirrel	*S.papillosus*	N	Reiber&Byrd 1942	D
Sciuridae	*Sciurus carolinensis*	grey squirrel	*S.robustus*	N	Conti et al 1984	P
Sciuridae	*Sciurus carolinensis*	grey squirrel	*S.robustus*	N	Davidson 1976	P
Sciuridae	*Sciurus carolinensis carolinensis*	grey squirrel	*S.robustus*	N	Chandler 1942	M
Sciuridae	*Sciurus niger rufiventer*	fox squirrel	*S.robustus*	N	Chandler 1942	M

TABLE 6:8. *STRONGYLOIDES* - HOST PARASITE LIST.
(see text for key to INF)

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.agoutii	Caviidae	*Cavia porcellus*	E+	Cameron&Reesal 1951
S.agoutii	Caviidae	*Cavia porcellus*	E+	Reesal 1951
S.agoutii	Caviidae	*Cavia porcellus*	E+	Griffiths 1940
S.agoutii	Dasyproctidae	*Dasyprocta agouti*	N	Cameron&Reesal 1951
S.agoutii	Dasyproctidae	*Dasyprocta agouti*	N	Griffiths 1940
S.agoutii	Leporidae	*Oryctolagus cuniculus*	E-	Griffiths 1940
S.akbari	Mustelidae	*Mellivora indica*	N	Srivastava 1964
S.akbari	Soricidae	*Crocidura coerula*	N	Mirza&Narayan 1935
S.amphibiophilus	Bufonidae	*Bufo peltocephalus*	N	Perez Vigueras 1942
S.ardeae	Ardeidae	*Butorides virescens virescens*	N	Little 1966b
S.ardeae	Ardeidae	*Nyctanassa violacea*	N	Little 1966b
S.avium	Anatidae	*Anas platyrhyncha domestica*	E-	Cram 1929
S.avium	Aramidae	*Aramus gnarauna pictus*	N	Barus 1969
S.avium	Meleagrididae	*Meleagris gallapavo*	E+	Cram 1932
S.avium	Meleagrididae	*Meleagris gallapavo*	N	Maxfield et al 1963
S.avium	Numididae	*Numida meleagris galeata*	N	Fabiyi 1972
S.avium	Phasianidae	*Colinus virginianus*	N	Davidson et al 1980
S.avium	Phasianidae	*Colinus virginianus*	N	Cram 1929
S.avium	Phasianidae	*Gallus gallus*	N	Cram 1929
S.avium	Rallidae	*Rallus aquaticus indicus*	N	Sakamoto&Sarashina 1968
S.avium	Rallidae	*Fulica americana*	N	Cram 1930
S.avium	Rallidae	*Gallinula chloropus*	N	Barus 1969
S.avium	Rallidae	*Junco hyemalis hyemalis*	N	Cram 1930
S.avium	Tetraonidae	*Bonasa umbellus*	E+	Cram 1930
S.bufonis	Bufonidae	*Bufo melanostictus*	N	Rao&Singh 1968
S.canis	Canidae	*Canis familiaris*	N	Brumpt 1922
S.canis	Homidae	*Homo sapiens*	E-	Augustine 1940
S.carinii	Leptodactylidae	*Leptodactylus gracilis*	N	Pereira 1935
S.cati (*S.planiceps*)	Canidae	*Nyctereutes procyonoides*	N	Fukase et al 1985
S.cati (*S.planiceps*)	Canidae	*Canis familiaris*	E+	Horie et al 1981
S.cati (*S.planiceps*)	Canidae	*Canis familiaris*	N	Horie et al 1980

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.cati (*S.planiceps*)	Canidae	*Canis familiaris*	N	Arizono et al 1976
S.cati	Felidae	*Felis catus*	E+	Rogers 1939
S.cati (*S.planiceps*)	Felidae	*Felis catus*	N+	Horie et al 1981
S.cati	Felidae	*Felis planiceps*	N	Rogers 1939
S.cati (*S.sp*)	Muridae	*Mus musculus*	E-	Horie et al 1974
S.cati (*S.planiceps*)	Mustelidae	*Mustela sibirica*	N	Fukase et al 1985
S.cati (*S.planiceps*)	Mustelidae	*Mustela sibirica*	N	Fukase et al 1985
S.cebus	Cebidae	*Ateles geoffroyi*	N	Little 1966a
S.cebus	Cebidae	*Cebus apella fatuella*	N	Little 1966a
S.cebus	Cebidae	*Cebus capucinus* (*Cebus hypoleucus*)	N	Darling 1911
S.cebus	Cebidae	*Cebus* sp.	E+	Darling 1911
S.cebus	Cebidae	*Lagothrix lagotricha*	N	Little 1966a
S.cebus	Cebidae	*Saimiri sciurea*	N	Little 1966a
S.cebus	Cercopithecidae	*Macaca mulatta*	E+	Little 1966a
S.cebus	Homidae	*Homo sapiens*	E-	Sandground 1925
S.chapini	Hydrochoeridae	*Hydrochoerus hydrochaeris*	N	Sandground 1925
S.cruzi	Gekkonidae	*Hemidactylus mabouia*	N	Rodrigues 1968,1970
S.cubaensis	Ardeidae	*Butorides virescens maculatus*	N	Perez Vigueras 1942
S.darevskyi	Lacertidae	*Lacerta armenica*	N	Shapilo 1976
S.darevskyi	Lacertidae	*Lacerta rostombekovi*	N	Shapilo 1976
S.darevskyi	Lacertidae	*Lacerta rudis*	N	Shapilo 1976
S.darevskyi (*S.sp*)	Lacertidae	*Lacerta saxicola*	N	Shapilo 1973
S.darevskyi	Lacertidae	*Lacerta saxicola*	N	Shapilo 1976
S.dasypodis	Dasypodidae	*Dasypus novemcinctus*	N	Little 1966b
S.elephantis	Proboscidae	*Elephas indicus*	N	Greve 1969
S.erschowi	Canidae	*Nyctereutes procyonoides*	N	Popova 1938
S.eryxi (*S.mirzai*)	Boidae	*Chondropython viridis*	N	Weisman&Greve 1982
S.eryxi (*S.mirzai*)	Boidae	*Eryx johnii*	N	Singh 1954

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.eryxi (*S.mirzai*)	Boidae	*Eryx tataricus*	N	Shapilo 1973
S.eryxi (*S.mirzai*)	Canidae	*Canis familiaris*	E-	Singh 1954
S.eryxi (*S.mirzai*)	Colubridae	*Coronella austriaca*	N	Shapilo 1973
S.eryxi	Colubridae	*Elaphe carinata*	N	☆
S.eryxi (*S.mirzai*)	Colubridae	*Natrix natrix*	N	Shapilo 1973
S.eryxi (*S.mirzai*)	Colubridae	*Ptyas mucosus*	N	Singh 1954
S.felis	Canidae	*Canis fmiliaris*	N-	☆
S.felis	Felidae	*Felis catus*	N	Chandler 1925a,b
S.felis	Felidae	*Sus scrofa*	E-	☆
S.fuelleborni	Canidae	*Canis familiaris*	E+	Sandground 1925
S.fuelleborni	Caviidae	*Cavia porcellus*	E-	Rego 1972
S.fuelleborni	Cebidae	*Ateles geoffroyi*	E+	Sandground 1925
S.fuelleborni	Cebidae	*Ateles geoffroyi*	N	Hayama&Nigi 1963
S.fuelleborni	Cebidae	*Ateles paniscus*	N	Hayama&Nigi 1963
S.fuelleborni	Cercopithecidae	*Baboon unspecified*	N	Blackie 1932
S.fuelleborni	Cercopithecidae	*Cercopithecus ascanius*	N	Hayama&Nigi 1963
S.fuelleborni	Cercopithecidae	*Cercopithecus sabaeus* (*Cercopithecus callitrichus*)	N	Chung 1937
S.fuelleborni	Cercopithecidae	*Cercopithecus cephus*	N	Hayama&Nigi 1963
S.fuelleborni	Cercopithecidae	*Cercopithecus mitis*	N	Dollinger&Ruedi 1974
S.fuelleborni	Cercopithecidae	*Cercopithecus mitis*	N	Hayama&Nigi 1963
S.fuelleborni	Cercopithecidae	*Cercopithecus pygerethus*	N	Blackie 1932
S.fuelleborni	Cercopithecidae	*Macaca fuscata*	N	Tanaka et al 1962
S.fuelleborni	Cercopithecidae	*Macaca irus* (*Macaca cynomolgus*)	N	Weinberg&Romanovitch 1908
S.fuelleborni	Cercopithecidae	*Macaca irus* (*Macaca fascicularis*)	N	Panaitescu&Potorac 1981
S.fuelleborni	Cercopithecidae	*Macaca irus* (*Macaca fascicularis*)	N	Wong&Conrad 1978
S.fuelleborni	Cercopithecidae	*Macaca irus*	N	Bisseru&Poopalachelvam 1968
S.fuelleborni	Cercopithecidae	*Macaca irus*	N	Tanaka et al 1962
S.fuelleborni	Cercopithecidae	*Macaca mulatta*	N	Little 1966a
S.fuelleborni	Cercopithecidae	*Macaca mulatta*	N	Sandground 1925
S.fuelleborni	Cercopithecidae	*Macaca nemestrina*	N	Wong&Conrad 1978
S.fuelleborni	Cercopithecidae	*Macaca nemestrina*	N	Weinberg&Romanovitch 1908
S.fuelleborni	Cercopithecidae	*Macaca nemestrina*	N	Jessee et al 1970
S.fuelleborni	Cercopithecidae	*Macaca sp*	N	Sandground 1925
S.fuelleborni	Cercopithecidae	*Macaca irus philippinensis* (*Macaca* sp)	N+	Wallace et al 1948
S.fuelleborni	Cercopithecidae	*Macaca speciosa*	N	Hansen et al 1969

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.fuelleborni	Cercopithecidae	*Papio cyanocephalus*	N	Gretillat et al 1967
S.fuelleborni	Cercopithecidae	*Papio cyanocephalus* (*Cyanocephalus babuin*)	N	von Linstow 1905
S.fuelleborni	Cercopithecidae	*Papio papio*	N	Goodey 1926
S.fuelleborni	Cercopithecidae	*Papio porcarius*	N	Blackie 1932
S.fuelleborni	Cercopithecidae	*Papio ursinus*	N	Goldsmid 1974
S.fuelleborni	Cercopithecidae	*Presbytis cristatus*	N	Arambulo et al 1974
S.fuelleborni	Cercopithecidae	*Presbytis cristatus*	N	Ow Yang 1965
S.fuelleborni	Felidae	*Felis catus*	E-	Sandground 1925
S.fuelleborni	Homidae	*Homo sapiens*	N	Pampiglione&Ricciardi 1971
S.fuelleborni	Homidae	*Homo sapiens*	N+	Blackie 1932
S.fuelleborni	Muridae	*Mus musculus*	E-	Rego 1972
S.fuelleborni	Muridae	*Rattus norvegicus*	E-	Sandground 1925
S.fuelleborni	Pongidae	*Gorilla gorilla*	N	Jaros et al 1966
S.fuelleborni	Pongidae	*Pan troglodytes*	N	von Linstow 1905
S.fuelleborni	Pongidae	*Pongo pygmaeus*	N	☆
S.fuelleborni-like	Homidae	*Homo sapiens*	N	Kelly et al 1976
S.gulae	Colubridae	*Coluber constrictor flaviventris*	N	Little 1966b
S.gulae	Colubridae	*Heterodon platyrhinos*	N	Little 1966b
S.gulae	Colubridae	*Lampropeltis getulis holbrooki*	N	Little 1966b
S.gulae	Colubridae	*Natrix cyclopion cyclopion*	N	Little 1966b
S.gulae	Colubridae	*Natrix sipedon confluens*	N	Little 1966b
S.gulae	Colubridae	*Natrix taxispilota rhombifera*	N	Little 1966b
S.gulae	Colubridae	*Natrix taxispilota taxispilota*	N	Little 1966b
S.gulae	Viperidae	*Arkistrodon contortrix contortrix*	N	Little 1966b
S.gulae	Viperidae	*Arkistrodon piscivorus leucostoma*	N	Little 1966b
S.herodiae (*S.ardeae*)	Ardeidae	*Ardea herodias herodias*	N	Boyd 1966,1967
S.lutrae	Mustelidae	*Lutra canadensis*	N	Little 1966b
S.martis	Mustelidae	*Lutra lutra*	N	Shakhmatova 1966
S.martis	Mustelidae	*Martes martes*	N	Shakhmatova 1966
S.martis	Mustelidae	*Martes zibellina*	N	Little 1966b
S.martis	Mustelidae	*Mustela ermina*	N	Little 1966b
S.martis	Mustelidae	*Mustela lutreola*	N	Shakhmatova 1966
S.martis	Mustelidae	*Mustela nivalis*	N	Shakhmatova 1966
S.martis	Mustelidae	*Mustela putorius*	N	Shakhmatova 1966
S.minimum	Anatidae	*Dafila bahamensis*	N	Travassos 1930b
S.mustelorum	Mustelidae	*Mustela ermina*	N	Cameron&Parnell 1933

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.myopotami	Echimyidae	*Myocastor coypus*	N	Artigas&Pacheco 1933
		(*Myopotamus coipus*)		
S.myopotami	Homidae	*Homo sapiens*	E-	Little 1965
S.myopotami	Homidae	*Homo sapiens*	N	Burks&Jung 1960
S.myopotami	Muridae	*Rattus norvegicus*	E+	Enigk 1952
S.nasua	Procyonidae	*Nasua narica*	N	Darling 1911
		(*Nasua nasica panamensis*)		
S.ophidae	Snake	*Drymobius bifossatus*	N	Pereira 1929
S.oswaldi	Phasianidae	*Gallus gallus*	N	Travassos 1930a,b
(*S.oswaldoi*)		(*Gallus domesticus*)		
S.papillosus	Antilocapridae	*Antilocapra americana*	N	Sandground 1925
S.papillosus	Antilocapridae	*Antilocapra americana*	N	Ransom 1911
S.papillosus	Bovidae	*Aepyceros melampus*	N	Round 1968
S.papillosus	Bovidae	*Ammotragus lervia*	N	Tilc&Hanuskova 1976
S.papillosus	Bovidae	*Antidorcas marsupialis*	E+	Mönnig 1931
S.papillosus	Bovidae	*Antidorcas marsupialis*	N	Ortlepp 1961
S.papillosus	Bovidae	*Bos sondaicus*	N	Krijgsman 1933
S.papillosus	Bovidae	*Bos taurus*	E+	Vegors&Porter 1950
S.papillosus	Bovidae	*Bos taurus*	E-	Woodhouse 1948
S.papillosus	Bovidae	*Bos taurus*	N	Brumpt 1921
(*S.vituli*)				
S.papillosus	Bovidae	*Bos taurus*	N	Ransom 1911
S.papillosus	Bovidae	*Bubalus bubalis*	N	Chuahan et al 1973
S.papillosus	Bovidae	*Capra hircus*	E+	Bezubik 1963
S.papillosus	Bovidae	*Capra hircus*	N	Ransom 1911
S.papillosus	Bovidae	*Capreolus capreolus*	N	Kotrly&Kotrla 1980
S.papillosus	Bovidae	*Damaliscus dorcas albifrons*	N	Monnig 1931
S.papillosus	Bovidae	*Ovis aries*	E+	Woodhouse 1948
S.papillosus	Bovidae	*Ovis aries*	N	Wedl 1856
(*Trichosoma papillosum*)				
S.papillosus	Bovidae	*Ovis musimon*	N	Kotrly&Kotrla 1980
S.papillosus	Caviidae	*Cavia porcellus*	E+	Brumpt 1921a
S.papillosus	Caviidae	*Cavia porcellus*	E-	Schwartz&Alicata 1930
S.papillosus	Cebidae	*Ateles paniscus*	N	Krynicka et al 1979
S.papillosus	Cebidae	*Lagothrix lagotricha*	N	Pillers&Southwell 1929
		(*Lagothrix humboldti*)		
S.papillosus	Cercopithecidae	*Cercopithecus mona*	N	Krynicka et al 1979
S.papillosus	Cercopithecidae	*Erythrocebus patas*	N	Krynicka et al 1979
S.papillosus	Cercopithecidae	*Macaca mulatta*	N	Poindexter 1942
S.papillosus	Cervidae	*Alces alces*	N	Wetzel&Enigk 1937

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.papillosus	Cervidae	*Cervus elephus*	N	Kotrly&Kotrla 1980
S.papillosus	Cervidae	*Dama dama*	N	Barth&Matzke 1984
S.papillosus	Cervidae	*Mazama ?*	N	Cameron 1936
S.papillosus	Cervidae	*Odocoileus virginianus*	N	Forrester et al 1974
S.papillosus	Cervidae	*Sika nippon*	N	Kotrly&Kotrla 1980
S.papillosus	Cricetidae	*Cricetus cricetus*	E-	Bezubik 1961
S.papillosus	Felidae	*Felis catus*	E+	☆
S.papillosus	Giraffidae	*Okapia johnstoni*	N	Smits&Jacobi 1965
S.papillosus	Homidae	*Homo sapiens*	E-	Tomita 1940
S.papillosus	Hylobatidae	*Hylobates hoolock*	N	Chandler 1925b
S.papillosus	Leporidae	*Lepus ruficaudatus*	N	Mirza&Narayan 1935
S.papillosus	Leporidae	*Oryctolagus cuniculus*	E+	Ransom 1907
S.papillosus	Leporidae	*Oryctolagus cuniculus*	N	Hall 1916
S.papillosus	Muridae	gerbil	E-	Worley&Barrett 1964
S.papillosus	Muridae	*Mus musculus*	E-	Worley&Barrett 1964
S.papillosus	Muridae	*Rattus norvegicus*	E-	Sandground 1925
S.papillosus	Muridae	*Rattus norvegicus*	N	Hall 1916
S.papillosus	Mustelidae	*Mephitis mephitis*	N	Stiles&Baker 1935
S.papillosus	Mustelidae	*Mustela nivalis*	N	Stiles&Baker 1935
S.papillosus	Mustelidae	*Mustela putorius*	N	Stiles&Baker 1935
S.papillosus	Phasianidae	*Gallus gallus*	E-	Schwartz&Alicata 1930
S.papillosus	Phasianidae	*Gallus gallus*	N	Krijgsman 1933
S.papillosus	Pongidae	*Gorilla gorilla*	N	Krynicka et al 1979
S.papillosus	Pongidae	*Pongo pygmaeus*	N	Krynicka et al 1979
S.papillosus	Sciuridae	*Sciurus carolinensis*	N	Reiber&Byrd 1942
S.papillosus	Suidae	*Sus scrofa*	E+	☆
S.papillosus	Tragulidae	*Tragulus javanicus*	N	Jaros et al 1966
S.pavonis	Anatidae	*Anas platyrhyncha domestica*	E-	Sakamoto&Yamashita 1970
S.pavonis	Columbidae	*Columba livia*	E-	Sakamoto&Yamashita 1970
S.pavonis	Leporidae	*Oryctolagus cuniculus*	E-	Sakamoto&Yamashita 1970
S.pavonis	Muridae	*Mus musculus*	E-	Sakamoto&Yamashita 1970
S.pavonis	Muridae	*Rattus norvegicus*	E-	Sakamoto&Yamashita 1970
S.pavonis	Phasianidae	*Coturnix coturnix japonica*	E-	Sakamoto&Yamashita 1970
S.pavonis	Phasianidae	*Gallus gallus*	E+	Sakamoto&Yamashita 1970
S.pavonis	Phasianidae	*Pavo cristatus cristatus*	E+	Sakamoto&Yamashita 1970
S.pavonis	Phasianidae	*Pavo muticus*	N+	Sakamoto&Yamashita 1970
S.pavonis	Ploceidae	*Passer montanus kaibatoi*	E-	Sakamoto&Yamashita 1970
S.pereirai	?	*Elosia rustica*	N	Travassos 1932
S.physali	Bufonidae	*Bufo valiceps*	N	Little 1966b

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.procyonis	Canidae	*Canis familiaris*	E+	Little 1966b
S.procyonis	Homidae	*Homo sapiens*	E+	Little 1966b
S.procyonis	Procyonidae	*Procyon lotor*	N	Little 1966b
S.putorii	Mustelidae	*Mustela putoris*	N	Morosov 1939
S.quiscali	Icteridae	*Quiscalus niger caribaeus*	N	Barus 1968
S.ratti	Caviidae	*Cavia porcellus*	E+	Sheldon&Otto 1938
S.ratti	Caviidae	*Cavia porcellus*	E-	Sandground 1925
S.ratti	Cricetidae	*Cricetus cricetus*	E+	Wertheim 1959
S.ratti	Gerbillidae	*Meriones tristrami*	E+	Wertheim 1959
S.ratti	Gliridae	*Eliomys quercinus*	E+	Roman et al 1970
S.ratti	Leporidae	*Oryctolagus cuniculus*	E-	Sandground 1925
S.ratti	Microtidae	*Clethrionomys glareolus*	N	Roman 1964
S.ratti	Microtidae	*Micromys minutus*	N	Schmidt 1962
S.ratti	Microtidae	*Microtus agrestris*	N	Roman 1964
S.ratti	Microtidae	*Microtus arvelis*	N	Roman 1964
S.ratti	Microtidae	*Microtus guentheri*	E+	Wertheim 1959
S.ratti	Muridae	*Acomys cahirinus*	E-	Wertheim 1959
S.ratti	Muridae	*Apodemis agrarius*	N	Schmidt 1962
S.ratti	Muridae	*Apodemis flavicollis*	N	Schmidt 1962
S.ratti	Muridae	*Apodemis sylvaticus*	N	Roman 1964
S.ratti	Muridae	*Bandicoota indica*	N	Sinniah 1979
S.ratti	Muridae	*Mus musculus*	E+	Brackett&Bliznick 1949
S.ratti	Muridae	*Mus musculus*	N	Prokopic&del Valle 1966
S.ratti	Muridae	*Rattus annandalai*	N	Sinniah 1979
S.ratti	Muridae	*Rattus argentiventer*	N	Sinniah 1979
S.ratti	Muridae	*Rattus exulans*	N	Sinniah 1979
S.ratti	Muridae	*Rattus fuscipes*	N	Ballantyne 1971
S.ratti	Muridae	*Rattus norvegicus*	N+	Little 1966a
S.ratti	Muridae	*Rattus norvegicus*	N	Sandground 1925
S.ratti	Muridae	*Rattus rattus*	N	Dollfus et al 1961
S.ratti	Muridae	*Rattus rattus*	N	Chu Tsio-chih 1937
S.ratti	Muridae	*Rattus rattus*	N	Hori et al 1967
S.ratti	Muridae	*Rattus rattus*	E+	☆
S.ratti	Muridae	*Rattus rattus alexandrinus*	N	Ash 1962
S.ratti	Muridae	*Rattus rattus alexandrinus*	N+	Tanabe 1938
S.ratti	Muridae	*Rattus rattus diardii*	N	Sinniah 1979
S.ratti	Muridae	*Rattus rattus diardii*	N	Seng et al 1979

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.ratti	Muridae	*Rattus sabanus*	N	Sinniah 1979
S.ratti	Muridae	*Rattus tiomanicus*	N	Sinniah 1979
S.ratti v.*ondatrae*	Microtidae	*Ondatra zibethica* (*Ondatra zibethicus*)	N	Chandler 1941
S.robustus	Sciuridae	*Sciurus carolinensis carolinensis*	N	Chandler 1942
S.robustus	Sciuridae	*Sciurus niger rufiventer*	N	Chandler 1942
S.rostombekovi	Erinaceidae	*Erinaceus europea*	N	Gamzemlidse 1941
S.serpentis	Colubridae	*Coluber constrictor flaviventris*	N	Little 1966b
S.serpentis	Colubridae	*Heterodon platyrhinos*	N	Little 1966b
S.serpentis	Colubridae	*Lampropeltis getulis holbrooki*	N	Little 1966b
S.serpentis	Colubridae	*Natrix cyclopion cyclopion*	N	Little 1966b
S.serpentis	Colubridae	*Natrix sipedon confluens*	N	Little 1966b
S.serpentis	Colubridae	*Natrix taxispilota rhombifera*	N	Little 1966b
S.serpentis	Colubridae	*Natrix taxispilota taxispilota*	N	Little 1966b
S.serpentis	Viperidae	*Arkistrodon contortrix*	N	Little 1966b
S.serpentis	Viperidae	*Arkistrodon piscivorus leucostoma*	N	Little 1966b
S.sigmodontis	Caviidae	*Cavia porcellus*	E-	Melvin&Chandler 1950
S.sigmodontis	Cricetidae	*Cricetus cricetus*	E-	Melvin&Chandler 1950
S.sigmodontis	Leporidae	*Oryctolagus cuniculus*	E-	Melvin&Chandler 1950
S.sigmodontis	Muridae	*Mus musculus*	E-	Melvin&Chandler 1950
S.sigmodontis	Muridae	*Rattus norvegicus*	E-	Melvin&Chandler 1950
S.sigmodontis	Muridae	*Sigmodon hispidus*	N	Melvin&Chandler 1950
S.simiae	Canidae	*Canis familiaris*	E	Azevedo&Meira 1947
S.simiae	Caviidae	*Cavia porcellus*	E-	Azevedo&Meira 1947
S.simiae	Cebidae	*Ateles geoffroyi*	E+	Beach 1936
S.simiae	Cebidae	*Cebus capucinus*	N	Beach 1935
S.simiae	Cebidae	*Cebus capucinus*	N	Beach 1936
S.simiae	Cercopithecidae	*Cercopithecus sabaeus* (*Cercopithecus callitrichus*)	N	Azevedo&Meira 1947
S.simiae	Cercopithecidae	*Papio papio*	N	Azevedo&Meira 1947
S.simiae	Homidae	*Homo sapiens*	E-	Azevedo&Meira 1947
S.spiralis	Ranidae	*Rana esculenta*	N	Grabda-Kazubska 1978
S.spiralis	Ranidae	*Rana lessonae*	N	Grabda-Kazubska 1978
S.spiralis	Ranidae	*Rana ribidunda*	N	☆
S.stercoralis	Canidae	*Canis familiaris*	E+	Fülleborn 1914
S.stercoralis	Canidae	*Canis familiaris*	E+	Dawkins&Grove 1982
S.stercoralis	Canidae	*Canis familiaris*	N	Horie et al 1980
S.stercoralis	Canidae	*Canis familiaris*	N	Ware&Ware 1923
S.stercoralis	Canidae	*Canis familiaris*	N+	Georgi&Sprinkle 1974

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.stercoralis	Caviidae	*Cavia porcellus*	E-	Dawkins&Grove 1982
S.stercoralis	Cebidae	*Cebus apella*	N	Jaros et al 1966
S.stercoralis	Cercopithecidae	*Erythrocebus patas*	N	Harper et al 1982
S.stercoralis	Cercopithecidae	*Macaca irus* (*Macaca cynomolgus*)	N	Brumpt 1913
S.stercoralis	Cercopithecidae	*Macaca mulatta*	N	Brumpt 1913
S.stercoralis	Cercopithecidae	*Macaca sinica* (*Macaca sinicus*)	N	Brumpt 1913
S.stercoralis	Felidae	*Felis catus*	E+	Horie et al 1980
S.stercoralis	Felidae	*Felis catus*	E+	Sandground 1925
S.stercoralis	Felidae	*Felis catus*	N	Froes 1976
S.stercoralis	Homidae	*Homo sapiens*	N	Bavay 1876
S.stercoralis	Hylobatidae	*Hylobates agilis*	N	Hayama&Nigi 1963
S.stercoralis	Hylobatidae	*Hylobates lar*	N	Hayama&Nigi 1963
S.stercoralis	Hylobatidae	*Hylobates lar*	N+	de Pauli&Johnsen 1978
S.stercoralis	Hylobatidae	*Hylobates moloch*	N	Hayama&Nigi 1963
S.stercoralis	Hylobatidae	*Hylobates pileatus*	N	Hayama&Nigi 1963
S.stercoralis	Leporidae	*Oryctolagus cuniculus*	E-	Dawkins&Grove 1982
S.stercoralis	Muridae	*Mus musculus*	E+	Horie et al 1974
S.stercoralis	Muridae	*Mus musculus*	E-	Dawkins&Grove 1982
S.stercoralis	Muridae	*Rattus norvegicus*	E-	Dawkins&Grove 1982
S.stercoralis	Pongidae	*Gorilla gorilla*	N	Penner 1981
S.stercoralis	Pongidae	*Pan troglodytes*	N	Desportes 1945
S.stercoralis	Pongidae	*Pan troglodytes*	N	Penner 1981
S.stercoralis	Pongidae	*Pongo pygmaeus*	N	Krynicka et al 1979
S.stercoralis	Pongidae	*Pongo pygmaeus*	N	Swellengrebel&Rijpstra 1965
S.stercoralis	Pongidae	*Pongo pygmaeus*	N	Fox 1923
S.stercoralis	Pongidae	*Pongo pygmaeus*	N	☆
S.stercoralis	Procyonidae	*Nasua nasua*	E+	Sandground 1926
S.stercoralis	Procyonidae	*Procyon lotor*	E+	Johnson 1962
S.stercoralis	Suidae	*Sus scrofa*	E+	Lushina et al 1971
S.stercoralis	Amphibia	frogs	E+	Tessier 1896
S.stercoralis	Amphibia	frogs	E-	Sandground 1925
S.stercoralis	Amphibia	frogs	N	Alfieri 1908
S.stercoralis v.*vulpi*	Canidae	*Vulpes alopex*	N	Mirza&Narayan 1935
S.suis (*S.ransomi*)	Canidae	*Canis familiaris*	E+	Kotlan&Vajda 1934
S.suis (*S.ransomi*)	Caviidae	*Cavia porcellus*	E-	Oshio 1956
S.suis (*S.ransomi*)	Caviidae	*Cavia porcellus*	E-	Schwartz&Alicata 1930

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.suis (*S.ransomi*)	Felidae	*Felis catus*	E+	Kotlan&Vajda 1934
S.suis (*S.ransomi*)	Felidae	*Felis catus*	E-	Schwartz&Alicata 1930
S.suis (*S.ransomi*)	Homidae	*Homo sapiens*	E+	Kotlan&Vajda 1934
S.suis (*S.ransomi*)	Leporidae	*Oryctolagus cuniculus*	E+	Kotlan&Vajda 1934
S.suis (*S.ransomi*)	Leporidae	*Oryctolagus cuniculus*	E+	Oshio 1956
S.suis (*S.ransomi*)	Leporidae	*Oryctolagus cuniculus*	E-	Schwartz&Alicata 1930
S.suis (*S.ransomi*)	Muridae	*Mus musculus*	E-	Oshio 1956
S.suis (*S.ransomi*)	Muridae	*Rattus norvegicus*	E-	Schwartz&Alicata 1930
S.suis (*S.ransomi*)	Phasianidae	*Gallus gallus*	E-	Schwartz&Alicata 1930
S.suis	Suidae	*Sus scrofa*	N	Tarczynski 1956
S.suis	Suidae	*Sus scrofa domestica*	N	von Linstow 1905
S.suis (*S.ransomi*)	Suidae	*Sus scrofa domestica*	N	Schwartz&Alicata 1930
S.thylacis	Muridae	*Mus musculus*	E-	Mackerras 1959
S.thylacis	Peramelidae	*Isoodon macrouris* (*Thylacis obesulus*)	N-	Mackerras 1959
S.tumefaciens	Felidae	*Felis catus*	N	Price&Dikmans 1941
S.tumefaciens	Felidae	*Felis catus*	N	Dubey&Pande 1964
S.turkmenica (*S.terkmenicus*)	Laridae	*Larus canus*	N	Barus et al 1978
S.turkmenica	Recurvirostridae	*Himantopus candidus*	N	Kurtieva 1953
S.venezuelensis	Muridae	*Rattus fuscipes*	N	☆
S.venezuelensis	Muridae	*Rattus norvegicus*	N	Brumpt 1934
S.venezuelensis	Muridae	*Rattus norvegicus*	N+	Little 1966a
S.venezuelensis	Muridae	*Rattus rattus*	N	Ballantyne 1971
S.vulpis	Canidae	*Vulpes lagopus*	N	Petrov 1940b
S.vulpis	Canidae	*Vulpes vulpes*	N	Petrov 1940b
S.westeri	Canidae	*Canis familiaris*	E-	Blieck&Baudet 1921
S.westeri	Equidae	*Asinus asinus*	N	Benbrook&Sloss 1962
S.westeri	Equidae	*Equus asinus*	N	Pande&Rai 1960

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.westeri	Equidae	*Equus caballus*	N	Ihle 1917
S.westeri	Equidae	*Equus caballus*	N+	Greer et al 1974
S.westeri	Suidae	*Sus scrofa*	?	Georgi 1984
S.westeri	Suidae	*Sus scrofa*	N	Miyamoto 1929
S.sp	Agamidae	*Physignathus cocincinus*	N	Maier 1980
S.sp	Anatidae	*Anas platyrhyncha domestica!*	E-	☆
S.sp	Anatidae	*Anas platyrhynchos fulvigula*	N	Kinsella&Forrester 1972
S.sp	Anatidae	*Malacorhynchus membranaceous*	N	Harrigan 1981
S.sp	Boidae	*Eryx jaculus*	N	Baylis 1923
S.sp	Boidae	*Liasus fuscus*	E+	☆
S.sp	Boidae	*Morelia spilotes*	N	☆
S.sp	*Boidae*	*Python reticulatus*	N	Holt et al 1979
S.sp	Bovidae	*Aepyceros malampus*	N	Horak 1980
S.sp	Bovidae	*Antidorcas marsupialis*	N	Horak 1980
S.sp	Bovidae	*Connochaetes taurinus*	N	Round 1968
S.sp	Bovidae	*Damaliscus dorcas dorcas*	N	Verster et al 1975
S.sp	Bovidae	*Gazella granti*	N	Eckert 1963
S.sp	Bovidae	*Gazella subgutturosa*	N	Chertova 1971
S.sp	Bufonidae	*Bufo marinus*	N	☆
S.sp	Camelidae	camel (unspecified)	N	Lim&Lee 1977
S.sp	Camelidae	*Camelus bactrianus*	N	Silva et al 1973
S.sp	Camelidae	*Camelus dromedarius*	N	Steward 1950
S.sp	Camelidae	*Camelus dromedarius*	N	Enyenihi 1972
S.sp	Camelidae	lama	N	Lim&Lee 1977
S.sp	Canidae	*Canis aureus*	N	Rodononya 1966
S.sp	Canidae	*Canis familiaris*	N+	Augustine 1940
S.sp	Canidae	*Canis familiaris*	N	Munro&Munro 1978
S.sp	Canidae	*Canis familiaris*	N	Enyenihi 1972
S.sp	Caviidae	*Cavia porcellus*	N	Krediet 1921
S.sp	Cebidae	*Ateles geoffroyi*	N	Kreis 1932
S.sp	Cebidae	*Ateles geoffroyi*	E+	Faust 1930
S.sp	Cebidae	*Ateles pentadactylus*	N	Leger 1921
S.sp	Cebidae	*Cebus apella*	N	Leger 1921
S.sp	Cebidae	*Cebus capucinus*	N	Noda 1962
S.sp	Cebidae	*Cebus capucinus imitator*	N	Faust 1930
S.sp	Cebidae	*Lagothrix lagotrica*	N	Noda 1962
S.sp	Cebidae	*Saimiri orstedi orstedi*	N	Faust 1930
S.sp	Cebidae	*Saimiri sciurea*	N	Noda 1962
S.sp	Cebidae	squirrel monkey	N	Cullum&Hamilton 1965

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.sp	Cercopithecidae	*Cercopithecus aethiops*	N	de Silva et al 1973
S.sp	Cercopithecidae	*Cercopithecus diana*	N	Eckert 1963
S.sp	Cercopithecidae	*Cercopithecus pygerythrus pygerythrus* (*Cercopithecus aethiops pygerythrus*)	N	Yamashiroya et al 1971
S.sp	Cercopithecidae	*Cercopithecus* sp	N	Weinberg&Romanovitch 1908
S.sp	Cercopithecidae	Cercopithecus spp	N	Pandey 1978
S.sp	Cercopithecidae	*Colobus geraza*	N	Cooper&Holt 1975
S.sp	Cercopithecidae	*Erythrocebus patas*	N	Noda 1962
S.sp	Cercopithecidae	*Macaca arctoides*	N	Jessee et al 1970
S.sp	Cercopithecidae	*Macaca cyclopis*	N	Noda 1962
S.sp	Cercopithecidae	*Macaca fuscata*	N	Noda 1962
S.sp	Cercopithecidae	*Macaca irus*	N	Weinberg&Romanovitch 1908
S.sp	Cercopithecidae	*Macaca irus* (*Macaca fascicularis*)	N	Sano et al 1980
S.sp	Cercopithecidae	*Macaca irus philippinensis* (*Macaca philippinensis*)	N	Haberman&Williams 1957
S.sp	Cercopithecidae	*Macaca mulatta*	N	Weinberg&Romanovitch 1908
S.sp	Cercopithecidae	*Macaca radiata*	N	Wong&Conrad 1978
S.sp	Cercopithecidae	*Macaca sinica* (*Macaca sinicus*)	N	Gonder 1907
S.sp	Cercopithecidae	*Macaca sp*	N	Höeppli 1927
S.sp	Cercopithecidae	*Macaca sylvanus* (*Macaca sylvana*)	N	de Silva et al 1973
S.sp	Cercopithecidae	*Mandrillus leucophaeus*	N	Noda 1962
S.sp	Cercopithecidae	*Papio anubis*	N	Jessee et al 1970
S.sp	Cercopithecidae	*Papio cyanocephalus*	N	Reardon&Rininger 1968
S.sp	Cercopithecidae	*Papio papio*	N	Weinberg&Romanovitch 1908
S.sp	Cercopithecidae	*Papio sp*	N	Weinberg&Romanovitch 1908
S.sp	Cercopithecidae	*Papio ursinus*	N	McConnell et al 1974
S.sp	Cercopithecidae	*Presbytis cristatus*	N	Palmieri et al 1977
S.sp	Cercopithecidae	stump-tailed monkey	N	Cullum&Hamilton 1965
S.sp	Cervidae	*Odocoileus hemonionus*	N	Reed et al 1976
S.sp	Cervidae	*Odocoileus virginianus*	N	Glazener&Knowlton 1967
S.sp	Cervidae	deer	N	Lim&Lee 1977
S.sp	Coenobitidae	*Coenovita clipeatus*	N	Rowland&Vandenbergh 1965
S.sp	Colubridae	*Amphiesma mairii*	N	Ballantyne 1971
S.sp	Colubridae	*Boiga dendrophila*	N	Schmidt&Kuntz 1972
S.sp	Colubridae	*Boiga irregularis*	N	☆
S.sp	Colubridae	*Demansia atra*	N	☆
S.sp	Colubridae	*Dendrelaphis punctulatus*	N	☆

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.sp	Colubridae	*Elaphe obsoleta obsoleta*	N	Holt et al 1978
S.sp	Colubridae	*Elaphe obsoleta quadrivittata*	N	Holt et al 1978
S.sp	Colubridae	*Lampropeltis getulis*	N	Holt et al 1978
S.sp	Columbidae	*Columba livia*	N	✫
S.sp	Crotalidae	*Trimeresurus fravoviridis*	N	Hori&Kaneko 1969
S.sp	Cuculidae	*Centropus phasianinus*	N	✫
S.sp	Didelphidae	*Didelphis aurita*	N	Froes 1976
S.sp	Didelphidae	*Didelphis virginiana*	N	Little 1966b
S.sp	Echimyidae	*Myopotamus coipus*	N	Sprehn 1930
S.sp	Elapidae	*Naja naja*	N	Schmidt&Kuntz 1972
S.sp	Elapidae	*Pseudonaja textilis*	N	✫
S.sp	Equidae	*Equus burchelli*	N	de Silva et al 1973
S.sp	Equidae	zebra	N	Eckert 1963
S.sp	Erinaceidae	*Erinaceus roumanicus*	N	Lukasiak 1939
S.sp	Felidae	*Felis catus*	N	Miyamoto&Katsumi 1980
S.sp	Felidae	*Felis catus*	N	Sandosham 1952
S.sp	Felidae	*Lynx rufus*	N	Little 1966b
S.sp	Felidae	*Panthera leo*	N	Enyenihi 1972
S.sp	Hapalidae	*Tamarin midas* (*Midas midas*)	N	Leger 1921
S.sp	Hapalidae	*Saguinus fuscicollis*	N	Cosgrove et al 1968
S.sp	Icteridae	*Agelaius phoeniceus*	N	Little 1966b
S.sp	Giraffidae	*Giraffa camelopardalis*	N	Frank et al 1963
S.sp	Giraffidae	*Okapia johnstoni*	N	Wetzel&Fortmeyer 1964
S.sp	Gruidae	*Grus canadensis*	N	Forrester et al 1974
S.sp	Hippopotamidae	*Hippopotamus amphibius*	N	Round 1968
S.sp	Homidae	*Homo sapiens*	N	van der Hoeven&Rijpstra 1962
S.sp	Homidae	*Homo sapiens*	N	Brown&Giradeau 1977
S.sp (ex PNG)	Homidae	*Homo sapiens*	N	Kelly&Voge 1973
S.sp	Hylidae	*Litoria caerulea*	N	✫
S.sp	Hylidae	*Litoria lesueurii* (*Hyla lesueuri*)	N	Ballantyne 1971
S.sp	Hylidae	*Litoria rubella*	N	✫
S.sp	Hylobatidae	*Hylobates concolor leucogenis*	N	Urbain&Nouvel 1944
S.sp	Lemuridae	*Lemur*	N	Weinberg&Romanovitch 1908
S.sp	Leporidae	*Oryctolagus cuniculus*	E-	Fleming et al 1979
S.sp	Leptodactylidae	*Adelotus brevis*	N	Ballantyne 1971
S.sp	Leptodactylidae	*Limnodynastes peroni*	N	Ballantyne 1971
S.sp	Leptodactylidae	*Platypectron ornatus*	N	✫

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.sp	Macropodidae	*Aepyprymnus rufescens*	N	Speare et al 1982
S.sp	Macropodidae	*Lagorchestes conspicillatus*	N	Speare et al 1982
S.sp	Macropodidae	*Macropus agilis*	N	Speare et al 1983
S.sp	Macropodidae	*Macropus antelopinus*	N	Speare et al 1982
S.sp	Macropodidae	*Macropus dorsalis*	N	Speare et al 1982
S.sp	Macropodidae	*Macropus giganteus*	N	Speare et al 1982
S.sp	Macropodidae	*Macropus parryi*	N+	Speare et al 1982
S.sp	Macropodidae	*Macropus robustus*	N	Speare et al 1982
S.sp	Macropodidae	*Onychogalea fraenata*	N	Speare et al 1982
S.sp	Macropodidae	*Onychogalea unguifera*	N	Speare et al 1982
S.sp	Macropodidae	*Petrogale inornata*	N	Speare et al 1982
S.sp	Macropodidae	*Thylogale stigmatica*	N	Speare et al 1982
S.sp	Macropodidae	kangaroo	N	Lim&Lee 1977
S.sp	Meleagrididae	*Meleagris gallopavo osceola*	N	Hon et al 1975
S.sp	Meleagrididae	*Meleagris gallopavo silvestris*	N	Prestwood 1968
S.sp	Microtidae	*Ondatra zibethicus*	N	Marval 1978
S.sp	Muridae	*Arvicanthus niloticus*	N	Paperna et al 1970
S.sp	Muridae	*Gerbil*	E+	Marval 1978
S.sp	Muridae	*Mastomys natalensis*	N	Paperna et al 1970
S.sp	Muridae	*Mus musculus*	E-	Fleming et al 1979
S.sp	Muridae	*Oryzomys palustris*	N	Little 1966b
S.sp	Muridae	*Rattus exulans*	N	Yap et al 1977
S.sp	Muridae	*Rattus norvegicus*	E-	Fleming et al 1979
S.sp	Muridae	*Sigmodon hispidus*	N	Baylis 1945
S.sp	Muridae	*Uromys caudimaculatus*	N	☆
S.sp	Muridae	*Zyzomys argurus*	N	☆
S.sp	Muridae	*Zyzomys woodwardi*	N	☆
S.sp	Mustelidae	*Meles meles*	N	Enyenihi 1972
S.sp	Mustelidae	*Mephitis mephitis*	N	Babero 1960
S.sp	Mustelidae	*Mustela lutreola*	N	Law&Kennedy 1932
S.sp	Mustelidae	*Mustela nivalis*	N	Dollfus et al 1961
S.sp	Myrmecophagidae	*Tamadua longicaudata*	N	Cameron 1939
S.sp	Ochotonidae	*Ochotona princeps*	N	Grundman&Lombardi 1976
S.sp	Phalangeridae	*Trichosurus vulpecula*	N	Gordon*S*ommerville 1958
S.sp	Phasianidae	*Gallus gallus*	N+	☆
S.sp	Pongidae	*Gorilla gorilla*	N	Noda 1962
S.sp	Pongidae	*Pan paniscus*	N	Hasegawa et al 1983
S.sp	Pongidae	*Pan troglodytes*	N	Blacklock&Alder 1922
S.sp	Pongidae	*Pongo pygmaeus*	N	McClure et al 1973
S.sp	Proboscidae	Elephant	N	Lim&Lee 1977

STRONGYLOIDES SPECIES	FAMILY	HOST	INF	REFERENCE
S.sp	Procyonidae	*Procyon lotor*	N	Chandler&Melvin 1951
S.sp	Pseudocheiridae	*Dactylopsila trivirgata*	N	Speare et al 1984
S.sp	Pseudocheiridae	*Pseudocheirus herbertensis herbertensis*	N	Speare et al 1984
S.sp	Rallidae	*Fulica americana*	N	Kinsella 1973
S.sp	Rallidae	*Fulica atra*	N	☆
S.sp	Rallidae	*Gallinula chloropus*	N	Dollfus et al 1961
S.sp	Rallidae	*Porphyrio porphyrio*	N	☆
S.sp	Rallidae	*Porphyrula martinica*	N	Kinsella et al 1973
S.sp	Ranidae	*Rana clamantans*	N	Little 1966b
S.sp	Ranidae	*Rana esculenta*	N	Vojthova&Moravec 1977
S.sp	Ranidae	*Rana pipens*	N	Rau et al 1978
S.sp	Rhinocerotidae	*Rhinoceros sondaicus*	N	Palmieri et al 1981
S.sp	Scincidae	*Eumeces laticeps*	N	Little 1966b
S.sp	Scincidae	*Tilique gerrardi*	N	Ballantyne 1971
S.sp	Scincidae	*Tilique scincoides*	N	Ballantyne 1971
S.sp	Sciuridae	*Marmota monax*	N	Fleming et al 1979
S.sp	Soricidae	*Sorex minutus*	N	Cameron&Parnell 1933
S.sp	Suidae	*Sus scrofa*	N	Lutz 1885
S.sp	Talpidae	*Talpa europaea*	N	Cameron&Parnell 1933
S.sp	Tetraonidae	*Bonasa umbellus*	N	Davidson et al 1977
S.sp	Threskiornithidae	*Eudocimus albus*	N	Bush&Forrester 1976
S.sp	Ursidae	*Ursus americanus*	N	Crum et al 1978

Strongyloides is only moderately host specific. Its specificity on the level of host species is poor, members of the same genus seem to be readily infected by the same species of parasite. Infection of other genera within the same family as the natural host seems to be the rule, although infections may not be as readily established. On the host generic level differences in infectivity seem to be not in terms of positivety or negativety, but more in terms of intensity and longevity. Some species will infect hosts of different orders from that of the natural host; e.g., *S.stercoralis* can infect Primata, Carnivora, Rodentia and Artiodactyla (pigs)(Lukshina et al, 1971); *S.papillosus* can infect Artiodactyla and Lagomorpha. No species of *Strongyloides* has been clearly shown to infect hosts outside the class of its natural host. An early record of *S.stercoralis* in frogs (Alfieri, 1898) lacks taxonomic details and must be suspect. Similarly the report of patent experimental infection of frogs by *S.stercoralis* (Tessier, 1896) is dubious particularly in view of his report of the development of a giant form of the parasite in infected frogs. Sandground's (1925) efforts in a similar endeavour were negative. Schwartz and Alicata (1930) could not infect a domestic fowl with *S.suis* (syn.*S.ransomi*) from the pig. Sakamoto and Yamashita (1970) were unable to infect a range of mammals with the avian parasite, *S.pavonis*.

Range of hosts able to be experimentally infected is not a useful taxonomic tool. It may lead to errors, particularly if the number of experimental infections attempted is small (Sandground, 1925). Schwartz and Alicata (1930) used the failure of *S.suis* (syn.*S.ransomi*) to infect rabbits as a feature to separate *S.suis* from *S.papillosus*. Kotlan and Vajda (1934) and Oshio (1956) contradicted this by obtaining patent infections. Reliance for differentiation of species on the range of hosts infected is usually an indication that the morphological taxonomy is inadequate; e.g. *S.sigmodontis* (Melvin and Chandler, 1950), unidentified species from the woodchuck, *Marmota monox* (Fleming et al, 1979). The inclusion of host range adds to an understanding of the biology of the parasite (Sakamoto and Yamashita, 1970), but it is only a minor taxonomic criteria.

6.9 CROSS FERTILIZATION OF FREE-LIVING ADULTS.

The free-living adult must mate to produce fertile eggs. The male, however, does not contribute genetic material, the penetration of sperm serving solely to initiate meiotic pathenogenesis in the ovum of the female (Triantaphyllon and Moncol, 1977). This is gynogenesis or obligatory pseudofertilization. Augustine (1940) attempted various combinations of matings of the free-living adults of strains from a chimpanzee, *Pan troglodytes*, a colombian capucin monkey, *Cebus apella*, rhesus monkeys, *Macaca mulatta* and a dog. No fertile cross-matings were produced. He considered the complete failure of hybridization of the strains indicated they were distinct species. Unfortunately, no concurrent taxonomic study was carried out. Thus the work was essentially valueless from the taxonomic viewpoint.

Fertile matings were obtained between free-living adults of *S.suis* (syn.*S.ransomi*) and *S.papillosus* (Triantaphyllon and Moncol, 1977). These authors discovered that mating was an obligatory pseudofertilization, and did not consider that successful fertilization meant the two species were synonymous, but that they were closely related.

Fertilization studies are not a useful criterion for species differentiation at our present state of knowledge, and considering the nature of the fertilization it may be too insensitive to distinguish between related species.

6.10 AUTOINFECTION.

Infective larvae in fresh faeces have only been seen for *S.stercoralis* and *S.felis*. These larvae in the case of *S.stercoralis* are responsible for autoinfection (Faust, 1937), a condition in which larvae migrate from the gut back into the tissues to complete the life cycle without passing outside the body. These infective larvae are morphologically similar, but are often smaller than the infective larvae developing normally (Nishigori, 1928; Faust, 1937). Infective larvae were found in faeces from cats naturally infected with *S.felis*. These were smaller than the normal infective larvae (Table 6:9), and suggested autoinfection could occur with *S.felis*. No evidence of hyperinfection was seen in cats infected with this species. The discovery of infective larvae, particularly dwarf infective larvae, in fresh faeces can be used to diagnose eiher *S.felis* or *S.stercoralis*, since this is unique to these species.

Rhabditoid larvae of *S.stercoralis* also have the ability to penetrate host tissues (Froes, 1931; Torres and Azevedo, 1938; de Pauli and Johnson, 1978; Penner, 1981). In a dog experimentally infected with *S.stercoralis* many rhabditoid larvae were found migrating down the crypts of the large intestine and were occasionally found passing into the lamina propria (Fig.6:16). Parasitic females were found only in the small intestine. This is a pathognomonic sign of the invasive tendency of *S.stercoralis*. It has not been seen in other species with the exception of *S.felis*. This tendency is present in both rhabditoid and filariform larvae and is responsible for autoinfection in *S.stercoralis*. Adult parasitic females found in the small intestine and rhabditiod larvae invading the large intestine is characteristic of *S.stercoralis*. A

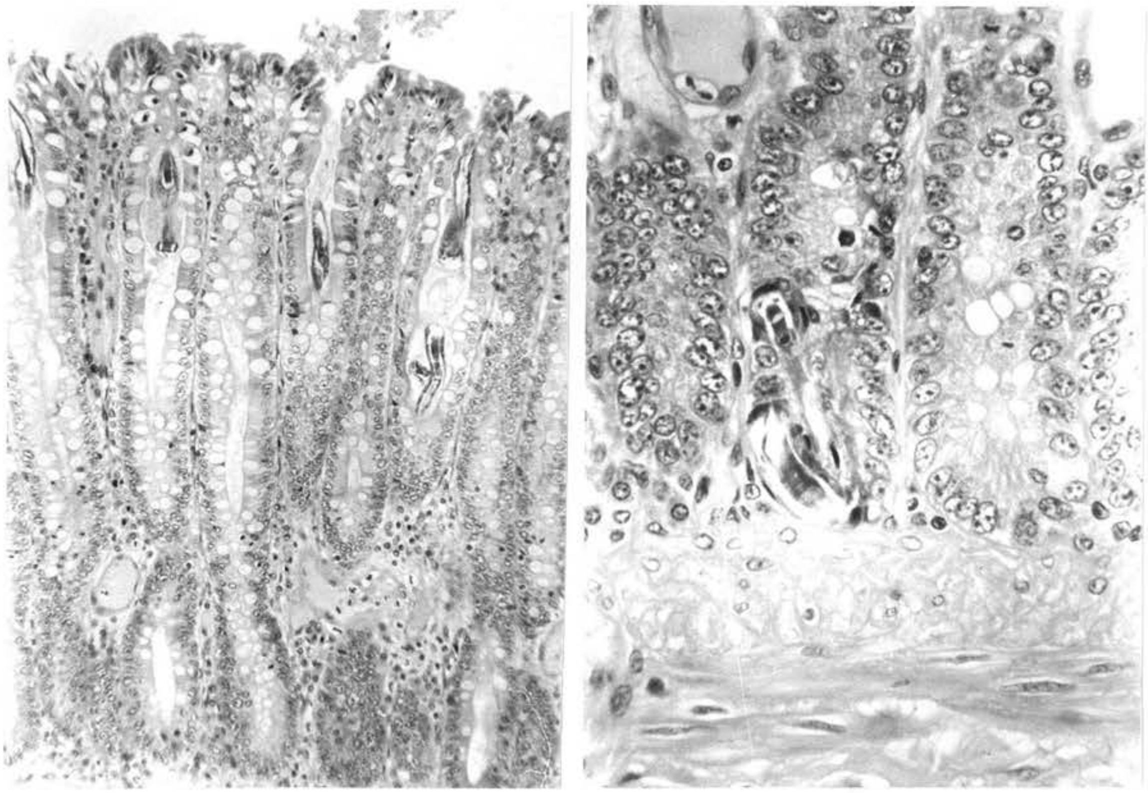

FIG.6:16. Autoinfective tendency in *Strongyloides stercoralis* : A. rhabditoid larvae migrating from lumen of colon down crypts; B. larva passing through mucosa at base of crypt in colon. Dog immunosuppressed by prednisolone and experimentally infected with *Strongyloides stercoralis*. H & E AX180; BX420.

FIG.6:17. Rhabditoid larva of *Strongyloides felis* in crypt of colon. Naturally infected cat. H & E X420.

pathologist aware of this feature can, in primates, change his diagnosis from "*Strongyloides sp*" to "consistent with *S.stercoralis*. Invasion of the crypts of the large bowel is seen very occasionally with *S.felis* (Fig.6:17), and provides further evidence of the autoinfective tendency suggested by the finding of infective larval in faeces. This feature has not been seen in histological preparations of large bowel in hosts infected with other species.

Infective larvae in faeces or evidence of autoinfection is a useful character. Finding infective larvae in faeces is rare in both *S.stercoralis* and *S.felis*. Infective larvae formed 0.16% of 5000 larvae examined from the faeces of 200 humans infected with *S.stercoralis* (Bandyopadhay and Chowdhury, 1961), while only 12 infective larvae of *S.felis* were seen in my study in which at least several million larvae were examined. The autoinfective tendency in *S.felis* is obviously less. Thus, although useful the character is not consistent, and its occurrence cannot be relied upon for diagnosis.

FIG.6:9. Infective larvae of *Strongyloides felis* : A. normal; B. dwarf larvae in faeces.

PARAMETER	A	B	REDUCTION (%)
n	10	3	
length (µm)	524.5±9.8 (808 - 538)	379.4±7.5 (373 - 388)	27.7
width (µm)	15.3±1.0 (14.6-16.7)	10.6±1.7 (9.4-12.5)	30.7
oes (µm)	226.4±5.7 (214.7-233.5)	168.2±3.2 (164.7-170.9)	44.0
ant end to GP (µm)	320.6±7.9 (304.4-327.3)	239.7±13.2 (230.4-249.1)	25.2
tail (µm)	59.8±1.5 (58.4-62.5)	40.6±7.4 (35.4-45.9)	32.1
oes/l (%)	43.2±0.9 (42.2-45.2)	44.3±0.4 (44.1-44.8)	-2.5
ant end-mid GP /l (%)	61.1±0.9 (59.8-62.7)	62.6±2.3 (61.0-64.2)	-2.4
tail/l (%)	11.4±0.3 (11.0-11.8)	10.6±2.2 (9.1-12.2)	7.0

6.11 SUMMARY.

The criteria used to differentiate species has been critically assessed in this chapter. The criteria were classified into major and minor, a major criterion being used as an initial tool for separating species, while minor criteria were used to distinguish between species of similar morphology demarcated at first by the major criteria. In the parasitic female the major criteria were the shape of the stoma in the *en face* view, the type of ovary, body length and the stage in freshly voided faeces. A useful minor criterion was the shape of the tail in lateral view.

Major criteria in the free-living male were the allignment of the subventral preanal and adanal papillae in the longitudinal axis, the position of the subventral preanal papillae with respect to the preanal organ, the distance between the preanal organ and the cloaca, and the type of spicule. In the free-living female the only criteria were the post-vulval narrowing and rotation of the vulva posteriorly.

Other criteria were only minor and included the presence of autoinfective larvae or evidence of an autoinfective tendency, and the taxonomic classification of the host, particular the order to which it belonged.

CHAPTER 7

APPLICATION OF CRITERIA.

7.1 Introduction.

An indication of the usefulness of criteria for speciation would be, one would expect, the number of new species described after the criteria were established. Seven new species were proposed after Little (1966a&b) published his criteria. One, *S.herodiae*, initially was described without knowledge of Little's work (Boyd, 1966&1967). Another, *S.bufonis*, was a poor quality upgraded version of an unavailable former attempt (see Chapter 3.2.1). Both Boyd (1967) and Rao and Singh (1968) subsequenlty ignored Little's suggestions. Of the remaining five new species described in the 19 years since Little's work was published, Little's criteria in two cases were incomplete but given to the best that the available specimens allowed (Greve, 1967 ;Grabda-Kazubska, 1978). The former, *S.elephantis*, was available only as parasitic females in fixed gut contents, while for the latter, *S.spiralis*, the free-living adults failed to develop in culture. For *S.quiscali* the *en face* view of the parasitic female, free living stages and stage in faeces were not described (Barus 1968). Sakamoto and Yamashita (1970) described all stages of *S.pavonis* but save a description of the free-living male which failed to conform to Little's generic definition in that nine pairs of caudal papillae were reported, rather than the six pairs typical of the genus. In describing *S.cruzi* Rodrigues (1968) appeared to be unaware of Little's work and gave a description reminiscent of the inadequate, almost generic, descriptions of the 1930's and 40's. Shapilo (1976) gave a mediocre description of only the parasitic female of *S.darevskyi*. Thus of the seven new species described since 1966 none were fully described. Only one species, *S.cati* (syn.*S.planiceps*), was redescribed using the new criteria (Arizono *et al*, 1976; Horie *et al*, 1980). Members of the genus are not scarce. Since 1966 at least 90 reports of *Strongyloides* sp. in new hosts have been made (Table 6:8). The inadequately described new species, the failure to redescribe "old" species and the large number of unidentified "new" records indicate that in practice Little's criteria are being ignored. Why is this so? What are the practical problems in applying Little's criteria?

7.2 Problems in Application.

A clue to these problems was provided by attempts to identify a species of *Strongyloides* found as a natural parasite of man in the Highlands of Papua Nuigini (Kelly and Voge, 1973; Kelly *et al*, 1976; Knight *et al*, 1979; Ashford *et al*, 1979; Vince *et al*, 1979; Ashford *et al*, 1981). This species has eggs in faeces, and in this respect resembles *S.fuelleborni*, reported from man in Africa (Blackie, 1932; Pampiglione and Riccardi, 1971; Hira and Patel, 1977) and the Philippines (Wallace *et al*, 1948). The free-living females obtained had a post-vulval narrowing (Kelly *et al*, 1976); again a characteristic of *S.fuelleborni*. No males were available. The parasitic female was obtained by anthelmintic therapy (Kelly *et al*, 1976), had spiral ovaries, and a stoma which in *en face* view was a modified X-shape, and a bluntly rounded tail. Why was this species not diagnosed as *S.fuelleborni*? Lesser information had led to the species in African man with eggs in faeces being diagnosed as *S.fuelleborni* (Pampiglione and Riccardi, 1971).

It seems that the major cause of reluctance was lack of non-human primates in PNG (Kelly *et al*, 1976). There was no excuse for short cuts. All stages were required. This is the first point. Parasitologists are often presented with fixed *Strongyloides* of whatever stages. If these are not unique, other stages are also required. The second point is that free-living males could not initially be cultured (Kelly *et al*, 1976); consequently, a key stage was missing. This illustrates the often encountered problem, that even when one makes the effort to collect all stages, the biology of the parasite foils ones efforts. The third point, is that even when all stages are available and have been adequately studied, one has to compare them with valid species, too few of which have been fully described. If the descriptions are inadequate, one therefore has to reexamine those species related to the specimens to be diagnosed and fully describe them.

Once those species which appeared to share key morphological features with the Kanabea *Strongyloides* were examined, the fourth point become obvious. Little's criteria were not precise enough. He had made a highly significant contribution in clarifying what the generic morphology of *Strongyloides* was, and how gross differences could be used to separate species, but one needed to know what degree of difference, in which features, justified creation of a new species. Chapter 6 has answered some of these questions.

When faced with specimens to be identified, even if a full suite of stages is available, how does one start? Firstly, all stages must be examined and adequately described in terms of key features. Next comes the tedious and often frustrating process of matching the specimens to a described species. The alogorithm presented in the form of flow charts (Fig.7:1; 7:2; 7:3) makes this process easier. The principle underlying this schema is that if one searches through descriptions of valid species in an attempt to match key features e.g. stomal shape, many possible diagnoses will be discarded owing to their descriptions being deficient and lacking that key feature. Consequently one needs a schema which allows these inadequately described species to be presented for consideration. This is allowed for in the flow charts by utilizing the host specificity of *Strongyloides*. If a species has been already described from a particular host, it should be among the

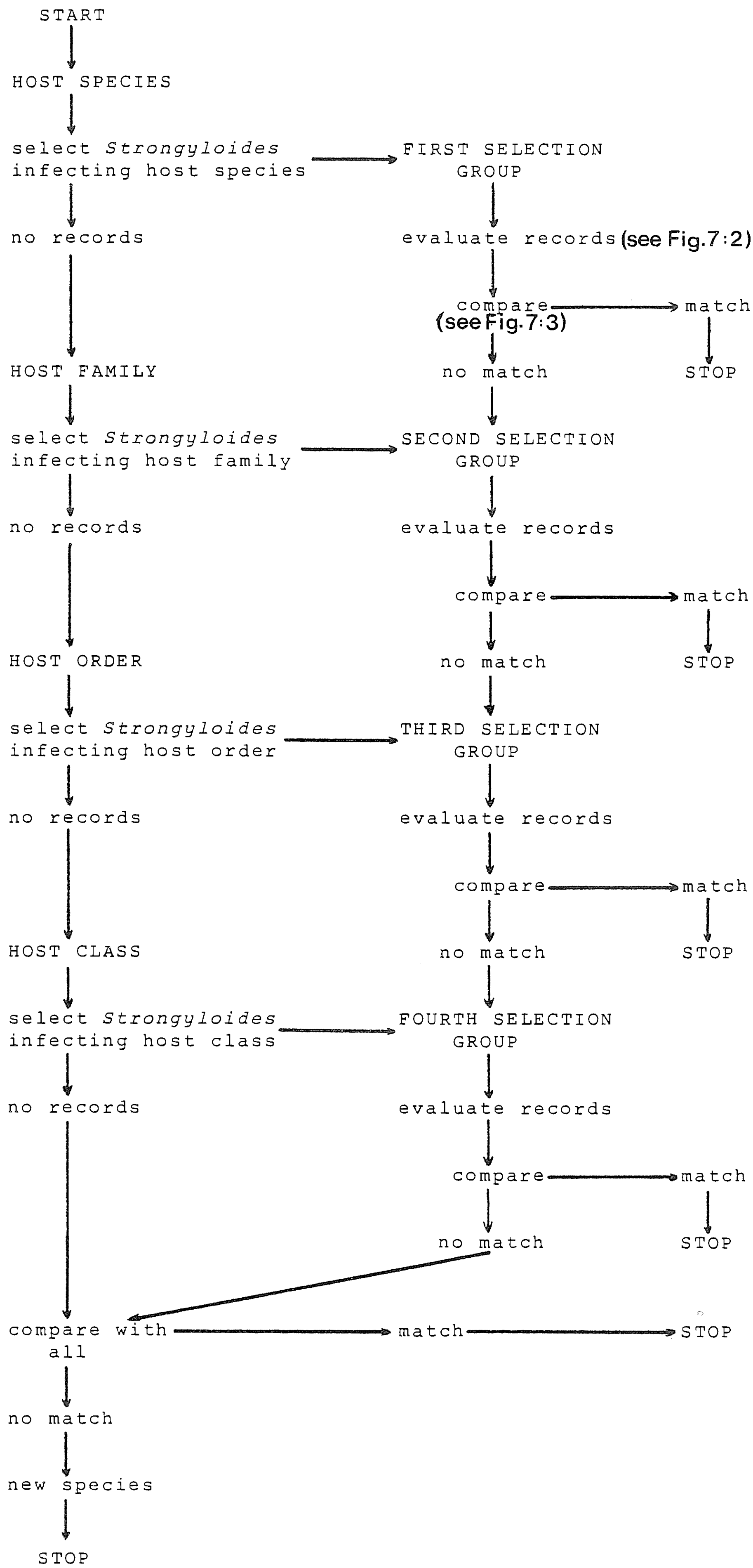

FIG.7:1. Algorithm for the diagnosis of unidentified specimens of *Strongyloides*.

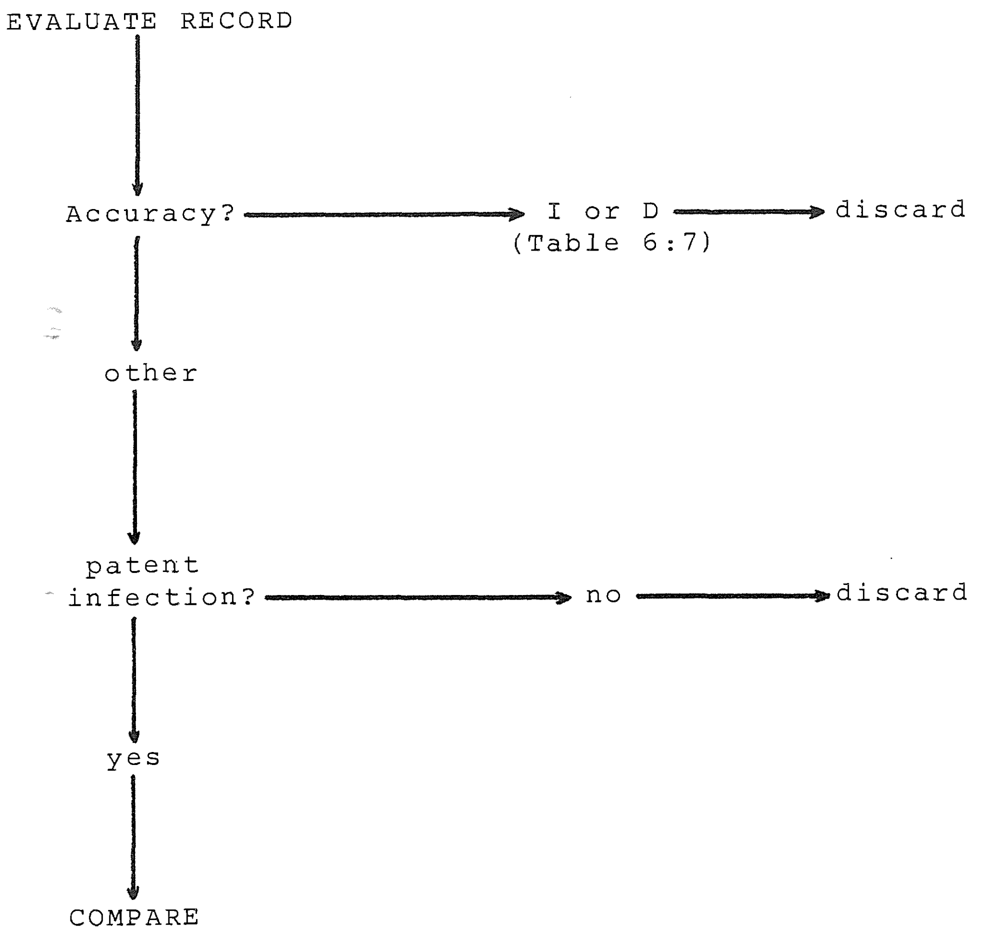

FIG.7:2. Flow chart for the evaluation of host - *Strongyloides* records as part of algorithm given in Fig.7:1.

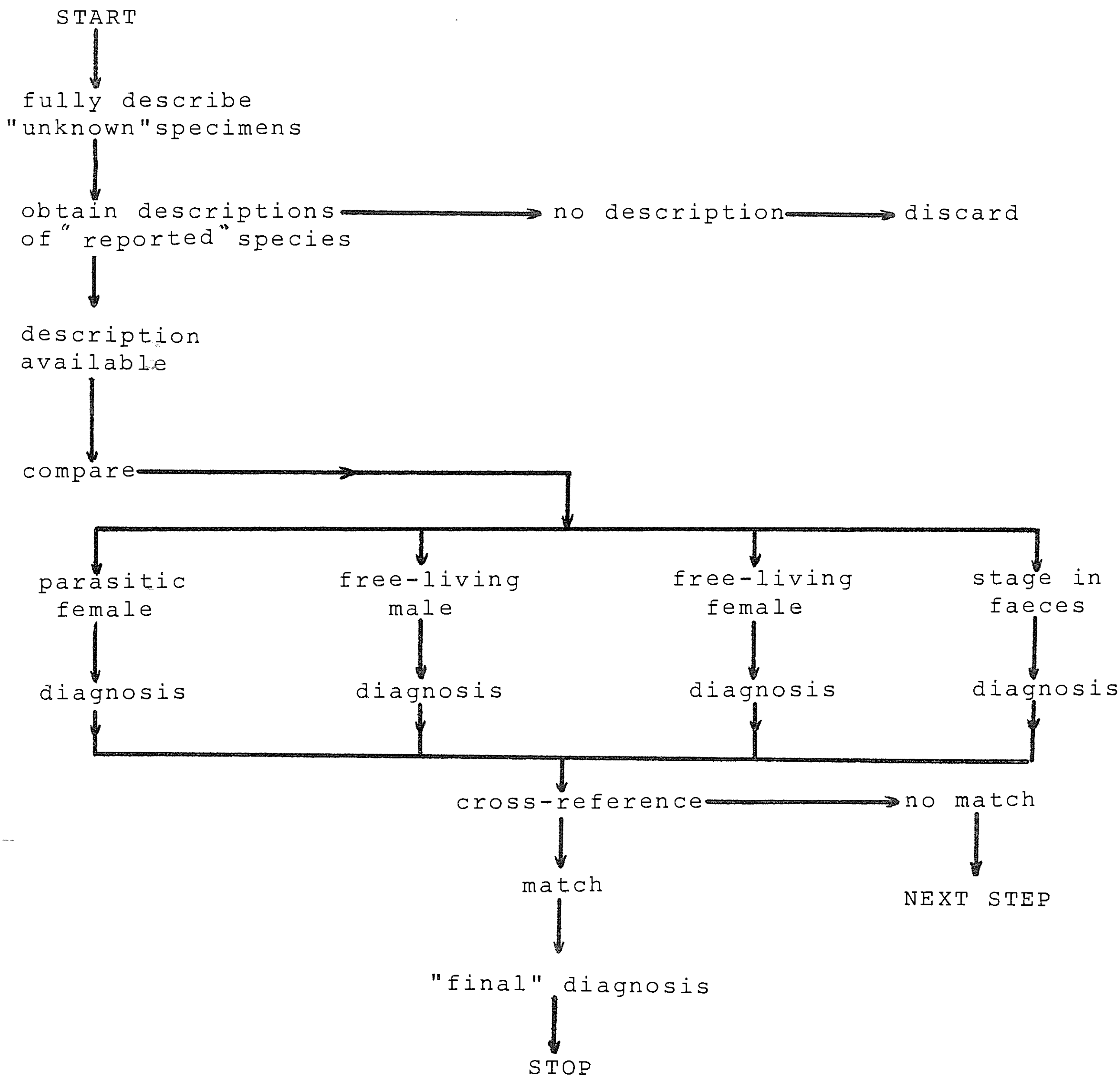

FIG.7:3. Flow chart for the comparison of "unknown" specimens with valid species to determine identity.

first to be considered in diagnosis, even if the description is inadequate. In such a case, a "consistent-with" diagnosis can be arrived at by matching up the described features in the named species with those in the specimen. If no match is obtained, one then considers the next selection group which is based on host family. This approach does not advocate diagnosis of a particular species solely on the basis of host, but uses host as a means of bringing first to one's attention the most likely diagnoses.

Fig.7:1 presents the overall schema, Fig.7:2 the preliminary steps in evaluating records in selection groups and Fig.7:3 the general schema for comparing the unknown with known species. Fig.7:1 relies heavily on the host-*Strongyloides* list (Table 6:7). Fig.7:2 also utilizes this list. Sources for the descriptions of species required in Fig.7:3 can be found in Table 3:1. In Fig.7:3 note that comparisons of the parasitic female, free-living male, free-living female and stage in faeces are made independently leading to four diagnoses. These are then checked for agreement and if one is found to match all four, the "final" diagnosis made. "Final" is qualified since the finality will depend on various factors, eg. adequacy of specimens, adequacy of descriptions, commoness of host-parasite association. This latter category is illustrated by a diagnosis of *S.papillosus* in a sheep. This is an expected diagnosis, whereas diagnosis of *S.stercoralis* in a cat, being uncommon, would make one look more critically at other alternatives, eg. *S.felis* or lead one to search further through the flow chart to enable other diagnosis to be eliminated. It is also obvious from Fig.7:3 that a diagnosis can be made using only one stage of a parasite, rather than four, but that this diagnosis will be less reliable than if the other three stages were also compared.

To illustrate how this schema can be used in a particular case, that of the *Strongyloides* found in man in PNG will be considered.

7.3 The Kanabea Strongyloides.

The distribution in man in PNG of the *Strongyloides* species with eggs in faeces is shown in Fig.7:4. The Karimui Plateau, Simbu Province, site of my own collection of the free living stages and stage in faeces, is also shown.

The literature contains a description of specimens collected from the Fly River region (Kelly *et al*, 1976). The free-living male was undescribed. No description, but a brief comment on the comparative morphology of free-living females collected from the Highland area of Kamea was made by Ashford *et al* (1979). No name has been formally proposed for the parasite, but a confusing array of names have been used. The specimens from the Fly River region have been refered to as *Strongyloides* species (Kelly and Voge, 1973), *S.fulleborni*-like (Kelly *et al*, 1976), *S.fuelleborni* (Knight *et al*, 1979, p565), *S.'fuellborni'* (Knight *et al*, 1979, p571), *S.fuelleborni*-like (Knight *et al*, 1979, p572), *S.cf.fuelleborni* (Ashford et al, 1981, p269), *fuelleborni*-like *Strongyloides* (Ashford *et al*, 1981, p270), and Kelly's *Strongyloides* (Ashford *et al*, 1981, p276). Those from Kamea in the Highlands have been called Kanabea *Strongyloides* (Vince et al, 1979; Ashford *et al*, 1979), *S.cf.fuelleborni* (Ashford *et al*, 1981, p269), *fuelleborni*-like *Strongyloides* (Ashford *et al*, 1981, p270), and Kelly's *Strongyloides* (Ashford *et al*, 1981, p276).

FIG.7:4. Distribution of the Kanabea *Strongyloides* in Papua Nuigini (from Ashford *et al*, 1981). Positive sites shown as larger dots; ? introduced positives as smaller dots; Karamui Plateau as indicated by arrow.

The present status is:

1. The parasitic female resembles *S.fuelleborni* but has not been diagnosed as such.

2. The parasitic female, free-living female, infective larvae and eggs have been described, but not the free-living male.

3. Undisclosed differences exist between free-living females from the Fly River region and from the Highlands of PNG (Ashford *et al* 1979).

4. These differences have led to a belief that two species of *Strongyloides* may occur (Ashford, pers. comm., 1985).

7.4 Application of Algorithm.

Only a brief resume will be given to merely illustrate the principles involved. This is presented in Fig.7:5. The first selection group is given in Table 7:1 and contains species extracted from Table 6:7. *S.myopotami* and *S.felis* were discarded since no patent infection has been demonstrated in man. *S.cebus* was retained since it naturally infects primates. The *S.*sp from the pretty faced wallaby which also failed to become patent on experimental infection was also discarded. All species discarded also were morphologically different from the Kanabea *Strongyloides*. In the course of events these species would normally be presented for reconsideration in another selection group. No descriptions were available for the *Strongyloides* sp. reported by Brown and Girardeau (1977) and van der Hoeven and Rijpstra (1962). The former authors found *Strongyloides* larvae, possibly *S.fuelleborni*, in breast milk, while the latter reported eggs in faeces of people in Dutch West New Guinea, possibly the same species under consideration in P.N.G.

The parasitic female described by Kelly *et al* (1976) had a stoma with a modified-X shape in *en face* view, spiral ovaries both anterior and posterior, was of medium length with a bluntly rounded tail. It was consistent with *S.cebus* and *S.fuelleborni*.

The free-living male had a sharply pointed spicule, with a moderate curvature and a prominent ventral membrane with a straight edge; the gubernaculum was curved, width/length 48.5%; SVP level with PO, AD1 was dorsal to line of SVP and AD2, and the postanals were moderaely separated; PO to cloaca was greater than body width, 1.34±0.16. It was consistent with that of *S.fuelleborni* and *S.suis* (Fig.7:5).

The free-living female had a post vulval constriction (reduction of 11.8±3.0%) but the vulva was not rotated posteriorly

TABLE 7:1. Species reported to infect man naturally or used for experimental infections.

SPECIES	INF	REFERENCE	AC
S.canis	E-	Augustine 1940	P
S.cebus	E-	Sandground 1925	M
S.felis	E-	this thesis	
S.fuelleborni	N+	Blackie 1932	M
S.fuelleborni	N+	Pampiglione&Ricciardi 1972	M
S.fuelleborni-like	N	Kelly et al 1976	M
S.myopotami	E-	Little 1965	M
S.myopotami	N?	Burks&Jung 1960	P
S.procyonis	E+	Little 1966b	G
S.simiae	E-	Azevedo&Meira 1947	M
*S.*sp	N	van der Hoeven&Rijpstra 1962	P
*S.*sp	N	Brown&Girardeau 1977	P
*S.*sp (ex PNG)	N	Kelly&Voge 1973	M
s.sp (*ex Macropus parryi*)	E-	this thesis	
S.stercoralis	N	Bavay 1876	M
S.stercoralis	N	Georgi&Sprinkle 1974	P
S.suis (*S.ransomi*)	E+	Kotlan&Vajda 1934	M
S.suis (*S.papillosus*)	E-	Tomita 1940	P

(angle 100.5±5.2°). *S.fuelleborni* and *S.cebus* have a post vulval narrowing which is variable (Little, 1966a). The variation in the orientation of the vulva has not been carefully examined, although Premvati (1958) in her illustrations showed the vulva rotated with temperature in *S.fuelleborni*. *S.suis* from PNG has a post vulval narrowing and a slightly rotated vulva.

All these species have eggs in faeces as does the Kanabea *Strongyloides*.

On comparing all four diagnoses only *S.fuelleborni* matches up, although the possible error in the free-living female reduces the degree of confidence with which the diagnosis is made. Further comparison using the same technique with other selection groups leaves only *S.papillosus* as a possible diagnosis, although its free-living female does not have a post vulval constriction like the Kanabea *Strongyloides*.

It is obvious a more comprehensive study both of the Kanabea *Strongyloides* and of *S.fuelleborni* is required before a confident diagnosis can be made. The intraspecific variation in key features shown by these species must be examined to determine the range of morphology shown by both, particularly for the free-living adults, and most notably the post-vulval constriction and vulval rotation of the free-living female. Nevertheless, the example illustrates how the algorithm can be applied in practice.

7.5 SUMMARY.

Little's criteria for the differentiation of species in *Strongyloides* has been rarely used since their publication. Problems in the application of these criteria were assessed and an algorithm proposed to enable unknown specimens to be identified in a practical way. An example of the use of the schema was provided using the Kanabea *Strongyloides*, a parasite of humans in Papua Nuigini. Although a tentative diagnosis of *S.fuelleborni* was made, significant reservations due to unknowns regarding the intraspecific variation in morphology of the free-living stages of this species and those species morphologically similar to it, make the diagnosis uncertain.

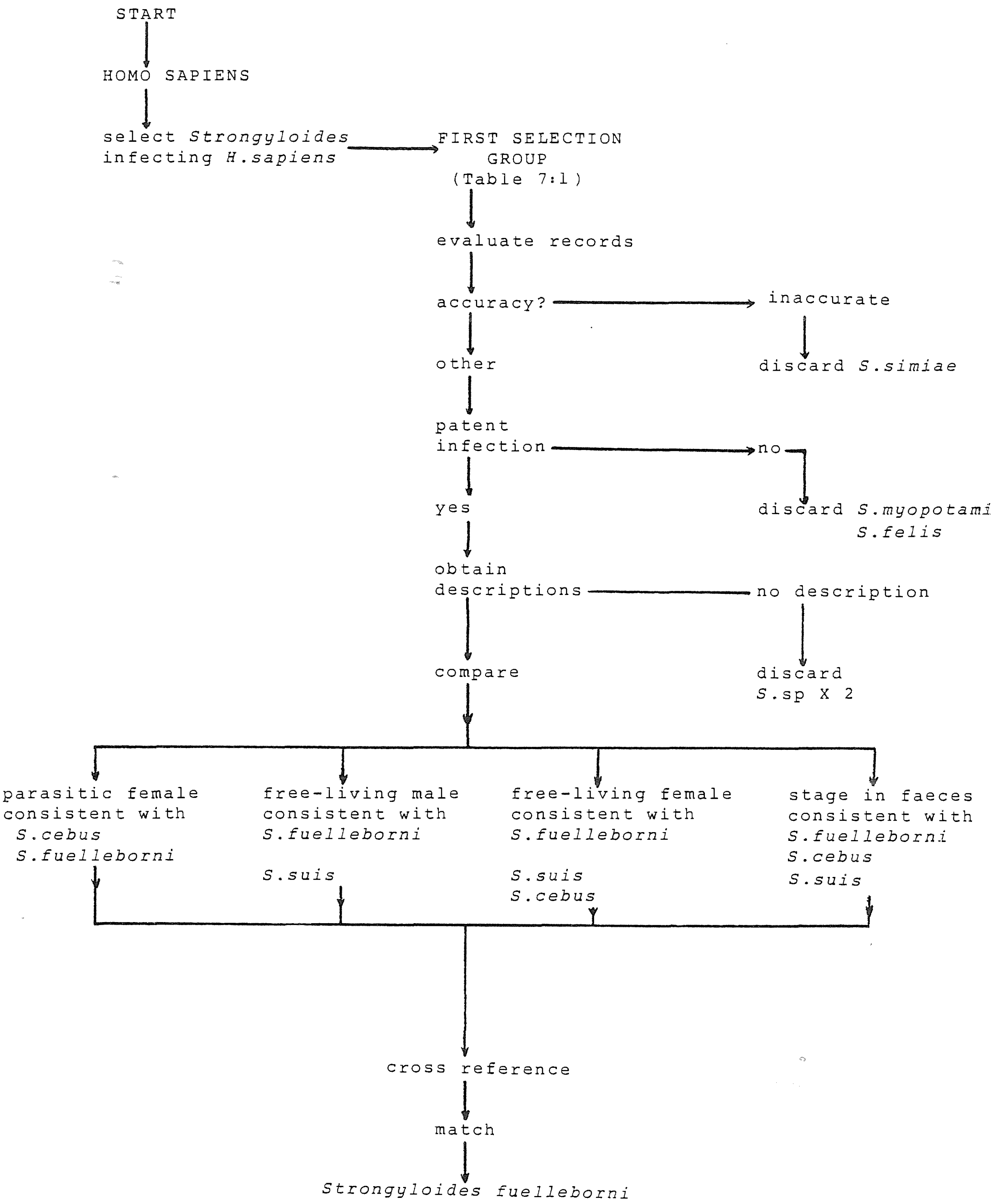

FIG.7:5. Illustration of the application of the algorithm for diagnosis of *Strongyloides*. The Kanabea *Strongyloides* is the test case.

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APPENDIX 1.
SPECIMENS OF *STRONGYLOIDES* EXAMINED.

ID	SPECIES	COLLECTION	STATUS	STAGE	D	H
1	*S.agoutii*	JP		P,FL	–	–
4	*S.ardeae*	USNMHC	paratypes	P	–	–
5	*S.avium*	USNMHC	cotypes	P	–	–
		self		P,FL	+	–
8	*S.cati*	MNHNLV		P	–	–
10	*S.chapini*	USNMHC	cotypes	P	–	–
14	*S.dasypodis*	USNMHC	paratypes	P,FL	–	–
15	*S.elephantis*	USNMHC	paratypes	P	–	–
17	*S.eryxi*	BMNH		P	–	–
18	*S.felis*	self		P,FL	+	+
19	*S.fuelleborni*	JP		P,FL	–	–
		self		FL	–	–
20	*S.gulae*	USNMHC	paratypes	P,FL	–	–
21	*S.herodiae*	USNMHC	paratypes	P	–	–
22	*S.lutrae*	USNMHC	paratypes	FL	–	–
26	*S.myopotami*	BMNH		P	–	–
30	*S.papillosus*	self		P,FL	+	+
34	*S.physali*	USNMHC	paratypes	P,FL	–	–
35	*S.procyonis*	USNMHC	paratypes	P,FL	–	–
38	*S.ratti*	self		P,FL	+	+
40	*S.robustus*	USNMHC	paratypes	P	–	–
		Davidson		P	–	–
42	*S.serpentis*	USNMHC	paratypes	P,FL	–	–
		self		P,FL	+	–
44	*S.spiralis*	G-K	paratypes	P	–	–
		self		P	+	–
45	*S.stercoralis*	self		P,FL	–	+
		MNHNLV		P,FL	+	–
47	*S.suis*	MNHNLV		P	–	–
		self		P,FL	+	+
		USMNHC	paratypes	P,FL	–	–

48	*S.thylacis*	QM	types	P,FL	–	
		self		P,FL	+	+
49	*S.tumefaciens*	USNMHC	paratypes	P	–	+
51	*S.venezuelensis*	MNHNLV		–	+	
		self		P	+	–
53	*S.westeri*	self		P,FL	+	+
	S.ovocinctus	USNMHC	paratypes	P	–	–
	S.vituli	MNHNLV		P	–	–
	Parastrongyloides perameles	QM	types	P,FL	–	–
	Parastrongyloides chrysocloris	MNHNLV	types	P	–	–
	Parastrongyloides trichosuri	QM	types	P,FL	–	–
	Strongyloides sp. ex :					
	Amphiesma mairii	self		P,FL	+	–
	Boiga irregularis	self		P,FL	+	–
	Centropus phasianinus	self		P,FL	+	–
	Dactylopsila trivirgata	self		P	+	–
	Demansia atra	self		P,FL	+	–
	Dendrelaphis punctulatus	self		P	+	–
	Fulica atra	self		P	+	–
	Gallus gallus	self		P,FL	+	+
	Homo sapiens	self		FL		
	Lagorchestes conspicillatus	self		P,FL	+	+
	Liasis fuscus	self		P,FL	+	–
	Litoria caerulea	self		P,FL	+	–
	Litoria rubella	self		P	+	–
	Macropus agilis	self		P,FL	+	+
	M.dorsalis	self		P,FL	+	+
	M.giganteus	self		P,FL	+	+
	M.parryi	self		P,FL	+	+
	M.robustus	self		P,FL	+	+
	M.rufogriseus	Obendorf		P	–	+
	M.rufus	self		P,FL	+	+
	Morelia spilotes	self		P,FL	+	–
	Onychogalea fraenata	self		FL	–	–
	Onychogalea unguifera	self		P,FL	+	+

Petrogale assimilis	self	P,FL	+	−
Petrogale inornata	self	P,FL	+	−
Platypectron ornatus	self	P,FL	+	−
Porphyrus porphyria	self	P	+	−
Pseudocheirus herbertensis	CSIRO	P	−	
Pseudonaja textilis	self	P,FL	+	−
Thylogale stigmatica	self	P	−	−
Trichosurus vulpecula	self	P,FL	+	−
Uromys caudimaculatus	self	P	+	+
Vombatus ursinus	Obendorf	P	−	+
Zyzomys argurus	PP	P	+	−
Zyzomys woodwardi	PP	P	+	−
Parastrongyloides sp. *ex* :				
Tachyglossus aculeatus	CSIRO	P,FL	−	−
	self	FL	−	−

Key to Collections: BMNH - Parasitic Worms, British Museum (Natural History), Cromwell Rd., South Kensington, London; CSIRO - Wildlife and Rangelands Research, CSIRO, Lynham, ACT;
G-K - Dr. B. Grabda-Kazubska, Research Centre of Parasitology, Polish Academy of Sciences, ul.Pasteura 3, S.p. 153, 00-973 Warsaw;
Davidson - Prof. W.R. Davidson, Department of Parasitology, College of Veterinary Medicine, University of Georgia, Athens, Georgia;
JP - Dr. J. Pearson, Department of Parasitology, Veterinary School, University of Queensland, St. Lucia, Brisbane, Queensland;
MNHNLV - Museum Nationale d'Histoire Naturelle, Labortoire der Vers, Rue Buffon, Paris; Obendorf - Dr. D. Obendorf, Department of Agriculture, Mt. Pleasant Laboratories, Launceston, Tasmania;
PP - Dr. P. Presidente, Atwood Veterinary Laboratory, Parkville, Victoria; QM - Queensland Museum, Petre Terrace, Bowen Hills, Brisbane, Queensland; USNMHC - United States National Museum Helminthological Collection, Smithsonian Institute, Washington, D.C.;

P = parasitic

FL = free living

D = specimen obtained from mucosa by dissection

H = specimen examined in histological section

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