STUDIES ON THE GENUS *KALICEPHALUS* IN SNAKES

by

Gerhard Adam Schad

A

Thesis

Submitted to the Faculty of Graduate Studies and Research of McGill University in partial fulfilment of the requirements for the degree of

Doctor of Philosophy

May 1955

Ph.D. PARASITOLOGY

Gerhard Adam Schad

STUDIES ON THE GENUS *KALICEPHALUS* IN SNAKES

The state of systematics in the genus *Kalicephalus* and the taxonomic characters used by previous authors are discussed. Several suggestions are offered as to the value of various taxonomic characters. The North American species are reviewed and three are redescribed, several formerly recognized species are reduced to synonomy and a key to the North American species is provided.

The life cycles of *K. parvus*, *K. agkistrodontis* and *K. rectiphilus* were investigated experimentally. Differences between the three species are noted in histotropism and rate of development. The parasitic third stage of *K. parvus* is given special attention, as is the development of the genital primordium and the spicular primordium in this species.

Infection *per os* was successful in all three species investigated. Skin penetration apparently also occurs. The mode of infection in nature is discussed and the life histories of *K. parvus*, *K. rectiphilus* and *K. agkistrodontis* are compared to those of related species. A host catalogue, world-wide in scope, is provided.

ACKNOWLEDGEMENTS

The author is greatly indebted to Dr. T.W.M. Cameron who directed this research. His advice and criticism have been invaluable. The use of the facilities of the Institute of Parasitology is also gratefully acknowledged.

The appreciation of the author is extended to Miss J. Smith of the Institute of Parasitology for her aid in securing the necessary literature and for reading the manuscript.

The San Diego Zoological Society, and especially its Research Committee and the Managing Director, Dr. C. Schroeder, are deservant of grateful thanks for the fellowship they provided, for the interest taken in this work and for the special grant of remaining funds which will enable the completion of the taxonomic studies begun here.

The author also wishes to thank Mr. W.A.Inglis of the British Museum (Natural History), Drs. Price and McIntosh of the United States National Museum, Dr. R.J. Ortlepp, Dr. P.O'Connor, Dr. R.J.Reiber, and The Institute Butantan for the loan of specimens. Dr. L. Goss of the New York Zoological Society generously provided space in the hospital of the New York Zoological Park where several collections of Kalicephalus were made.

The author is grateful to Mr. W.H.Woodin of the Arizona-Sorona Museum for his generosity and co-operation in sending some of the snakes required for life history experiments. Messrs. Perkins and Shaw of the San Diego Zoological Society made the facilities and library of the Reptile House at the Society's gardens

available to the author. Their help as regards care, nomenclature and distribution of snakes is greatly appreciated and special thanks are due them for the broods of gopher snakes which they reared from eggs.

The co-operation of Drs. L.M. Klauber, E.R. Dunn, A. Loveridge, R.F. Inger and K.P. Schmidt in matters of snake nomenclature is greatly appreciated.

The author is indebted to Mr.K. Ronald of the Institute of Parasitology for photographically reproducing the illustrations contained herein.

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

Two nematode genera, Kalicephalus Molin, 1861 and Diaphanocephalus Diesing, 1851, form the small family Diaphanocephalidae. Members of this family are bursate, small to medium in size and are characterized by laterally compressed, bivalved buccal capsules bearing internally one or two transverse cuticular ridges and externally three parenchymatous bands terminating in the circumoral papillae. They are parasitic in reptiles, where, attached to the walls of the digestive tract, they feed on the host's tissue (Hoeppli and Hsu, 1931).

The genus Diaphanocephalus, which is confined to South American lizards, is comprised of but two species, Diaphanocephalus galeatus (Rudolfi, 1819) and Diaphanocephalus diesingi de Freitas and Lent, 1938. Structural characters of the buccal capsule separate this genus from the closely related Kalicephalus.

The latter, composed of approximately 50 species, is normally parasitic in snakes and occurs in all sections of the digestive tract from oesophagus to rectum. Species of Kalicephalus have been recovered from snakes inhabiting all zoogeographical regions and all major habitats i.e. marine, arboreal etc.

The snakes from which the majority of Kalicephalus are known may be placed in two groups. These are: 1. Snakes frequently displayed in zoological gardens, and 2. Snakes which are common and readily collected by the parasitologist surveying a local fauna. Those snakes shown in zoological gardens tend to be spectacular species, i.e. those which, by virtue of their large size, their poisonous nature or by the awe they inspire in the public, make a good display. The author does not wish to minimize the value of parasitic material from this source,

but he does desire to point out that its study has resulted in a great imbalance in the degree to which individual ophidian species have been investigated for helminth parasites. Thus the bushmaster, Lachesis muta, apparently rare in nature, has a relatively well-known helminth fauna, while the small South American vipers, certainly as common as the bushmaster, have been very incompletely surveyed.

There is a similar imbalance in the survey work of the parasitologist. In this case, the small, secretive species, found abundantly only by the herpetologist, are poorly known as regards their intestinal helminths, while the larger, more conspicuous serpents have been surveyed often. The need, then, is for more extensive collections of material from the smaller, the arboreal, the fossorial and the nocturnal snakes.

Before turning more directly to the parasites themselves, the author also wishes to point out the inadequacy of many host designations. Too often the snake is identified only by a museum or collection number, a provisional museum name which has never reached the herpetological literature, or by a designation such as "Snake-East Africa." The identification of these snakes is now next to impossible. Less exasperating, but still most difficult, is a tendency for the earliest host names to be carried forward through the literature by more recent workers, with no effort to include also the extant designation. The longer a name is out of use, the more difficult it is to find its current equivalent. Admittedly most helminthologists are not in the position to make accurate host designations in all the groups they may encounter, nor are they always acquainted with the necessary

literature. However, the author wishes to register a plea for greater attention to proper host designation. In the catalogues included in this thesis, an attempt has been made to check the accuracy of the host name used and, wherever possible, a specialist in the particular group of snakes or in the snakes of the particular region concerned has been consulted.

There is no comprehensive treatment of the genus Kalicephalus presently available, but papers by Molin (1861), Ortlepp (1923), Maplestone (1931), Harwood (1932, 1934) and Hsü (1934) are important. Baylis (1936) in "Nematoda: Fauna of British India", provides a good revision of the species known from snakes of the Indian subregion.

Taxonomically the genus Kalicephalus is difficult. The established systematic characters are frequently more variable within a species than they are between two species described as distinct. In general, one or two morphological criteria do not permit the separation of species of Kalicephalus; rather a group of characters must be considered. However, the configuration of the dorsal ray of the bursa and the direction taken by the uteri from the ovejector, whether divergent or convergent, suffice in identifying unknown material to a species complex. More definite identification is often difficult. One worker, Sandground (1933), would not attempt specific identification under the prevailing conditions.

The problems facing a student of Kalicephalus today are not only those inherent in the genus. These difficulties have been greatly multiplied by inadequate descriptions, often based on few specimens or on males or females alone, and by the failure of most authors to restudy type material of early workers. The resultant chaos has led

even the most reliable nematologists into error and today the student is confronted by a tangle of species which are most difficult to separate.

Therefore, when attempting to identify several collections of Kalicephalus from snakes dying at the New York Zoological Park, the author found it necessary to undertake studies toward a complete revision of the genus. A project involving taxonomy, life history, variability and geographical distribution has developed.

This thesis will include that part of the total study which has been completed as a student at the Institute of Parasitology and during a year apart as Research Fellow at the San Diego Zoological Gardens. The material herein reported consists of 1. The bibliographical research basic to the problem, which is represented in the main by the historical review and the catalogues concluding the thesis; 2. A taxonomic revision of the North American species, which establishes the identity of the species on which 3. Life history studies are reported. Exotic species have been studied, but this material is not included here except as a check on the conclusions reached in the study of North American species. Its description must await the completion of investigations approaching complete world-wide coverage. Such a study, leading to a revision of the genus, is planned and should be possible at the termination of work on the collections of the British Museum (Natural History), the United States National Museum and the Vienna Museum.

The project outlined above is important from the point of view of pure zoology, but it should not be overlooked that the bursate nematodes constitute a most important group economically. These

nematodes, the Strongylina, include the hookworms of man and domestic animals, the lungworms, the gapeworms and several other groups injurious to the health of animals. Of this important suborder, the Syngamidae (gapeworms) and the Diaphanocephalidae are most primitive on the basis of the cephalic papillae (Dougherty, 1951). It seems to the author, then, that this family offers excellent opportunities for comparative studies which could yield information applicable to the medically important strongylins.

Noteworthy here also is the parallelism in the evolution of both snakes and parasites. As has been pointed out by Schmidt (1950), snakes constitute a fruitful area for evolutionary studies, since, in spite of their homogeneous structure, they have been able to invade almost all available habitats. Morphologically the genus Kalicephalus is also unusually homogeneous, yet it has been able to follow its ophidian hosts into all the various habitats the snakes have entered. This suggests the possibility of marked life history modifications, which, should they occur, would be interesting indeed.

HISTORICAL REVIEW

The earliest report of nematodes belonging to the family now known as the Diaphanocephalidae is that of Rudolfi (1819). In his "Entozoorum Synopsis" he listed Strongylus galeatus, Strongylus costatus and Strongylus viperae. Present day authors assign the first species to the genus Diaphanocephalus and the latter two to the genus Kalicephalus; these genera comprise the family Diaphanocephalidae as it now stands.

In 1845, Dujardin separated S. costatus and S. galeatus from the all inclusive Strongylus, placing them in the equally heterogeneous Sclerostoma. Diesing (1851, 1861) contributed the genus Diaphanocephalus and included in it the three species as reported by Rudolfi (1819). In his "Revision der Nematoden" (1861), he placed these diaphanocephalids in the subfamily "Deletrocephalidea" of the family "Strongylidea."

Molin (1861), in his lengthy "Il Sattordine Degli Acrofalli", greatly advanced the classification of parasitic nematodes by breaking up the large, heterogeneous genera of his contemporaries. He accepted the genus Diaphanocephalus with the species as placed therein by Diesing. However, for seven new bursate nematodes from South American snakes, he created the genus Kalicephalus. Essentially this arrangement is a modern one. Furthermore Molin indicated a definite awareness of the close relationship between Kalicephalus and Diaphanocephalus --- "Un genere affine Diaphanocephalus e Deletrocephalus e il genere Kalicephalus." (Deletrocephalus, of course, can no longer be regarded as closely related to the other two genera). Of the seven species described, only one is figured and none is designated as type of the genus. One, K. bothropis, is listed as species inquirenda.

Wücherer (1872) and Blanchard (1886) mentioned bursate nematodes from snakes; however they confused these with ancylostomes. In a general account of ancylostomiasis, the former discussed a collection of strongylins from the stomach of Lachesis muta, the bushmaster. The description indicates that these were kalicephalids, although Wücherer himself considered them closely related to the ancylostomes. Blanchard's (1886) material was from a boa constrictor and his illustration shows the specimens to be a species of Kalicephalus. Blanchard, however, erroneously described oral hooks for what were certainly sections of an anterior chitinous ridge and placed his new species in the genus Ankylostoma.

Von Linstow (1878), in his compendium of helminthology, accepted Kalicephalus as a generic name but rejected Diaphanocephalus in favour of Strongylus.

In 1895, Stossich produced two papers, one a review of the genus Ankylostoma including a restatement of Blanchard's (1886) description of A. boae, and another in which he described a new species, Dochmius vallei. In the years immediately following, 1896 to 1900, Stossich dealt with species of Kalicephalus repeatedly. In 1896, he described Strongylus ersillae from a python, and in 1897 he synonomized his D. vallei with Rudolfi's (1819) Strongylus viperae and placed the species in the genus Sclerostomum. Then, in 1899, he reviewed the Strongylidae, but unfortunately his concept of the strongylin genus was not as modern as that of Molin (1861). Stossich returned the species in Molin's smaller, more homogeneous genera to the large heterogeneous Strongylus, Sclerostomum etc. Thus Molin's

seven species of Kalicephalus were assigned to Sclerostomum. This change necessitated the renaming of K. mucronatus Molin, 1861, since Ascaris mucronata Fröhlich, 1791, was also included in Sclerostomum. Stossich renamed K. mucronatus, Sclerostomum kalicephalum.

Looss (1902), discussing parasitic nematodes in general, noted a need to divide the genera then generally accepted into more natural groupings. He observed that Molin was probably closer to true generic division than either his contemporaries or subsequent helminthologists.

Von Linstow (1904, 1906, 1908), working in India and Ceylon, published three papers in which he again recognized the genus Kalicephalus.

Allessandrini (1905), in a review of the genus Uncinaria, listed one species from an atypical host, a snake, and identified it as conspecific with A. boae (Blanchard, 1886). He showed no recognition, however, of the true affinities of this nematode with the genus Kalicephalus.

Stiles and Hassall (1905), in "The Determination of Generic Types", listed Molin's seven species and noted that K. inermis should probably be selected as type of the genus Kalicephalus, since, of the original seven, it was the only species figured. (It might be added that this species was also the first one listed and thus can also be considered type by page priority). Sambon (1907, 1909) recognized the genus Kalicephalus. He reported Kalicephalus spp. from several snakes.

Leiper (1908), in a succinct discussion of the classification of bursate nematodes, indicated the need to reinstate many of Molin's suppressed genera into any modern classification. Among these he included Kalicephalus. He divided the bursate nematodes into three

families; the Strongylidae, the Metastrongylidae, and the Eustrongylidae and placed Kalicephalus in the Strongylidae in a subfamily of its own, but proposed no name for such a subfamily. Railliet and Henry (1909), however, considered Kalicephalus a synonym of Diaphanocephalus and included this genus as one of uncertain position in the subfamily Ankylostominae of the family Strongylidae. Looss (1911) recognized that several bursate nematodes of reptiles previously placed in various genera constitute a homogeneous group and furthermore suggested that they probably form a separate family within the order "Strongyles".

MacCallum (1918) described Camallanus bungari from a krait and later (1921) he described Strongylus boae from a boa constrictor. The written descriptions of these species are very poor but re-examination of the types has identified them as species of Kalicephalus.

Travassos (1919) originated the name Diaphanocephalidae. He included therein only the genus Diaphanocephalus, Kalicephalus receiving no recognition.

In the "Index Catalogue of Medical and Veterinary Zoology" dealing with nematodes, Stiles and Hassall (1920) listed 12 species of Kalicephalus, and noted that the designation of a generic type is a peculiar case, one which is "not altogether clear under the Code". However, they believed K. mucronatus (K. kalicephalum) to be the type of the genus rather than K. inermis, which they had tentatively designated in 1905. The basis for the selection of K. mucronatus is as follows:

Molin (1861) designated no generic type among his original species of Kalicephalus. Stossich (1899), in removing Molin's species

to Sclerostomum, was forced to change the specific name of K. mucronatus, since there was another species, Sclerostomum mucronatum Fröhlich, 1791, with priority. Stossich changed Kalicephalus mucronatus to Sclerostomum kalicephalum, the latter name becoming a synonym of K. mucronatus upon the reinstatement of Kalicephalus as a valid genus. This synonomy then created the tautonomy establishing the type of the genus.

Baylis and Daubney (1922) and Daubney (1923) followed Railliet and Henry (1909) in considering Kalicephalus a synonym of Diaphanocephalus. They placed several new kalicephalids in the genus Diaphanocephalus, subfamily Deletrocephalidae, of the family Strongylidae.

However, Ortlepp (1923), in the first extensive modern study of the group, again separated the genera Kalicephalus and Diaphanocephalus and also included a third genus, Occipitodontis, in this group. No discussion of the higher categories was given.

Yorke and Maplestone (1926) accepted Ortlepp's three genera as constituting the Diaphanocephalidae, and listed 24 species of Kalicephalus. They noted, however, that many of these were probably synonymous; K. mucronatus was considered the generic type. Baylis and Daubney (1926), in their "Synopsis of Families and Genera of Nematoda", recognized the name Diaphanocephalidae as the correct family designation and synonymized the genus Occipitodontis Ortlepp, 1923 with Kalicephalus. They pointed out that the characters used as the basis of separation were ones which are variable within a strongylin genus. Rauther (1930), in the nematode section of Kükenthal and Krumbach, "Handbuch der Zoologie", accepted the genus Kalicephalus with K. mucronatus as the generic type.

Maplestone (1931) described seven species of Kalicephalus from snakes dying in the Calcutta Zoological Gardens. Several of these were new to science. Hsü (1934) published an excellent paper on the genus Kalicephalus in China, therein describing three new species and supplying additional measurements and morphological data on known Asiatic species. He noted the difficult systematics encountered in the genus Kalicephalus, and offered a review of the systematic characters of the genus. Baylis (1936) gave nematology its first acceptable systematic account of the kalicephalids from a large faunal area, namely the Indian subregion. By the restudy of type material, he was able to reduce considerably the number of Indian species and replace the taxonomic confusion with clearly characterized species. However, he stated:

> It seems at present almost impossible to construct a satisfactory key to the Indian species of this genus, owing to the great amount of variation and overlapping in their measurements, and the great uniformity of their morphological characters.

Harwood (1932, 1934) described several North American species and gave a key to the Nearctic species described to the time of his publication.

Chitwood and Chitwood (1937, 1950), in an outline classification of nematodes, included the Diaphanocephalidae in the superfamily Strongyloidea, along with the Strongylidae, Ancylostomidae, etc. Elsewhere in "Introduction to Nematology", the family designation Kalicephalidae is used. The latter name was never formally proposed by either previous workers or by the Chitwoods themselves, and no doubt represents a lapsus. As such, the name has no nomenclatural status and should not be considered as a valid synonym.

Dougherty (1946, 1951) considered the Diaphanocephalidae and the Syngamidae the most primitive strongylins, the latter being the more primitive morphologically. He listed these within the Strongylina without superfamilial grouping. Hyman (1951) recorded the genera Kalicephalus and Diaphanocephalus in the family Diaphanocephalidae of the order Strongyloidea.

This review traces the history of the genus Kalicephalus from the time of Rudolfi to the present. It does not, however, trace the history of individual species. Papers dealing solely with the description of individual species have been largely omitted. In general, only those papers involving the recognition or rejection of Kalicephalus as the appropriate generic designation and those establishing higher taxonomic categories have been included. The published information on the anatomy, ecology and life history of species of Kalicephalus is scant and is more appropriately discussed in subsequent sections of this thesis.

TAXONOMY

Introduction

Systematic problems encountered in the genus Kalicephalus have been attributed to difficulties inherent in the group (Baylis, 1936; Hsü, 1934; Campana and Chabaud, 1950). These authors suggest that intraspecific variability and interspecific homogeneity are the basis of these difficulties. Campana and Chabaud (1950) state:

> Le genre Kalicephalus Molin, 1861, répresenté par une quarantaine d'espèces, est très homogène; même pour les espèces récemment décrites, les déterminations ne reposent souvent que sur des variations très faibles, plus faibles parfois d'une espèce à une autre qu'au sein d'une même espèce.

In the introduction to this thesis, the author comments on the chaos presently characterizing the systematics of this genus, but indicates that the confusion existing today is not entirely resultant from variability within a species and great similarity between species. To some degree the problem is one of the helminthologists' own making. It results, in part, from the failure of the first modern authors (1900-1926) to restudy and redescribe the species created by the early workers whose written descriptions are inadequate and whose inaccurate figures do no more than indicate that their specimens were indeed kalicephalids! Thus we inherit two species from Rudolfi (1819), seven from Molin (1861) and one from Blanchard (1886). Of these K. viperae (Rudolfi, 1819) and K. subulatus Molin, 1861 have been subsequently redescribed.[1] Two species, K. costatus (Rudolfi, 1819)

---

[1] Redescriptions by Dollfus and Chabaud (1949) and Ortlepp (1923) respectively. However, there is some doubt that K. subulatus Ortlepp, 1923 is conspecific with K. subulatus Molin, 1861 (see page 52).

and K. appendiculatus Molin, 1861, have been redescribed by Skrjabin (1916) and Stossich (1900a,b) respectively, but K. costatus of Skrjabin (1916) is certainly not K. costatus of Rudolfi (1819). Similarly, Stossich's (1900) K. appendiculatus, which was redescribed by Boulenger (1926), is distinct from its homonym described by Molin (1861). Leiper, who has seen Molin's types, has suggested that K. appendiculatus may not even be a kalicephalid![1] One cannot solve the problem of these old species by ignoring them and nomenclaturally considering them nomina dubia. Presumably the material still exists and we invite further complications should it be redescribed and the original names resurrected. The types could and should be restudied.[2]

A second failure of these early authors of the modern school, whose work is accurate as far as it goes, is that their own species are not positively identifiable. There was misplacement of emphasis in the original description. Unimportant characters were stressed and important ones ignored. These descriptions were frequently based on small, uniform collections and this allowed subsequent authors to describe larger or smaller variants as new species.

The result was that by 1926 Yorke and Maplestone were able to list 24 species. Fourteen of these were described prior to 1900, and only one or two of these can be identified at present. Remaining are 10 species attributable almost entirely to Baylis and Daubney (1922),

---

[1] Personal communication from Leiper, who saw Molin's types in the Vienna Museum.

[2] Restudy of this material by the author prior to the writing of this thesis was impossible, but it is planned for the near future.

Daubney (1923) and Ortlepp (1923). A few of these are certainly synonymous with species described in the earlier period, and this would be a minor problem if subsequently many variants of already known species had not been described as new.

It is clear, when one begins a review of this genus and has sufficient material at hand in both numbers of species and individuals of one species, that subsequent authors could not have identified their small collections with the narrow descriptions of their predecessors.

In the period 1930 to 1950, new names were given variants of known species, the list of species grew and the differences between them became ever smaller. Of course, some valid species were also described.

According to Campana and Chabaud (1950), approximately 40 species of Kalicephalus are recognized at present. The author's count, based on an intensive search of the literature, reveals 50 species of which, in his opinion, as many as 40% may be synonyms.

This pattern of discovery and early inaccurate characterization, followed by an era of description of numerous species, in turn followed by integration, evaluation and understanding is well-known. The beginnings of the last phase are found in Baylis (1936), who has revised the Indian species, in Harwood (1934), who provides a key to North American species, and in papers by Hsü (1934) and Campana and Chabaud (1950), who have discussed the relative value of certain systematic characters. In the author's opinion, the papers by Hsü (1934) and Campana and Chabaud (1950) present a basis for satisfactory identification of species in the genus Kalicephalus. Their suggestions, however, require evaluation and therefore the author desires to discuss the taxonomic

characters which have been used by previous authors before redescribing the North American species, K. parvus Ortlepp, 1923, K. rectiphilus Harwood, 1932, and K. agkistrodontis Harwood, 1932.

The following discussion is based on a study of

I. Personal collections

A. Native material[1]

1. An extensive series of K. parvus from several hosts, all specimens of which were examined and 100 specimens of which were measured.

2. A large series of K. agkistrodontis mainly from Coluber c. constrictor, 50 of which were measured.

3. A smaller series of K. rectiphilus found almost exclusively in the rectum of Coluber c. constrictor.

B. Exotic material

1. The South American species K. subulatus collected from a bushmaster, Lachesis muta, which died in the New York Zoological Park.

2. The Australian species, K. novae-brittanae, collected from an Australian copperhead, Denesonia superba, at the New York Zoological Park.

II. Several collections given or loaned by other individuals or institutions.

A. African species collected by R.J.Ortlepp, Onderstepoort Veterinary College, P.O'Connor, Veterinarian, Staten Island

---

[1]Complete listings of the hosts are to be found in the sections dealing specifically with each of the kalicephalids.

Zoological Park, and the United States Navy Medical Research Unit #3, Cairo.

B. Two South American species loaned by the Institute Butantan, Sao Paulo, Brazil.

C. Type and other material loaned by the United States National Museum, the British Museum (Natural History), and R.J. Reiber, University of Georgia.

Review of the Taxonomic Characters

Recognizing that the gross subdivisions of the genus as advocated in the discussion following may be artificial (formal subgeneric division is not proposed), the author follows Ortlepp (1923) in considering the divergence or convergence of the uteri as the basis for a primary division of the genus. A secondary division, based on the pattern of the terminal branching of the dorsal ray, is suggested. It is modified and expanded from Hsü (1934).

The uteri: Ortlepp's (1923) division of the genus into Groups A and B on the basis of the uteri, whether divergent or convergent, has been used by some subsequent authors. However, to refer to species as belonging to "Group A" or "Group B" of Ortlepp is an undesirable practice in that it tends toward the elevation of these to subgeneric status. The groups are artificially divided, and indeed a division does not really exist. K. laticaudae Yamaguti, 1935 is variable in this uterine character and the author has studied another species, K. simus (Daubney, 1923), in which the uteri may sometimes begin as divergent but the posterior branch, after a short course posteriorly,

turns forward to converge with the anterior branch. However, in a description of a species, the course taken by the uteri should be mentioned since this appears to be constant for most species.

The dorsal ray: Hsü (1934) proposed a system of groups based on the configuration of the terminal branches of the dorsal ray by which he felt one could arrive at a species complex. The terminal ramification invariably consists of three pairs of branches.[1] Hsü's scheme is quoted below (see also schematic presentation page 20).

1. One branch on each side takes its origin from the base of the dorsal ray, from which it is widely separated throughout its whole length. The common stem of the dorsal ray after a varying length divides into two branches, each of which subdivides again into two terminal branches. These two last ones are comparatively short and more or less of the same length. K. naiae is the representative.

2. The dorsal ray divides into two short main branches each of which subdivides into three terminal branches which may be equal or unequal in length. K. nankingensis and K. sinensis are the representatives.

   The second type may be subdivided into two subtypes based upon determining whether the anterior terminal branch is or is not definitely separated from the two posterior branches. K. nankingensis and K. sinensis are the representatives of the two subtypes.

Campana and Chabaud (1950) suggest that the dorsal ray pattern in conjunction with the characters 1. Course taken by the uteri (convergent or divergent); 2. Position of the cervical papillae and excretory pore; and 3. Shape of the female tail, permits identification of material to a group of related species.

---

[1] In Kalicephalus agkistrodontis the terminal branching is variable to some degree. Typically three pairs of branches occur but occasionally variants with fewer branches or with an extra branch occur.

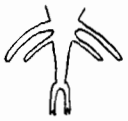
The latter view is more nearly correct. The configuration scheme of Hsü (1934) is insufficient in itself. His category 1 emerges as a specific character; there is but one described species having this type of ray. Category 2 contains the remaining 40-odd species. While only four species can be assigned to subdivision 2a (the "nankingensis" type), the remainder fall into group 2b (the "sinensis" type).

If Hsü's scheme is used in conjunction with the uterine characters already suggested, a number of smaller groupings emerge, and, in the author's opinion, the recognition of these groups facilitates the comparison and identification of species. Therefore, he presents the following categories, which are modified and expanded from Hsü (1934).[1,2]

---

[1]The list of species for each category is tentative. All described species are not included since the author has not studied many of these and the available descriptions of some species are not complete enough to permit placement. Some dorsal rays are figured so schematically that identification to one or other of the groups here recognized is impossible. Some species listed are probably synonymous.

[2]This classification does not contradict the previous statement concerning the primary division of the genus on the basis of uterine characters. The dorsal ray characters are given prominence over uterine characters in this discussion to emphasize their value.

I. (Group 1 of Hsü)		"minutus" type (naiae type of Hsü)	K. minutus (= K. naiae)
II. (Group 2 of Hsü)			
A. (Group 2a of Hsü)		"nankingensis" type uteri divergent	K. enygri K. rectiphilus K. brachycephalus K. nankingensis
B. (Group 2b of Hsü)			
1 (a)		"indicus" type uteri convergent	K. indicus K. parvus K. philodryadus K. obesus K. elongatus K. novae-brittanae
(b)		"indicus" type uteri divergent	K. agkistrodontis[1] K. subulatus K. coronellae K. conoidus
2 (a)		"sinensis" type uteri divergent	K. sinensis K. colubri of Lopez-Neyra K. appendiculatus of Stossich and Boulenger
(b_1)		"longior" type uteri divergent	K. longior K. chunkingensis K. colubri K. bitisi K. willeyi K. rotundatus K. obliquus
(b_2)		"longior" type uteri convergent or variable	K. simus K. nigeriensis K. laticaudae

[1]Occasional specimens have variable terminal branching.

Discussion of the proposed species groupings: Definitions of groups already defined by Hsü (1934) and quoted on page 18 are not repeated here. Certain dorsal ray patterns which were not considered particularly useful previously are given special significance by the author. In the case of these, appropriate examples as figured by Hsü are cited. This course seems desirable since in the literature some reference has already been made to patterns illustrated by Hsü.

Group I: This group is identical with group 1 of Hsü and, as already pointed out, it is monotypic. K. minutus, a common parasite of cobras in Asia, is its sole representative. This species is unique in both its dorsal ray pattern and in the character of its spicules, which are markedly unequal.

Group II: This group corresponds to Hsü's group 2 and contains all species other than K. minutus. Hsü subdivides this group into two lesser groups. One of these is retained by the author but with some elaboration, while the other is divided into five lesser groups.

Division A of Group II (Group 2a of Hsü): This division is represented by species possessing bursae in which the dorsal ray exhibits the "nankingensis" pattern. This ray is intermediate between the "minutus" type and the "indicus" type. In some specimens, it approaches one or the other of these allied forms and therefore there is no clear-cut separation. However, species with the "nankingensis" pattern

have divergent uteri in common and occur in the rectum of snakes.[1] Taken together, these characteristics clearly separate this group from others. K. rectiphilus is the Nearctic representative.

Division B of Group II (Group 2b of Hsü): Group 2b of Hsü contains the majority of known species, about 30,[2] and clearly without modification offers little help. When uterine characters are considered, about six species, characteristically possessing convergent uteri, are separated easily from the remainder. It is found that these have a dorsal ray type in common. The author therefore proposes:

> Subdivision 1a of IIB: All terminal branches arise distally and remain closely associated. The anterior terminal branches originate, elbow and more or less parallel the stems of the posterior terminal branches. The common stems of the posterior terminal branches are distinct entities. This terminal branch pattern is designated as the "indicus" type figured by Hsü but given no special significance by him. K. parvus is the Nearctic representative.

---

[1] K. willeyi, as reported by von Linstow in several papers (1904, 1906, 1908), has been recognized as a heterogeneous assemblage by both Ortlepp (1923) and Baylis (1936). They indicate that von Linstow's records of this parasite from snakes other than Vipera russelli require confirmation. Von Linstow noted that his material from Typhlops braminus was recovered from the rectum. A species of group 2a should, therefore, be expected.

[2] The figures here given do not add up to the total number of species recognized since some descriptions do not include these major characters. Some are based on females alone and therefore no description of the bursa is available.

Subdivision 1b of IIB: In these species, the dorsal ray is similar to the "indicus" pattern in that a definite common stem exists after the anterior terminal branches originate, but occasional specimens have variable posterior terminal branching (footnote page 18) and there is a tendency toward intergradation with the "longior" pattern as seen in IIB, 2b. These species all have divergent uteri. The author is as yet uncertain as to how many species are members of this category. He, therefore, assigns only the related New World species of the K. agkistrodontis group to this category.

Remaining is the large group of species having a dorsal ray in which all the terminal branches arise at almost the same level. A distal, common stem, if present, is not as distinct an entity as it is in the preceding groups. The approximately 14 species so characterized are tentatively subdivided on the basis of smaller dorsal ray characters and characteristics of the uteri.

Subdivision 2a of IIB: Stossich (1900a,b), Boulenger (1926), Hsü (1934), and Lopez-Neyra (1949) furnish illustrations of dorsal rays which are remarkably similar. Indeed, those of Stossich, Boulenger and Lopez-Neyra are almost identical (text Fig.1).

The author has not seen any species with a dorsal ray as illustrated in text Fig.1, but he is willing to accept it as a distinct type on the basis of its description by these three authors who figure it almost identically.

Furthermore, two of these authors found the same morphological type in the same host, namely the East Indian snake, Boiga irregularis (= Dipsadormorphis irregularis). This group is then defined as one in which all terminal branches arise at approximately the same level. These branches are knob- or spike-like and, in this respect, differ from the group following, which has longer branches. The "sinensis" type of Hsü (1934) is representative. The uteri are divergent. No Nearctic representative is known.

Subdivision 2b of IIB: The species included herein show a dorsal ray pattern such as is found in the "longior" type. However, this group is further divided on the basis of the uteri. Most species possess divergent uteri; these are thereby separated from those with convergent or variable uteri.

It is suggested that the type specimen selected in describing new species of Kalicephalus should be a male in view of the taxonomic value of the dorsal ray of the bursa.

The vulva: The vulvar ratio and whether the vulva is a simple slit, level with the ventral surface of the nematode, or opens on a distinct prominence, are characters which have received considerable attention in taxonomic accounts from the time of Ortlepp's (1923) publication to the present.

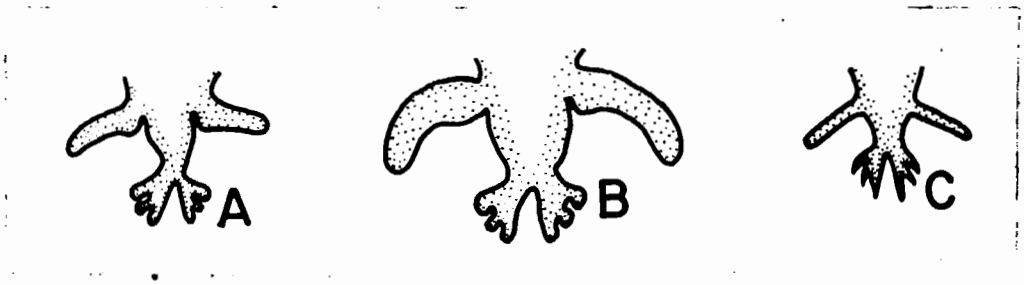


Figure 1. The Dorsal Ray of Kalicephalus sinensis Hsü, 1934 and of Kalicephalus appendiculatus Stossich, 1900. A. K. appendiculatus Stossich (after Stossich 1900a, b) B. After Boulenger, 1926 C. K. sinensis Hsu (after Hsü, 1934).

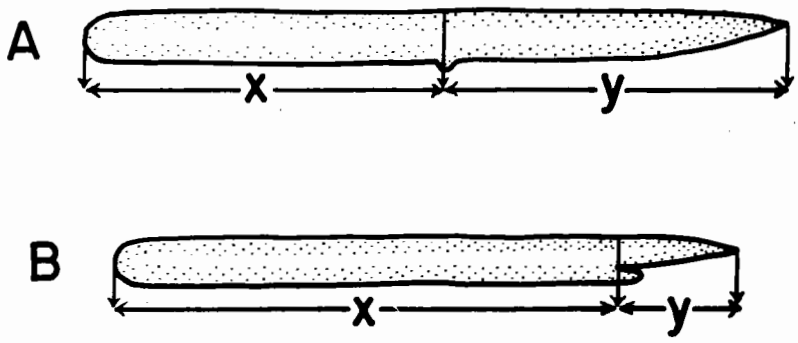


Figure 2. Illustrations of Methods of Computing Vulvar Ratio.

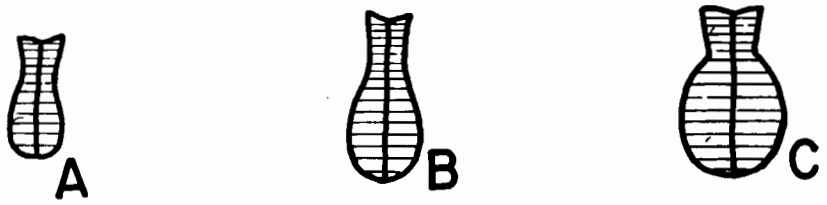


Figure 3. The Oesophagus of Kalicephalus parvus, Kalicephalus agkistrodontis and Kalicephalus rectiphilus. A. K. rectiphilus B. K. agkistrodontis C. K. parvus

In the case of the vulvar ratio, measurements based on 50 female K. parvus yielded ratios of 3.45-10.66:1. However, Hsü (1934) found a more constant ratio, 2.89-4.26:1, in 50 specimens of K. indicus Ortlepp, 1923. He concluded that both the pre- and postvulvar portions of the worm grow until the final length is attained. It has been observed in Camallanus americanus that the prevulvar portion of the female is more constant in length than the postvulvar portion.[1] This is the case in K. parvus. In ratios showing the greatest departure from the average, one usually finds that the postvulvar rather than the prevulvar portion is abnormally short or long. In the author's experience, species possessing convergent uteri tend to be more variable in this character than those possessing divergent uteri.

In most specimens of K. parvus, the postvulvar body contains only the end of the intestine and the few structures of the female tail. Occasional specimens, however (possibly senile females), have several ovarian coils extending into the postvulvar body. A sufficient number of specimens of this type are not yet available to the author to permit a definite conclusion, but those seen to date have longer postvulvar lengths. This, however, can be only a partial explanation since specimens do not occur frequently and a series containing no such specimens has been measured and found extremely variable (vide supra).

It is desirable, however, that this ratio be included in

---

1 Magath, T. B., 1919. Camallanus americanus, nov. spec., a monograph on a nematode species. Tr. Am. Micr. Soc. 38: 49-170.

descriptions. In species with convergent uteri, one should recognize this character as one of great variability, but in species having divergent uteri, where the ratios tend to be more constant, it has some use. However, vulvar ratios should never be used as the sole criteria in separating closely allied species.

The author has found an error in the vulvar ratio given for several species. The types of some of these have been remeasured and the ratio calculated. The cause for error is not apparent, but may possibly result from the ratio being taken in different ways. Therefore, illustrations are given to indicate the manner in which the author has calculated the vulvar ratio (text Fig.2).

The female tail: Hsü (1934) finds the absolute length of the female tail too variable to be of much taxonomic value. He concludes, however, that its shape is constant within a species and quite different between species.

The author's measurements on the female tail of K. parvus varied from 0.09-0.15 mm; Hsü found a variation in the case of K. indicus ranging from 0.090-0.188 mm. In a species of a different morphological group, K. subulatus, the female tail is described by Ortlepp (1923) to measure 0.36 mm, yet the author's series shows a variation of 0.25-0.52 mm.

The morphology of the tail appears to be fairly constant within a species and there are distinct differences between certain species. At present, however, it would seem to the author that the morphologically distinct tails occur mainly between species which are readily separable on other characters. The character, therefore, fails where needed most,

i.e. in the separation of the similar species of the same complex. Here the tails are, like most other characters, interspecifically similar.

The head capsule: In the character of the head capsule, it is found that closely related species are very similar. Species with markedly distinct head capsules are usually separable on more obvious characters. Furthermore, it is difficult to convey the distinctive form of this structure in either words or illustrations.

The oesophagus: It is as yet impossible for the author to evaluate this character. The three North American species, K. parvus Ortlepp, 1923, K. agkistrodontis Harwood, 1932 and K. rectiphilus Harwood, 1932, are usually separable on morphology of the oesophagus (text Fig.3). But the separation of these three species is relatively simple. On the other hand, the American complex of which K. agkistrodontis is a member and which also includes K. coronellae Ortlepp, 1923, K. conoidus Comroe, 1948 and a South American species whose proper designation is in doubt, is not separable on the basis of this character.

The spicules: Almost all described species of Kalicephalus possess a pair of spicules equal in length. Exceptions to this generalization are the two species, K. minutus (Baylis and Daubney, 1922) and K. conoidus Comroe, 1948. The spicules of the former are of distinctly different lengths, while in the latter the difference is small (0.05 mm). The type material of K. conoidus was examined

by the author and this small difference in length was verified.

Hsü (1934) was of the opinion that spicule length was an important taxonomic character since variation within a species was relatively small, while between species it was relatively great. Hsü cites intraspecific variation within the several species he studied as ranging from 0.03-0.11 mm; from the literature he concluded the intraspecific variation ranged between 0.01 and 0.12 mm, but interspecific variation ranged from 0.236-0.780 mm. He concluded that the difference was sufficiently great to make this character valuable.

The author found a variation of only 0.06 mm between the minimum and maximum length in spicules of K. parvus (0.25-0.31 mm). In another species, however, a variation of 0.30 mm was found. Actually the range of interspecific variation of spicule lengths is greater than that given by Hsü. Some Kalicephalus sp. from Bothrops jararaca have spicules ranging up to 1.00 mm. Then the range is increased to about 0.80 mm between the species with the shortest spicules and the species with the longest.

In the related species, K. parvus, K. indicus and K. philodryadus Ortlepp, 1923, spicule lengths range from 0.25-0.31, 0.30-0.41 and 0.43-0.70 mm respectively. Spicule length is, therefore, a useful taxonomic character.

The excretory pore: Its position relative to the oesophagus is fairly constant. Therefore, in a description, it is desirable to note between which levels the excretory pore is found. A good illustration is essential in species where the character of the

excretory pore is distinctive, e.g. K. simus (Daubney, 1923) has a very noticeable excretory pore marked by a distinct depression in the cuticle. This character was noted in passing by its describer, but not figured, and consequently means little. Actually it is one of the most characteristic features of this species. The author has examined two series of African material, one from the Egyptian cobra, Naja haja, and one from the African spitting cobra, N. nigricollis. In both collections, the excretory pore resembles a button-like elevation within a cuticular depression. The general body contour, however, is not markedly affected by this depression.

In the case of K. parvus (= K. tennesseensis Harwood, 1934), the excretory pore in itself is a simple opening, but usually there is a marked increase in the width of the worm at this level. Harwood's (1934) illustration clearly shows this character.

Cervical papillae: The location of the cervical papillae has been given considerable weight as a taxonomic character by Campana and Chabaud (1950). In the author's experience, this character is relatively constant, but its worth at present is minimized since many descriptions omit reference to the location of the cervical papillae and thus descriptions are not comparable. In general, the cervical papillae in the genus Kalicephalus are minute and thus are probably overlooked.

Campana and Chabaud found these structures shifted surprisingly far to the rear in K. bitisi Campana and Chabaud, 1950, and it is one of their main points in recognizing this species as distinct from K. viperae (Rudolfi, 1819). In the author's experience, an exception

to the generalization that the cervical papillae are difficult to locate is the species K. novae-brittanae Baylis, 1933. In this species they are prominent.

This character may prove valuable but the author is not yet in a position to assess its worth.

The Taxonomic Position of the Genus Kalicephalus

The Family Diaphanocephalidae Travassos, 1920

Diagnosis: Strongylina with bivalved buccal capsule; externally each lateral jaw bears three parenchymatous bands leading to the cephalic papillae; internally each half of the buccal capsule possesses one or two transverse cuticular ridges; submedian cephalic papillae of the external circle not fused; meromyarian; parasitic in the digestive tract of snakes and lizards.

The Genus Kalicephalus Molin, 1861

Synonomy: Strongylus Goeze, 1782 in part, Rudolfi (1819) 37, 647-648
Sclerostoma Rudolfi, 1809 in part, Dujardin (1845) 260
Diaphanocephalus Diesing, 1851 in part, 297-298
Kalicephalus Molin, 1861, 538-549
Ankylostoma Lutz, 1885 in part, Blanchard (1886) 295-296
Dochmius Dujardin, 1845 in part, Stossich (1895) 34
Uncinaria Fröhlich, 1789 in part, Allessandrini (1905) 42-45
Occipitodontis Ortlepp, 1923, 69

Diagnosis: Diaphanocephalidae; each valve of the buccal capsule having one internal transverse ridge; corona radiata usually absent.[1] Uteri convergent or divergent. Genital cone does not extend far beyond the posterior limit of the bursa; monoxenous; parasitic in the digestive tract of snakes.[2]

---

[1]Rudimentary corona radiata present in K. fimbriatus Ortlepp, 1923.

[2]Records from lizards and mammals are accidental.

Abbreviations Used in Host Lists for K. parvus, K. rectiphilus and K. agkistrodontis (pages 34, 40 , and 44).

Host localities

Aca., Mex. - Acapulco, Mexico
Am., Mass., - Amherst, Massachusetts
Ath., Ga. - Athens, Georgia
Col., Ga. - Columbus, Georgia
Houst., Tex. - Houston, Texas
Kiss., Fla. - Kissemee, Florida
Lond. Zoo. - London Zoological Garden
Nash., Tenn. - Nashville, Tennessee
N.A. - North America
N.Y.Z.P. - New York Zoological Park
N.Z.P., Wash. - National Zoological Park, Washington, D.C.

Institutional and personal collections

Br. Mus. (Nat. Hist.) - British Museum (Natural History)
Coll. Reiber - Collection Dr.R.J.Reiber, University of Georgia
I.P. - Institute of Parasitology, Ste. Anne de Bellevue, Quebec, Canada
U.S.N.M. - United States National Museum

Parasitic habitat

duo. - duodenum
g.i. - gastrointestinal tract
lu. - lung
oesoph. - oesophagus
rect. - rectum
sm. int. - small intestine
st. - stomach

Authors

The asterisk (*) denotes identification by the present author
Cab. - Caballero
Har. - Harwood
Ort. - Ortlepp
Rank.- Rankin
Reib.- Reiber, Byrd and Parker

North American Species of Kalicephalus

Kalicephalus parvus Ortlepp, 1923 not Maplestone, 1932

Synonomy

K. parvus Ortlepp, 1923, J. Helminth., 1:65 [type: in Lampropeltis getulus (= Coronella getula) North America (Lond. Zoo) Br. Mus. Nat. Hist.)] . Yorke and Maplestone, 1926, The Nematode Parasites of Vertebrates, Churchill, London. (List described species).

K. tennesseensis Harwood, 1934 not Reiber et al, 1940 J. Tennessee Acad. Sci. 9: 192 [type: in Coluber constrictor, Nashville, Tenn., U.S.A., U.S.N.M.] .

K. floridanus Reiber, Byrd and Parker, 1940 in part, Lloydia 3:125 [type: in Coluber c. constrictor, Kissemee, Fla., U.S.A., U.S.N.M.] .

Type Specimen

K. parvus Ortlepp, 1923, Br. Mus. (Nat.Hist.); from Lampropeltis getulus - stomach, North America (Lond. Zoo.).

Hosts

Lampropeltis getulus - st., N.A. (Lond. Zoo.), Ort. '23
duo., Fla., U.S.A. I.P.*
Coluber c. constrictor - duo., Nash., Tenn., U.S.A., Har. '34
st., duo., Kiss., Fla., U.S.A., Reib. '40
st., duo., Fla., U.S.A., I.P.*
Masticophis f. flagellum - duo., N.Y.Z.P., U.S.A., I.P.*
Elaphe obsoleta deckerti - duo., Fla., U.S.A., I.P.*
Elaphe vulpina - g.i., N.Z.P., Wash., D.C., U.S.A. (USNM 43954)*
Heterodon platyrhinos - lu., N.Z.P., Wash., D.C., U.S.A. (USNM 31954)*

History

Ortlepp (1923) described Kalicephalus parvus from the stomach of the North American snake Coronella getula. (The extant designation of this snake is Lampropeltis getulus). Only three specimens, one male and two females (immature), were available and thus the original description is inadequate.

Harwood (1934) described K. tennesseensis from Coluber c. constrictor and in his key he separated this species from K. parvus on a difference

in vulvar ratio.

Reiber, Byrd and Parker (1940) report several collections of nematodes from snakes in Florida as K. tennesseensis, but this is an error. The species reported by these authors as K. tennesseensis is K. agkistrodontis Harwood, 1932, whereas their new species, K. floridanus from the stomach and duodenum of Coluber c. constrictor, is, in part, K. parvus.

New Synonomy

The following are new synonyms of K. parvus:

K. tennesseensis Harwood, 1934 not Reiber et al, 1940

K. floridanus Reiber, Byrd and Parker, 1940

Diagnosis

Kalicephalus; uteri convergent; dorsal ray of the "indicus" type; head capsule and oesophagus robust; body increases abruptly in width immediately behind excretory pore; known only from North American snakes.

Description (Plate I; A,B,C,D)

A relatively stout species; its width usually maximum immediately behind the excretory pore; at this point the general body contour is broken on the ventral side by the sudden unilateral increase. The excretory pore opens through the cuticle in the area bounded by the anterior level of the oesophageal bulb and the level of the bulb's greatest diameter. It is a simple pore.

The head capsule is robust; the oesophagus relatively short and stout. The nerve ring surrounds the oesophageal isthmus at

varying levels from just anterior to the bulb to the midpoint of the isthmus.

The male: The alate spicules are equal and relatively short. The gubernaculum viewed ventrally is dart-shaped; it has smooth contours. In each lateral wall of the cloaca, there is a sclerotization in the form of a low crest. The dorsal ray of the bursa is stout; the externo-dorsal rays arise near its midpoint; bifurcation occurs and from each short common stalk the anterior terminal branch originates, elbows almost 90° and extends posteriad; after giving rise to the anterior terminal branches the common stalks extend posteriad as two distinct stems and bifurcate only at their tips; the inner branch is elbowed.

The female: The uteri are convergent; usually the postvulvar body is free of reproductive structures.[1] The ovejector is bent into an arc. The vulva is variable; it may merely open on a prominence or be markedly pedunculate. Immediately posterior to the vulva, the body narrows abruptly. The tail is short; its tip is bent ventrally.

---

[1] The occasional specimen contains postvulvar ovarian coils.

Measurements

Table 1. Measurements (mm) of Adult *Kalicephalus parvus*.

Item	Male	Female
Number of specimens	50	50
Total length	3.39-4.91	4.38-7.80
Maximum width	0.21-0.32	0.23-0.35
Head diameter	0.17-0.21	0.18-0.24
Depth of buccal capsule	0.11-0.14	0.12-0.18
Nerve ring from anterior end	0.18-0.24	0.21-0.35
Excretory pore from anterior end	0.29-0.31	0.30-0.41
Length of oesophagus	0.26-0.30	0.27-0.38
Greatest width oesophagus	0.14-0.18	0.15-0.23
Length of spicule	0.25-0.31	
Vulva from anterior end		3.54-6.68
Vulvar ratio		3.5-10.6:1
Length of tail		0.09-0.15
Egg length		0.07-0.10
Egg width		0.04-0.05

Discussion

The author has collected a large series of *K. parvus* Ortlepp, 1923 from *Lampropletis getulus*, *Coluber constrictor* and *Masticophis flagellum*. In addition, he has found this species contained in several vials of previously unidentified material in the collection of the United States National Museum. Host, habitat and locality data have already been listed.

Ortlepp's description of *K. parvus* does not permit identification; his illustrations do not show the distinctive characteristics of the species and his measurements are low in the range of variation. The author's examination of the type material, three subadults, confirms the measurements originally given, but the vulvar ratio (4.3:1) was found to be incorrect; on recalculation this was found to be 5.5-5.6:1.

Harwood (1934) described K. tennesseensis but in his discussion he does not compare this species with K. parvus. However, in the key presented in the same paper he separates the two species on the basis of the vulvar ratio. As has already been stated, the vulvar ratio given by Ortlepp was incorrect and this difference between the descriptions of K. parvus and K. tennesseensis is, therefore, narrowed.

Considering the inadequacy of Ortlepp's original description, it is understandable that this species has not been recognized by subsequent workers. Although Harwood's measurements are higher in the range of variation than those found by the author, his excellent morphological description permits one to identify conspecific material with certainty. Significant morphological differences were not found between K. tennesseensis as described by Harwood, the type material of K. parvus and the author's personal collections. This is the basis for synonomizing these species.

The type specimens K. floridanus of Reiber, Byrd and Parker (1940) were studied and found to represent K. parvus. The species reported by these authors as K. tennesseensis is K. agkistrodontis Harwood, 1932. The paratypes of K. floridanus, however, are heterogeneous. Among six slides labelled paratypes and loaned to the author by Reiber, one was found to consist of a male and female K. rectiphilus Harwood, 1932. It is apparent that these authors were confused as to the identity of their material. The original description of K. floridanus indicates no reason for the separation of this species from K. parvus as here redescribed, and re-examination of the types and paratypes has not brought to light any morphological

differences which would require this species to be retained. *K. floridanus* is, therefore, considered a synonym of *K. parvus*.

Attention should be called to the robust buccal capsule and the stout oesophagus of *K. parvus*. These are characteristic and Harwood (1934) has captured the essential features of the former in his illustration. He mentions that he was unable to locate the dorsal gutter. This structure is present but difficult to find in some specimens. The increase in body width at the excretory pore is also worthy of special mention as a taxonomic character. *K. parvus* is the only known North American species in which the uteri are convergent.

In the author's experience, adult *K. parvus* are normally restricted to the duodenum. All snakes examined by him immediately after death displayed this localization of the parasite. Snakes which were examined long after death occasionally showed parasites in the stomach. This condition may be attributed to post-mortem wandering.

Kalicephalus rectiphilus Harwood, 1932

Synonomy

K. rectiphilus Harwood, 1932, Proc. U.S. Nat. Mus., 81:1-71 [type: in *Coluber constrictor flaviventris* Houston, Tex., U.S.A., U.S.N.M.].

K. floridanus Reiber, Byrd and Parker, 1940 in part, Lloydia 3:125 [in *Coluber c. constrictor*, Kissemee, Fla., U.S.A., among paratypes of *K. floridanus* Coll. Reiber].

Type Specimen

K. rectiphilus Harwood, 1932, U.S.N.M. Helminth Coll. #31708; from *Coluber constrictor flaviventris* - rectum, Houston, Texas, U.S.A.

Hosts

Coluber c. constrictor - (?)st., Kiss., Fla., U.S.A., Reib. '40
rect., Fla., U.S.A. I.P.*
Coluber c. flaviventris - rect., Houst., Tex., U.S.A., Har. '32
Lampropeltis getulus - rect., Fla., U.S.A., I.P.*

History

This species, originally described by Harwood (1932), has been subsequently collected by Reiber, Byrd and Parker (1940) and confused by them with *K. parvus*, (= *K. floridanus* in part).

New Synonomy

The following is a new synonym of *K. rectiphilus*:

K. floridanus Reiber, Byrd and Parker, 1940 in part.

Diagnosis

Kalicephalus; uteri divergent; dorsal ray of the "nankingensis" type; a pair of pronounced globose papillae at either side of the male cloacal opening; oesophagus short and not markedly bulbed; female tail a long, narrow cone with rounded tip; adults confined to the rectum of North American snakes.

Description (Plate II; A, B, C, D, E, F, G)

This is a small slim species with a relatively large buccal capsule and a weakly developed oesophagus; the latter is short and not markedly bulbed; its width at the origin equals or may even exceed the width at the midpoint of the bulb. The nerve ring surrounds the oesophageal isthmus at its narrowest point. The excretory pore, usually difficult to observe, is located between the posterior end of the oesophagus and the level of greatest oesophageal width. The cervical papillae lie a short distance anterior to the posterior end of the oesophagus. The cuticle is finely striated.

The male: The spicules are relatively simple, slim and alate. The gubernaculum is complex, with three longitudinal ridges, and ends anteriorly in a "v"-shaped "tail". In each wall of the cloaca, there exists a long, wavy cuticular crest. The end of the genital cone possesses a pair of obvious globular papillae and a smaller pair of cone-shaped papillae. The bursa gives an impression of delicacy. The rays tend to be pointed and relatively thin for their length. The lateral rays are usually distinctly separated. The dorsal ray of the bursa is of the "nankingensis" type; after giving rise to the anterior terminal branches, which are distinctly separated from the posterior terminals, the dorsal ray bifurcates and, after a short distance, each branch gives rise to the posterior terminal branches.

The female: The uteri are divergent; the ovejector is relatively short and narrow, yet heavily muscularized. The vulva may be a simple slit or slightly pedunculate. The tail has the shape of a slender cone with its distal end rounded off.

Measurements

Table 2. Measurements (mm) of Adult *Kalicephalus rectiphilus*

Item	Male	Female
Number of specimens	13	18
Total length	4.28-5.69	4.73-7.35
Maximum width	0.19-0.24	0.20-0.29
Head diameter	0.17-0.20	0.20-0.24
Depth of buccal capsule	0.12-0.14	0.12-0.17
Nerve ring from anterior end	0.21-0.25	0.25-0.27
Excretory pore from anterior end	0.29-0.37	0.24-0.39
Length of oesophagus	0.18-0.24	0.21-0.29
Greatest width of oesophagus	0.08-0.11	0.09-0.13
Length of spicule	0.24-0.28	
Vulva from anterior end		2.67-4.70
Vulvar ratio		1.0-1.5:1
Length of tail		0.11-0.30
Egg length		0.05-0.06
Egg width		0.02-0.03

Discussion

This species appears to be among the rarest of North American kalicephalids. It has been previously reported by its describer, who found it once, and unknowingly by Reiber, Byrd and Parker (1940) who confused two specimens of *K. rectiphilus* among their paratypes of *K. floridanus*. The original description is based on five specimens, two males and three females. This is a very distinctive species in several respects and there is no reason to confuse it with other North American species. Its habitat in the rectum of North American snakes is diagnostic in itself. It is the author's opinion that records of this parasite from other localities within the host are to be doubted (vide infra).

There are several morphological points that are extremely characteristic and deserve special note. The combination of buccal

capsule and oesophagus presents an unusual morphology as compared to other North American species. The weakly developed oesophagus appears dwarfed by the buccal capsule. In the female, the long, narrow tail is rounded off at the tip. A cuticular welt behind the anus is present in all specimens that have been examined by the author.

The bursa of the male is characteristic. It is a much more delicate structure in this species than in the other North American species; its rays tend to be thin for their length but this is not invariable. However, a constant feature in the specimens examined is that the rays end as points distally. The three lateral rays generally present a symmetrical morphology and are usually well separated distally. The outstanding feature is the presence of two large, globose papillae situated laterally on the ventral surface of the genital cone. The author knows of no other species of Kalicephalus possessing such papillae.

The author has never found the adults of this species anywhere but attached to the rectal wall. In this location they are often difficult to find amid the faeces which sometimes clings to the wall.

Kalicephalus agkistrodontis Harwood, 1932

Synonomy

K. agkistrodontis Harwood, 1932, Proc. U.S. Nat. Mus., 81:1-71 [type: in Agkistrodon mokasen, Houston, Tex., U.S.A., U.S.N.M. (and also other hosts)] ; Harwood, 1933, Parasitol., 25: 130 (new host); Harwood, 1934, J. Tenn. Acad. Sci., 9:192 (Key N.A. species); Harwood, 1936, Ecology 17:697 (larvae in soil).

K. agkistrodontis flagellus Harwood, 1932, Proc. U.S. Nat. Mus., 81: 1-71 [type: in Masticophis flagellum, Houston, Tex., U.S.A., U.S.N.M. (and also other hosts)] , Rankin, 1945, J. Parasitol., 31:142 (new hosts).

K. humilis Caballero, 1938, Ann. Parasitol., 16: 327, [type: in Bothrops atrox, Omealca, Vera Cruz, Mex., cotype U.S.N.M.] , Caballero 1939, An. Inst. Biol., 10:73 (new host).

K. tennesseensis Reiber et al 1940 (not Harwood, 1934) Lloydia 3:125 (new host).

Type Specimen

K. agkistrodontis Harwood, 1932, U.S.N.M. cat. #31704 loc. T26F (cotype 31705, T26G); from Agkistrodon mokasen - stomach, Houston, Texas, U.S.A.

Hosts

Agkistrodon mokasen - st., Houst., Tex., U.S.A. Har. '32
Agkistrodon piscivorus - st., Houst., Tex., U.S.A., Har. '32
Agkistrodon piscivorus - lu., N.Z.P., Wash., U.S.A., U.S.N.M. 31963*
Bothrops atrox - sm. int., Omealca, Vera Cruz, Mex., Cab. '38
Coluber c. constrictor - st. & oesoph., Kiss., Fla., U.S.A., Reib. '40
Coluber c. constrictor - st. & oesoph., Fla., U.S.A., I.P.*
Coluber c. constrictor - int., Am., Mass., U.S.A., Rank. '45
Coluber c. flaviventris - st., Houst., Tex., U.S.A., Har. '32
Masticophis f. flagellum - st., Houst., Tex., U.S.A., Har. '32, U.S.N.M.
Masticophis f. flagellum - st., oesoph., Ath., Ga., U.S.A., Reib. '40
Drymarchon corais melanurus - oesoph., st., int., Aca. Gro., Mex., Cab.'39
Elaphe obsoleta deckerti - oesoph., Fla., U.S.A., I.P.*
Heterodon platyrhinos - st., Houst., Tex., U.S.A., Har. '32
Lampropeltis getulus holbrooki - st., Houst., Tex., U.S.A., Har. '32
Lampropeltis getulus nigra - st., oesoph., Col. Ga., U.S.A., Reib. '40
Micrurus fulvius - st., Houst., Tex., U.S.A., Har. '32
Natrix r. rhombifera - st., Houst., Tex., U.S.A., Har. '32
Natrix sipedon fasciata - st., Houst., Tex., U.S.A., Har. '32
Pituophis sayi sayi - st., Houst., Tex., U.S.A., Har. '32
Sistrurus sp. - lu., N.Z.P., Wash., U.S.A., U.S.N.M. #32193*
Thamnophis sirtalis - int., Mass., U.S.A., Rank. '45
Thamnophis sirtalis proximus - st., Houst.,Tex., U.S.A., Har. '32

History

Harwood (1932) described K. agkistrodontis from Agkistrodon mokasen and eight other snakes collected near Houston, Texas. At this time he also reported a subspecies, K. agkistrodontis flagellus, from Masticophis flagellum (= Coluber flagellum) and Coluber constrictor flaviventris (= C. flaviventris). In 1933 he recorded an additional host, Agkistrodon piscivorus, for K. agkistrodontis.

K. humilus was described by Caballero (1938) from the fer-de-lance, Bothrops atrox, and subsequently (1939) he also reported this species from Drymarchon corais. Both these records are from Mexico.

Reiber, Byrd and Parker (1940) reported kalicephalids from several snakes in the southeastern United States as K. tennesseensis. This is a misidentification of K. agkistrodontis.

Fantham and Porter (1954) published a long paper on the endoparasites of North American snakes. Many of their herpetological and helminthological results are so in error that the author finds it difficult to trust any identifications they report.

K. mucronatus Fantham and Porter, 1954 from Crotalus horridus cannot be considered seriously as conspecific with K. mucronatus Molin, 1861. Recent authors have been unable to identify Molin's species and most have totally ignored them. K. mucronatus is certainly not identifiable on the basis of the available description. Therefore, it is doubtful that Fantham and Porter were able to identify their material by comparison with Molin's description.

In Molin (1861) and in subsequent compendia such as Yorke and Maplestone (1926) for example, K. mucronatus Molin, 1861 is listed from

Crotalus horridus. This is the only species listed from this host in the literature. Presumably, then, this identification was made by simply choosing the name of a kalicephalid that had previously been recovered from the above host. This is always a dangerous method of identification, but in this case it is especially misleading. Molin's host designations leave much to be desired, some of them being unrecognizable, but since there is only one South American rattlesnake, it is certain that Crotalus horridus reported by Molin is actually Crotalus durissus. Considering the location in which the rattlesnakes reported by Fantham and Porter (1954) were collected, it is probable that Crotalus horridus was the correct identification; they were certainly not Crotalus durissus. It is obvious that these authors have made several errors and it is extremely improbable that their material from a timber rattler collected in New York is conspecific with K. mucronatus Molin, 1861 from a rattlesnake in Brazil.

It should also be noted that Fantham and Porter, in the same paper, record K.agkistrodontis from a water moccasin, Agkistrodon piscivorus, from Lantier, Quebec. The host identification is certainly incorrect; Agkistrodon piscivorus does not occur north of Virginia in eastern North America. The host was probably Natrix sipedon sipedon, this being the only water snake found in the region of Canada concerned.

Fantham and Porter (1954) provide no measurements or morphological data by which one can check their identifications. The author has not examined any of their material and it is doubtful that these specimens still exist. Fantham and Porter state that the best of their material was destroyed in the bombings of London. The author is of the opinion

that the best of alternatives is to consider all kalicephalids reported by Fantham and Porter (1954) as nomina dubia.

New Synonomy

The following are new synonyms of K. agkistrodontis:

K. agkistrodontis flagellus Harwood, 1932

K. humilus Caballero, 1938

K. tennesseensis Reiber, Byrd and Parker, 1940 not Harwood, 1934.

Diagnosis

Kalicephalus; uteri divergent; bursa well-developed; rays stout, dorsal ray variable, but usually of the "indicus" pattern; maximum width not in the area immediately behind the excretory pore; excretory glands comparatively large and well-developed; oesophagus is relatively long, its bulb is normal; phasmids are obvious and their level is often marked by a constriction in the female tail; cuticle with obvious transverse striations; parasitic in the oesophagus and stomach of many North American snakes.

Description (Plate III; A,B: Plate IV; A,B,C)

This is a medium-sized species with a maximum width usually at the level at which the excretory cells are widest. From the point of greatest diameter, the body tapers anteriorly and posteriorly. The excretory glands are large and, in the male, extend posteriorly about one-third of the length of the body. The excretory pore is a simple opening and is variable in position. In some specimens it is found as far anterior as the posterior level of the nerve ring, while in others it opens at a level just behind the greatest oesophageal diameter.

The cuticle of the head is characteristic when the worm is viewed laterally. The cuticle is raised across the anterior face, and where this bends posteriorly, the relatively smooth arc of the cuticle is broken by an abrupt angle. The head capsule itself is not particularly distinctive.

The oesophagus is relatively long and possesses a normally developed bulb. The nerve ring, variable in position, surrounds the isthmus of the oesophagus at varying levels from just anterior to the bulb to the midpoint of the isthmus. The cervical papillae also vary in position from just anterior to the level of greatest oesophageal width to the level just anterior to the end of the oesophagus. The cuticle bears obvious transverse striations.

The female: The uteri are divergent and the ovejector is well-developed. The vulva is variable in morphology; it may be pedunculate or only slightly raised. The tail is long and is usually constricted at the phasmids; its tip is blunt but not distinctly rounded.

The male: The bursa is large, well-developed and obliquely truncate. The terminal branching is variable to some extent but the "indicus" pattern is typical. Aberrant specimens occur, some of which show a "longior" type pattern. Occasionally fusion of the posterior terminal branches occurs, and extra branches are sometimes in evidence. The spicules, which are equal and alate, are of medium length as compared to other members of the genus. The lateral cloacal walls bear sclerotizations in the form of a relatively high crest.

Measurements

Table 3. Measurements (mm) of Adult Kalicephalus agkistrodontis

Item	Male	Female
Number of specimens	25	25
Total length	5.21-8.30	7.64-11.16
Maximum width	0.18-0.30	0.26-0.45
Head diameter	0.17-0.20	0.21-0.24
Depth of buccal capsule	0.11-0.12	0.12-0.15
Nerve ring from anterior end	0.18-0.23	0.23-0.26
Excretory pore from anterior end	0.27-0.38	0.29-0.36
Length of oesophagus	0.27-0.30	0.30-0.36
Greatest width oesophagus	0.12-0.15	0.14-0.18
Length of spicule	0.48-0.56	
Vulva from anterior end		5.15-7.26
Vulvar ratio		1.2-2.0:1
Length of tail		0.27-0.42
Egg length		0.07-0.08
Egg width		0.04-0.05

Discussion

Kalicephalus agkistrodontis belongs to a group of North American species which are morphologically very homogeneous. K. agkistrodontis Harwood, 1932, K. coronellae Ortlepp, 1923, K. humilus Caballero,1938, K. tennesseensis Reiber, Byrd and Parker, 1940, and K. agkistrodontis flagellus Harwood, 1932 are indistinguishable on the basis of their structural characteristics. In addition, K. conoidus Comroe, 1948 is very similar. One South American species also conforms to this group in general morphology.

As already noted, K. humilus, K. tennesseensis Reiber, Byrd and Parker, 1940 not Harwood, 1932, and K. agkistrodontis flagellus are here synonomized under the name K. agkistrodontis. In the case of K. humilus, cotypes deposited in the United States National Museum were studied and no morphological differences could be found between

these and known K. agkistrodontis material. A difference in vulvar ratio does not exist; Caballero's calculation of 2.6:1 is incorrect. This ratio was determined on the cotypes and found to be 1.5:1, a ratio within the range of variation found in K. agkistrodontis.[1] Caballero also cited a difference in spicule length. A comparison of the data in Table 4 shows that the spicule length of K. humilus is within the range of that of K. agkistrodontis.

K. tennesseensis Reiber, Byrd and Parker, 1940 requires no special explanation. Specimens borrowed from the senior author were found to be morphologically identical with K. agkistrodontis; the measurements are also in agreement. This, then, is a simple case of misidentification.

K. agkistrodontis flagellus Harwood, 1932 is here synonomized with K. agkistrodontis Harwood, 1932 in that it does not meet the specifications of a subspecies.[2] The characteristics set forth as those distinguishing K. agkistrodontis flagellus are encompassed in large series of typical K. agkistrodontis and, therefore, K. agkistrodontis flagellus does not differ taxonomically from the typical K. agkistrodontis.

---

[1] Harwood's original description of K. agkistrodontis (1932) is also in error as regards the vulvar ratio. He gives a ratio of 1.6:2.0. This is corrected in his later paper (1934).

[2] Subspecies are "----populations which differ taxonomically from other such subdivisions of the species." E.Mayr, E.G. Linsley and R.L. Usinger, Methods and Principles of Systematic Zoology, p.30. New York: McGraw-Hill Book Company, 1953.

There now remain those species which belong to this complex but which are, or are provisionally considered, valid. Of these, K. conoidus Comroe, 1948 is the most distinct. The inequality in the length of its spicules is sufficient to separate this species from other closely allied forms.

K. coronellae Ortlepp, 1923 is taxonomically difficult. The type specimens of this species were examined and found to be indistinguishable from K. agkistrodontis on structural grounds alone. The measurements given by Ortlepp are correct in all respects, and it is in measurements that the difference lies. The K. agkistrodontis specimens measured by the author were taken from a collection of about 200 and included the largest individuals collected, yet none of these approached K. coronellae in size. Most of the author's specimens are only half the length of Ortlepp's. Harwood's original description of K. agkistrodontis was based on specimens collected from different host species and presumably was based on an adequate series of specimens. His measurements also fail to encompass those given for K. coronellae. The fact that Harwood's material came from several snakes reduces the possibility that the size differences between K. agkistrodontis and K. coronellae may be attributable to a growth variation in different hosts.

The author, therefore, recognizes K. agkistrodontis and K. coronellae as distinct, but he desires to point out that these species are very similar indeed and the occasion may arise, when sufficient material is available, where the two species will be shown to be conspecific.

The South American species, K. subulatus, mentioned previously, is discussed here since it may well be conspecific with either K. agkistrodontis or K. coronellae and, indeed, it partially bridges the gap between these two. Should these emerge as conspecific, the name of the South American species would have priority. As yet the author cannot definitely assign a name to the species. Undoubtedly the designation K. subulatus of some authors has been applied to members of this species and this designation goes back to Molin (1861). However, the identifications of this species by recent authors, including the writer, are based on Ortlepp's (1923) redescription. Recently the author has found evidence that Ortlepp may have based his redescription on another species.[1] Therefore, the proper name for certain South American kalicephalids from Lachesis muta and Constrictor constrictor cannot be determined with certainty.

The specimens of K. subulatus in the author's collection are similar in structure to both K. agkistrodontis and K. coronellae. They overlap the former in overall size and in this respect approach K. coronellae. Their spicules actually exceed the length of those found in the latter.

The solution of this problem also awaits the study of larger collections, but until then it seems advisable to retain the three species as distinct. K. subulatus is separable from these closely related forms only on the basis of measurements. Tables 4 and 5 give the measurements supplied by various authors for the species in the "agkistrodontis" group. Also included are the author's measurements on

---

[1] Through the courtesy of R.T.Leiper, the author has studied some of his sketches drawn from Molin's original material and these suggest that Ortlepp's K. subulatus may not be the same species as that of Molin.

his own collections and on previously described type material wherever measurements were not given or were inaccurate.

TABLE 4. Comparative Measurements (mm) of Some Species Synonymous With or Closely Related to K. agkistrodontis (Males)

Species	Characters Measured								
	Total Length	Maximum Width	Head Diameter	Depth of Buccal Cap.	Nerve ring From Ant.	Excret. Pore From Anterior	Length of Oeso-phagus	Width of Oeso-phagus	Length of Spicule
K. coronellae Ortlepp, 1923	11.00-11.50	0.28	0.22	0.15	0.28	-------	0.42	0.24	0.78
K. agkistrodontis Harwood, 1932	6.50- 9.50	0.20-0.30	0.16	0.13-0.16	0.22-0.28	0.33-0.40	0.31-0.34	0.10	0.46-0.58
K. agkistrodontis[1]	5.21- 8.30	0.18-0.30	0.17-0.20	0.11-0.12	0.18-0.23	0.27-0.38	0.30-0.36	0.14-0.18	0.48-0.56
K. conoidus Comroe, 1948	6.30- 7.00	0.30-0.33	0.15-0.16	0.12	0.21-0.22	--------	0.31-0.33	0.15	0.76&0.81
K. humilus Caballero, 1938	8.32	0.33-0.35	0.14	0.12	0.22	0.39	0.34	0.15	0.54-0.58
K. subulatus Ortlepp, 1923	6.50-8.00	0.30	0.24	-------	-------	--------	0.37	-------	over 0.50
K. subulatus[1]	7.50-11.12	0.24-0.37	0.22-0.28	0.15-0.18	0.27-0.31	0.40-0.46	0.37-0.45	0.19-0.24	0.76-0.90

[1] Author's measurements; specimens from his personal collection.

Figures underlined in red - Measurements not supplied in original description. These measurements taken by author on type specimens.

TABLE 5. Comparative Measurements (mm) of Some Species Synonymous With or Closely Related to K. agkistrodontis (Females)

Species	Characters Measured										
	Total Length	Maximum Width	Head Diameter	Depth of Buccal Capsule	Nerve Ring From Anterior	Excretory Pore From Anterior	Length of Oesophagus	Width of Oesophagus	Vulvar Ratio	Length of Tail	Egg Size
K. coronellae Ortlepp, 1923	19.00-20.00	0.35	0.25	0.18	0.34	0.52	0.54	0.25	1.6:1	0.60	0.06 x 0.03
K. agkistrodontis Harwood, 1932	10.00-13.70	0.26-0.33	0.16	0.16-0.18	0.28-0.32	0.40-0.51	0.35-0.47	0.12	1.6:1	0.37	0.06-0.07 x 0.03-0.04
K. agkistrodontis[1]	7.64-11.16	0.26-0.45	0.21-0.24	0.12-0.15	0.23-0.26	0.29-0.36	0.30-0.36	0.14-0.18	1.2-2.0:1	0.27-0.42	0.07-0.08 x 0.04-0.05
K. conoidus Comroe, 1948	10.70	0.48	0.19	0.12	0.25	0.30	0.38	0.18	1.6:1	0.38	0.08 x 0.03
K. humilus Caballero, 1938	12.30-16.00	0.42-0.48	0.18	0.14-0.16	0.25	0.35	0.34-0.37	0.17-0.18	1.5:1	0.58	0.06-0.07 x 0.04
K. subulatus Ortlepp, 1923	7.00-9.50	0.43	------	------	------	------	0.45	------	2.0:1.0	0.36	0.06-0.07 x 0.03
K. subulatus[1]	7.80-15.70	0.30-0.60	0.24-0.33	0.15-0.21	0.30-0.37	0.45-0.55	0.40-0.52	0.19-0.28	1.5-20:1	0.25-0.49	0.06 x 0.04

[1]Author's measurements; specimens from his personal collection.

Figures underlined in red - Measurements not supplied in original description. These measurements taken by author on type specimens.

Figures underlined in black - Measurements incorrectly given in original description but later corrected (Harwood, 1934).

Figures underlined in green - Ratio or measurements in original description inaccurate; remeasured on type by author.

A Key to the North American Species[1]

1. Uteri convergent..... K. parvus
   Uteri divergent..... 2

2. Dorsal ray of the bursa of the "nankingensis" pattern cloacal papillae prominent and globose..... K. rectiphilus

   Dorsal ray of the bursa variable but usually of the "indicus" pattern; cloacal papillae not prominent and globose..... 3

3. Spicules subequal..... K. conoidus
   Spicules equal..... 4

4. Total length female over 19.00 mm, spicules 0.78 mm..... K. coronellae
   Total length female to 14.00 mm, spicules 0.46-0.58 mm.... K. agkistrodontis

General Discussion

It became obvious soon after undertaking this study that three distinct species of Kalicephalus parasitized the available host species and that in freshly killed snakes these were localized in definite regions in the digestive tract. If, however, a snake had been dead for 10 to 12 hours, or had died and been placed in the refrigerator for a day, then the distribution of the various species in the host was found no longer to be specific. The author has seen several tubes of museum specimens, the collectors of which are reliable workers, containing K. agkistrodontis and K. parvus from the lungs.

---

[1] K. simplex (Leidy, 1856) Walton, 1927 from a porcupine has been omitted from this key and the preceding discussions in that the author has not been able to study these specimens. Walton noted that they were partly macerated and attributed this to death in an abnormal host.

These parasites were collected from snakes which had died in zoos and it probably was some time before the corpse reached the helminthologist. Undoubtedly the abnormal position of the nematodes in the host represents post-mortem wandering. The author feels that all reports of K. agkistrodontis from any location other than the oesophagus or stomach can be explained in this manner. It is the author's opinion then (and from his personal experience with material collected from hosts immediately after death this is invariable) that each of the three species emphasized in this paper is restricted, as an adult, to definite localities in the digestive tract. K. agkistrodontis, as mentioned, is confined to the oesophagus and stomach, K. parvus to the duodenum and K. rectiphilus to the rectum. All three species may coexist in the same host individual and specific identification of the adult offers no problem when these are separated on the basis of distribution in the freshly killed host.

It is interesting to note the reactions of these three species when recovered and placed in tap water. Most K. parvus burst after a short period in this medium. This is seen to begin as a prolapse of the excretory glands through the excretory pore. K. rectiphilus does not burst, but the females lay few eggs and usually die overnight or soon thereafter. On the other hand, K. agkistrodontis may survive for three to five days in tap water, the females depositing large numbers of eggs for the first day or two. After this time many of the eggs hatch in the body.

These differences in tolerance to tap water are no doubt correlated with the individual species' adaptation to the particular area of the

digestive tract in which it occurs normally. Thus K. parvus from the highly specialized habitat, the duodenum, is much less tolerant of tap water than is K. agkistrodontis from the oesophagus.

MATERIALS AND METHODS FOR LIFE HISTORY STUDIES

Snakes Used As a Source of Parasitic Material

Several snakes purchased for studies on Entamoeba invadens from Ross Allen's Reptile Institute were found to harbour species of Kalicephalus in considerable numbers. The snakes infected were the black racer (Coluber c. constrictor), the southern Florida rat snake (Elaphe obsoleta deckerti) and the Florida king snake (Lampropeltis getulus floridana). Of these, C. c. constrictor was found to be the species most consistently and heavily infected. Some individuals were parasitized by all three species of Kalicephalus on which life history studies were to be carried out. Such an ideal source of material was not found in any other snake and, therefore, it was decided to use black racers from the supplier indicated above as a source of material for all life history studies.

Snakes Used For Experimental Infections

On the other hand, snakes to be used as experimental hosts constituted a more difficult problem. It was considered necessary to obtain snakes that one could be certain were not already infected with species of Kalicephalus. Therefore, the snakes already mentioned could not be used. Other species from this supplier were eliminated on the basis of price or their venonmous nature. Furthermore, it was found that snakes from this source often survived poorly. Survival was not a factor in the snakes used as a source of supply. However, in the case at hand, where the individual under experiment had to survive until the date set for its sacrifice, it was essential that the snakes be healthy.

An ideal source of snakes for experimentation was found in those reared from eggs by Perkins and Shaw of the San Diego Zoological Society. These herpetologists succeed regularly in hatching eggs laid by gopher snakes (Pituophis catenifer annectans). Soon after deposition, the eggs are removed to an earthenware crock where they are placed on several thicknesses of paper towelling, the bottom towel being thoroughly moistened and the top one dry. A glass plate is used as a cover. Water is added carefully around the sides of the crock whenever the eggs begin to wrinkle. Upon hatching, the snakes are removed to clean glass gallon jars. Snakes obtained in this manner have been reared under helminthologically sterile conditions and thus infection with species of Kalicephalus prior to experimentation is precluded. It should also be noted that other advantages exist in the use of these snakes. The San Diego gopher snake , (Pituophis catenifer annectans), is hardy in captivity, requires a minimum of attention and feeds readily. Furthermore, in hatchlings the search for larval stages is greatly facilitated in that the organs are small and the digestive tract thin-walled as compared to older specimens.

Disadvantageous in this source was the impossibility of obtaining large series of experimental hosts. Indeed, these snakes were never available in sufficient numbers to enable their use except in the most critical experiments. They were, therefore, used mainly in attempts to infect by skin penetration.

The larvae of Kalicephalus were known by the author to possess no resistance to desiccation. It was, therefore, reasoned that desert snakes might be suitable as experimental hosts. To test this hypothesis,

Chionactus occipitalis annulata, Rhinocheilus lecontei clarus, Pituophis catenifer annectans and Pituophis catenifer affinis from arid areas were examined for Kalicephalus. Natural infections of Kalicephalus were never found in these.[1] Therefore, Pituophis spp. from arid areas were used in some kalicephalid life history studies; faecal examinations were nevertheless carried out before a snake was considered negative.

A series of garter snakes (Thamnophis s. sirtalis) and Dekay's snakes (Storeria dekayi) were collected in the vicinity of Ste. Anne de Bellevue, Quebec, Canada, and found negative for Kalicephalus. Previous collections of these snakes used for other experimentation were also free of these nematodes. It was felt, however, that these snakes should be used for life history experiments only with great care. Therefore, several (3-4) faecal examinations were made on each snake before it was placed into an experiment and several controls (3-4 snakes per series of 8-12) were used. In no case was there any evidence of natural infection with Kalicephalus in a total of about 80 snakes from the vicinity of Ste. Annes.

A number of Thamnophis s. sirtalis and Storei dekayi caught in the early summer of 1954 at Ste. Anne de Bellevue, Quebec, were pregnant. These species bear their young alive and thus the author was provided with an additional source of excellent material for life history studies. The small size of the organs in the new-born of these species greatly facilitates the recovery of introduced larvae. Disadvantageous, however,

---

[1]Enquiries were also made among southern California parasitologists concerning Kalicephalus in desert reptiles. Their replies were in agreement with the negative findings of the author.

is the delicacy of these snakes in captivity and their reluctance to feed.

Maintenance and Feeding of Hosts

Stock Coluber constrictor were housed in either large wooden boxes (3' x 4' x 3') with tight fitting screen lids or similar galvanized metal containers with similar lids. Food was refused consistently, but water was taken from shallow pans with which each container was supplied.

Snakes used in experimental work were maintained in wide-mouthed glass jars of various sizes. Small "Mason jars" provided with a wire screen insert into the screw cap served as containers for newly-hatched and small species, while gallon jars with punched lids were used to house larger snakes. Survival was good in these containers provided water was supplied frequently.

Gopher snakes were fed on baby mice which were readily accepted, whereas the poorly feeding garter snakes received both earthworms and small fish. Adult Dekay's snakes fed on earthworms readily.[1]

The Culture of Larvae

Two types of cultures were attempted. These were tap water cultures and sand-faeces-charcoal cultures.

Tap Water Cultures

Eggs were obtained from female kalicephalids dying in tap water

---

[1]The fish (smelts from the Gulf of St.Lawrence) had been frozen for a considerable period of time, which condition is known to kill third-stage larvae of K. parvus in one hour (page 80). Furthermore, it is highly improbable that such fish would be infected. Mice used as a food for snakes were laboratory-reared under conditions precluding infection with Kalicephalus. Earthworms were collected in a greenhouse into which no new soil had been brought for many years and in which only chemical fertilizers had been used.

and/or from dead females by dissection. These eggs were introduced into tap water contained in a 5 cm Petri dish. As had already been noted by both Ortlepp (1923) and Harwood (1936), larvae of Kalicephalus spp. undergo considerable development in tap water. However, many larvae from these cultures die before reaching the third stage, and those which do reach the infective stage give variable results in infection experiments.

Sand-Charcoal-Faeces Cultures

1. Eggs directly from female worms: Sand, charcoal and snake faeces were ground together with a mortar and pestle and autoclaved. This helminthologically sterile medium was then moistened, introduced into a 5 cm Petri dish and inoculated with bacteria isolated from snake faeces. After an interval of two days to allow the bacteria to multiply, kalicephalid eggs were introduced into the prepared medium. This method of culture proved to be unreliable; only occasionally were infective larvae obtained in this way.

2. Eggs from snake faeces: Faeces collected from an experimentally infected snake (a pure infection with K. parvus), helminthologically sterile sand and charcoal were mixed in equal quantities and made into a thick paste with tap water. Equal parts of sand and charcoal were then added until there appeared to be no free water. These cultures invariably yielded larvae in quantity. Infection experiments with larvae so cultured were uniformly good. However, attempts to culture K. rectiphilus in this manner never succeeded.

3. Recovery of larvae from sand-charcoal-faeces cultures: Larvae were recovered from these cultures by the Baermann apparatus. This method was found to be satisfactory, giving high yields.

Infection Techniques

Per os: Larvae were introduced orally by either a blunted Pasteur pipette or by a hypodermic syringe, the needle of which was sheathed by catheter tubing. In using this method great care must be exercised to avoid entering the respiratory system and to avoid puncturing the oesophagus. One does not enter the trachea if the distal end of the pipette or catheter is held against the roof of the mouth as one pushes down toward the oesophagus. It is necessary to restrain contractions on the part of the snake to avoid oesophageal puncture. However, it is desirable to get the tip of the instrument well down into the oesophagus to avoid regurgitation of the larvae. Gentle posterior stroking of the ventrum beginning just behind the head and extending almost to the stomach, immediately after administering the larvae, is helpful in counteracting any tendency toward regurgitation.

Per cutaneous: Snakes to be used for these experiments were restricted from water until immediately before experimentation, when they were allowed to drink. After the cessation of drinking, the snakes were thoroughly dried. Narrow strips of "Scotch Tape" were applied to the head in many windings and cross-windings. Firstly, longitudinal strips attached from well back on the ventrum of the neck to the distal end of the lip were brought up and over the anterior face between the nostrils and back between the eyes, over the cranium and well back along the dorsal side of the neck. These preliminary wrappings were pressed down with the

fingernail by applying as much pressure as was considered safe. Secondly, transverse windings were made behind the skull. These bound down the ends of the longitudinal strips. Following this operation, transverse windings were made between the eyes and nostrils, the first described longitudinal strips were again laid down and the entire process was repeated. After several repetitions of this taping procedure, the entire head was so wrapped that openings were left only at the nostrils and the eyes. The snakes were then introduced into gallon jars or finger bowls, the receptacle being dependent on the size of the snake. Larvae were introduced in water so as to almost cover the floor of the container with fluid. Snakes were confined in contact with larvae in this manner overnight. The following day they were dried, swabbed with 70% alcohol and placed in clean glass bottles.

This method of restricting drinking was not completely satisfactory, since water tends to loosen the tape and snakes may rub it off even in perfectly smooth glass containers by rubbing against their own bodies. On one occasion, a snake shed its skin under the tape, the tape being cast along with the exuvium.

Furthermore, it has been demonstrated that some skin-penetrating larvae must be contained in a solid medium before skin penetration can be achieved (Spindler, 1933a). Probably water does not supply the necessary traction. However, the solid medium was avoided since it would have increased the ability of the snakes to shed the tape.

Fixation, Staining, Mounting

All stages were fixed in hot 70% alcohol. This fixative provides

excellent results on all parasitic stages, although many free-living third-stage larvae fixed in this manner showed a prolapse of the buccal tube and distortions of the oesophagus and intestine. The nervous system and genital rudiment, however, are satisfactorily fixed. Subsequent staining is good on alcohol-fixed material.

Larvae of all stages were stained in alcoholic hydrochloric acid carmine[1] and in Delafield's haematoxylin (commercial stock diluted 1:10 with distilled water). The alcoholic carmine stain was found particularly convenient since hydration and dehydration were unnecessary. Fixation, staining and destaining, therefore, were all accomplished in 70% alcohol. Delafield's haematoxylin, however, was useful as an alternative stain to bring out certain details not visible in carmine preparations. Most noteworthy in this respect were the oesophageal nuclei, the rudimentary excretory glands of the free-living third-stage larvae and the coelomocytes. Carmine-stained preparations were destained in a solution of one drop of concentrated hydrochloric acid in 100 cc of 70% alcohol. Haematoxylin-stained specimens were similarly destained but in distilled water instead of alcohol.

All larval material was cleared in glycerine and mounted in glycerine jelly. Adults were cleared and studied in lactophenol.

Some parasitic third-stage larvae were double embedded in celloidin and paraffin and sectioned at 5 μ. Host tissue, containing encysted larvae, was embedded in paraffin, sectioned at 10 μ, stained in Ehrlich's haematoxylin and counterstained with eosin.

---

[1] J.B. Gantenby and H.W. Beams, The Microtomist's Vade-Mecum (Bolles Lee), page 135, London; Churchill, 1950.

Hard parts, oral plates, spicules and oesophageal linings, etc. were isolated from host tissue by bacterial decomposition and studied in temporary preparations of glycerine or lactophenol.

Illustrations and Photographs

All drawings were made with the aid of a camera lucida. Kodachrome A was the film used for color microphotography. Phase contrast microscopy was found especially useful only in studying the fine cuticular structures associated with the provisional buccal capsule of the fourth-stage larva. The photograph of a shed provisional buccal capsule in this paper was taken with phase contrast.

LIFE HISTORY AND DEVELOPMENTAL ANATOMY

General Introduction

The life history of no kalicephalid is known completely. However, Ortlepp (1923) published an account of the free-living stages of K. philodryadus. He described this species from the stomach, duodenum and intestine of the South American snake Philodryas serra. His observations on the development of this species may be summarized as follows:

Females left in normal saline overnight lay eggs in an advanced state of segmentation. These eggs and others obtained by uterine dissection develop in tap water. In 24 hours, at laboratory temperature, the eggs become fully embryonated and some hatch. The first-stage larvae are active, possess a rhabditiform oesophagus and persist for slightly more than a day. The measurements given are total length, 0.312 mm; width, 0.016 mm; oesophagus, 0.09 mm long; buccal tube, 0.012 mm long; tail, 0.06 mm long. The genital rudiment is 0.135 mm from the tip of the tail, the excretory pore 0.029 mm in front of the base of the oesophagus and the nerve ring 0.012 mm anterior to the excretory pore.

The second stage is similar to the first, but these larvae grow considerably in size, attaining a length of 0.48 mm and a width of 0.02 mm. The oesophagus measures 0.105 mm in length and the tail 0.09 mm. The genital rudiment is composed of two cells. This stage persists for four to five days.

The third-stage larva is ensheathed and sluggish, measures 0.48-0.51 mm in length and is 0.027 mm in thickness. The oesophagus measures

up to 0.188 mm.

All further work was negative (i.e. infection experiments, skin penetration experiments, etc.) and this, in Ortlepp's opinion, resulted from weakness of the larvae since they were not cultured in a nutrient medium.

Other than Ortlepp's account, there are only incidental observations available in the literature. Harwood (1936) mentions the larvae of K. agkistrodontis in four soil types and remarks further that these undergo appreciable development in aqueous culture.

There is, of course, a wealth of literature concerning the life histories of the economically important nematodes within the other strongylin families. Surprising, however, is the lack of information on detailed developmental anatomy. The publications of Alicata (1935), Cameron (1927), Eisma (1932), Ihle and Oordt (1924), Looss (1897, 1911), Lucker (1935, 1936), Mönnig (1926), Ortlepp (1937), Veglia (1915) and Wetzel (1940a, b) were found especially useful for comparative purposes.

In the field of developmental anatomy of the free-living stages, Alicata (1935), Eisma (1932), Looss (1911), Lucker (1935, 1936), Mönnig (1926), and Wetzel (1940a, b) are of special interest.

Detailed accounts of the fourth-stage larvae and the development of the adult buccal capsule are to be found in Alicata (1935), Cameron (1927), Ihle and Oordt (1924) and Looss (1897).

Unless otherwise noted, all life history data pertaining to K. parvus are based on experimental infections in garter snakes (Thamnophis sirtalis) and Dekay's snakes (Storeria dekayi) . Similarly, all work with K. agkistrodontis and K. rectiphilus is based on experimental infections

of gopher snakes (Pituophis catenifer).

Kalicephalus parvus Ortlepp, 1923 (Plates V-X; text Fig. 4-6).

The Egg (Plate V; A-D).

The eggs of K. parvus measure 0.08-0.10 mm in length by 0.04-0.05 mm in width. They are transparent, thin-walled, flatter on one side than on the other and have slightly dissimilar poles. Eggs laid in tap water by females shortly after removal from a freshly killed host were in the morula stage. Under these conditions it is to be expected that the first eggs are laid in a state of development similar to those normally passed by the kalicephalid in the snake. Eggs studied in preparations made from fresh snake faeces were in all stages of development from an early gastrula to a well-developed, actively moving embryo. No count was made of the number of eggs in each stage of development in freshly passed faeces, and, although fully embryonated eggs were predominant, other stages were also represented in large numbers. This is surprising in that snakes as occasional feeders defecate at long intervals, and one might, therefore, expect most of the eggs to be fully embryonated. This would indicate that development of the egg in the snake proceeds slowly.

The development of eggs recovered from females dying in tap water is relatively rapid. In six hours at room temperature, development has reached the tadpole stage. The embryo is doubled back on itself and consists of a broad, anterior portion almost as long as the egg and a wide tail about three-quarters of the length of the anterior part. In nine hours, the embryo is in the late tadpole stage; it appears longer and slimmer, but still noticeably possesses the tadpole shape. By the eighteenth hour, all embryos are fully developed and active. In

20 hours, the earliest hatching is seen, and in 24 to 26 hours, hatching is at its height.

The First-Stage Larva (Plate V; E.F)

Shape: Newly hatched larvae are still faintly reminiscent of the embryo in that they are widest at the anterior end and taper from there to the tail. The gradual posterior taper becomes increased in slope near the anus; midway between the anus and the tail, the slope again changes causing the end of the tail to be long and narrow.

The cuticle: The cuticle is fine and bears no visible striations.

The musculature: The musculature is not yet well-developed and only the narrow muscle nuclei can be identified with certainty.

The alimentary tract: The oral opening, surrounded by a small collar, is of slightly greater diameter than the buccal tube which extends posteriad from it to the oesophagus. The oesophagus is rhabditiform and the isthmus is relatively long, in some specimens equalling the corpus in length. The bulb is not especially distinctive, three pairs of nuclei being visible in each sector. The primordium of the oesophago--intestinal valve is comparatively large and is composed of about six cells. The intestine in living preparations appears granular and its more transparent lumen is seen as a sinuous tract enclosed between roughly triangular cells. There are approximately 20 to 22 intestinal cells which alternate, and this, combined with their triangular shape, causes the lumen to take its sinuous course. Since the intestinal cells are dorsal and ventral, this condition is only visible

when the specimen is viewed in lateral aspect. The intestine is joined to the slightly raised anus by the delicate rectum. The latter is a fine, cuticle-shaped canal.

The nervous system: In the first-stage larva of K. parvus the nervous system is only partially differentiated. Surrounding the isthmus near its midpoint is the nerve ring, immediately anterior to which are a series of nuclei representing the rudimentary ganglia of the six cephalic papillary nerves. The latter, represented by chains of nuclei, are seen to extend anteriad from the anlagen of cephalic papillary ganglia.

Immediately posterior to the nerve ring, there is visible dorsally a small mass of cells from which evolve the dorsal and subdorsal ganglia of later stages. While this mass is clearly separate from the other ganglionic rudiments, it is not as yet differentiated into its two component parts. Ventrally a large ganglionic mass is seen which probably combines the still undifferentiated subventral and postero-ventral ganglia. Continuing ventrally and posteriorly, one sees, at the level of the oesophago-intestinal valve, the primordium of the retrovesicular ganglion. The lateral ganglia are visible, when the specimen lies in dorso-ventral aspect, as two spindle-shaped masses of nuclei extending posteriorly from the nerve ring to the oesophageal bulb. The ventral ganglionic chain, usually referred to as the ventral nerve, is represented by a series of nuclei extending along the ventral side of the body. The retrovesicular ganglion, already mentioned, is merely an enlargement in this chain. Masses of nuclei near the rectum represent the lumbar ganglia, which are paired and lateral, and the anal ganglion,

another enlargement in the ventral chain.

The excretory system: This system is composed of a minute pore situated ventrally immediately behind the nerve ring and a fine duct leading posteriorly which is soon lost among the crowded nuclei of this area.

The genital rudiment (text Fig.4): The genital rudiment is a small elliptical or ovoid body ventrally situated just behind the seventh intestinal cell. It is composed of two crescent-shaped, polar, epithelial cells which enclose two medially situated, oval germinal cells.

The coelomocytes: There is a coelomocyte associated with the genital rudiment. However, sex differentiation by the relative position of this coelomocyte and the genital rudiment (as determined by Alicata (1935) for Hyostrongylus rubidus) was not found possible.

Measurements:

Table 6. Measurements (mm) of First-Stage Larvae of Kalicephalus parvus.

Number of larvae measured	15
Total length	0.30-0.38
Maximum width	0.02-0.03
Length of buccal tube	to 0.01
Length of oesophagus	0.09-0.13
Nerve ring from anterior end	0.06-0.08
Excretory pore from anterior end	0.08-0.10
Genital primordium from anterior end	0.19-0.22
Length of tail	0.05-0.07

The Second-Stage Larva (Plate V; G)

Size and shape: This stage is considerably longer than the first. In shape, it tapers gradually both anteriorly and posteriorly from about the level of the fifth intestinal cell.

The cuticle: The cuticle is thin and transparent; striations are fine.

The musculature: As in the preceding stage.

The alimentary tract: The mouth and buccal tube have undergone no appreciable change in morphology. A projection may now be seen arising from the anterior end of the oesophagus and enclosing the base of the buccal tube. The oesophagus has a proportionately shorter isthmus. A greater number of nuclei appear in the oesophageal bulb. The oesophago-intestinal valves, the intestine and the rectum remain essentially the same as in the first stage.

The nervous system: As in the preceding stage.

The excretory system: As in the preceding stage.

The genital rudiment (text Fig.4): The genital primordium remains at the level of the seventh intestinal cell. In the number of contained cells there is no increase until the transition to the third stage. A maximum of seven epithelial cells and two germinal cells was counted in larvae which had not completed transition to the third stage.

The coelomocytes: All four coelomocytes are now clearly distinguishable, the anterior coelomocyte lying immediately behind the retrovesicular ganglion, and the posterior one lying just anterior to the genital rudiment. The remaining coelomocytes are situated about equidistant from each other and from the first and fourth.

The structure of the tail (text Fig.5): Sex differentiation is possible on the basis of this character. In larvae beginning the transition to the third stage, some larvae, interpreted as males, have a relatively more complex tail. In these, the cells of the spicular primordium are visible as a compact mass of cells lying dorsal to the rectum (see detailed discussion of the spicular primordium following).

In both sexes the rectal glands, not seen in the first stage, are now in evidence.

Measurements:

Table 7. Measurements (mm) of Second-Stage Larvae of Kalicephalus parvus.

Number of specimens measured	15
Total length	0.46-0.50
Maximum width	0.02-0.03
Length of buccal tube	0.01-0.02
Length of oesophagus	0.11-0.13
Nerve ring from anterior end	0.07-0.09
Excretory pore from anterior end	0.10-0.11
Genital primordium from anterior end	0.29-0.33
Length of tail	0.06-0.09

The Free-Living Third-Stage Larva (Plate V; H, I, J: Plate VI ; A,B,C)

Morphology and measurements

Shape and size: In this stage, the larvae, ensheathed in the cuticle of the preceding stage, appear longer and thinner than those of the second

stage, although there is actually little difference in absolute dimensions. The largest second-stage larvae overlap the shortest third stage in length; however, in width, only the very largest larvae of the third stage are wider than those of the preceding stage.

The cuticle: The retained exuvium ensheathing the third-stage larva is transversely striated. It is transparent and distinctly separate from the larva itself throughout its entire length. The cuticular linings of the excretory pore and rectum are seen as small appendages to the old skin. Anteriorly an indentation at the old mouth opening and small elevations at the former sites of cephalic papillae are visible. The cuticle of the larva itself is marked by fine, transverse striations.

The musculature: The musculature is more strongly developed than in the earlier stages. In ideal preparations, the rhomboidal shape of the individual cells can be seen. The nuclei are visible as rows of small bodies lying in the four sublateral sectors; they are not as elongate as those of preceding stages.

The alimentary tract: The mouth is no longer a wide, gaping opening; it has been considerably reduced. The narrow buccal tube is surrounded at its base by two projections from the oesophagus.

The oesophagus is long and slim; the bulb is much reduced but the corpus remains set off from the isthmus in being slightly wider. Striations representing the oesophageal musculature are visible. There is a nucleus in each oesophageal sector at the base of the bulb. The oesophago-intestinal valve is comparatively smaller than that of the previous stages.

The intestine appears narrow as compared to that of earlier stages and, in living larvae, presents the appearance of a granular tube in which the granulation is broken at more or less regular intervals by a clear patch. These clear areas represent the location of the intestinal nuclei. In stained preparations, the nuclei, 32 in number, are seen to be large and circular or oval. The lumen is straight rather than sinuous. The rectum has not changed appreciably from that seen in the second stage. Rectal glands are present.

The nervous system (Plate VI, A, B, C): There are six papillary nerves (PN) represented in the larva by chains of nuclei arising from nuclear masses immediately adjacent to the anterior face of the nerve ring. The chains proper, two subdorsal, two subventral and two lateral, are the primordia of the adult cephalic papillary nerves, while the denser, proximal nuclear masses represent the future cephalic papillary ganglia (CPG). The nerve ring is clearly indicated by a relatively colourless band encircling the oesophagus at its isthmus. Immediately posterior and adjacent to the nerve ring are the primordia of several cephalic ganglia. Viewed dorsally, the small dorsal (DG) and subdorsal ganglia (SDG) are represented by a tri-lobed, closely associated nuclear grouping. The two outer lobes, the subdorsal ganglia, enclose the small dorsal ganglion. In lateral aspect, the dorsal and subdorsal ganglia are visible encroaching upon the nerve ring to the dorsal side of the oesophagus; posterior and lateral to these a large nucleate mass, one of a pair of lateral ganglia (LG) extends to the oesophageal bulb. Ventrally three ganglia can be seen in sequence extending posteriorly

from the nerve ring. These are: 1. One of the large, paired ventral ganglia (VG); 2. A nucleate mass surrounding the excretory duct and termed the posteroventral ganglion (PVG) by Alicata (1935), but considered primordium of the excretory complex by Looss (1911), and 3. Most posterior, i.e., just behind the oesophageal bulb, the retrovesicular ganglion (RVG) (ventral cephalic ganglion of Looss).

The ventral nerve is represented by a chain of nuclei with sharply defined longitudinal margins which extends from close to the anterior end of the oesophagus into the retrovesicular ganglion, and from there continues posterior to another enlargement, the anal ganglion. From this, after passing around the anus, it again extends posteriad to gradually diminish in width and terminate in the tail close to the posterior end. The paired lumbar ganglia lie laterally at a level just behind the anal ganglion.

The excretory system: The excretory pore is as in the preceding stages. However, the primordia of the excretory glands are now visible lying between the intestine and the body wall a short distance anterior to the genital primordium. The rudimentary excretory cells are spindle-shaped; their nuclei are long and narrow and stain poorly with alcoholic acid carmine although haematoxylin gives satisfactory preparations. Long, narrow anterior prolongations of these cells are sometimes visible.

The genital rudiment (text Fig.4): The sexes are distinguishable with certainty on the basis of the genital rudiment alone. In the female, it is elliptical, while in the male it is oval or comma-shaped. The blunt

end of the male genital rudiment lies toward the anterior. There are approximately eight epithelial cells and two germinal cells, the latter lying in the posterior part of the rudiment.

The female rudiment is composed of two germinal cells, one of which lies at or close to each end, and eight epithelial cells. A pair of these are polar or tend to encroach on the polar position, while three pairs are symmetrically arranged along the middle of the rudiment body.

The coelomocytes: As in the preceding stage.

The structure of the tail: As in the preceding stage.

Measurements:

Table 8. Measurements (mm) of Free-Living Third-Stage Larvae of Kalicephalus parvus.

Number of specimens measured	15
Total length	0.47-0.59
Maximum width	0.02-0.03
Length of buccal tube	0.01-0.02
Length of oesophagus	0.12-0.15
Nerve ring from anterior end	0.09-0.10
Excretory pore from anterior end	0.10-0.11
Genital primordium from anterior end	0.27-0.34
Length of tail	0.05-0.09

Table 9. Summary of the Rate of Development of K. parvus in Tap Water at Room Temperature.

Hours	Stage
0	morula
6	early tadpole
9	late tadpole
20	hatching beginning
24-26	hatching at its height
48	first stage
72	first ecdysis in progress
96	second stage
120	second ecdysis beginning
144	third stage

Effects of Various Physical Environmental Factors[1]

The lethargic larvae are activated by warmth and touch and, when they are contained in a liquid medium, agitation of the fluid brings about activity of the larvae. There is a rapid positive response to an increase in light intensity. Removal of the source of light with subsequent replacement after five minutes did not elicit a positive response. The larvae are not resistant to desiccation. It was found that once the dish containing larvae appeared dry by inspection with the dissecting microscope, the larvae could no longer be revived by flooding. Freezing was found to kill within one hour.[2]

Attempts to Induce Skin Penetration

Three experiments employing the cork ring method of Goodey (1922) were carried out with negative results. Skin of a young mouse was used and the experiments were conducted in both a 37° incubator and at room temperature with approximately 100 larvae per trial.

The hair was clipped from the posterior part of the body and from the hind legs of two, young white mice. These areas were exposed to 150 larvae in 50 cc of water as follows:

The larvae in water were poured into a 100 ml beaker and the mouse was confined therein for one hour. After this interval, the mouse was removed and the water examined for larvae. Approximately 128

---

[1] No attempt was made to carry out thorough investigations of the effects of various physical and chemical factors on these larvae. Observations here reported were made incidental to other studies.

[2] Lesser times were not tested.

larvae were recovered in one experiment and more than 100 in the other. One mouse was sacrificed after two weeks and the other after one month. Each was thoroughly examined for encysted larvae. No larvae were found.

Attempts to Infect Intermediate Hosts

White mice: In addition to the two mice mentioned above, three other mice, all young males, received approximately 100 K. parvus larvae orally. One male of the same age and from the same source was reserved as a control. The larvae were introduced from a syringe via a catheter. One mouse died immediately after introduction of the larvae. The remaining two were killed and examined as those used in the skin infection trials and were also found to be negative.

Cockroaches: Cockroaches, Periplaneta americana obtained from the Department of Entomology, Macdonald College, Quebec, Canada, were tested as possible intermediate hosts. These were reared in the laboratory under conditions which would preclude infection with species of Kalicephalus. Ten roaches were used in this experiment, two being designated as controls. The remaining eight were starved and kept without water for several days. A paste consisting of ground dog checkers mixed with water containing several hundred larvae was then introduced into the roach colony. At the same time a dish of approximately 250 larvae contained in 10 cc of water was introduced. The roaches were observed to drink and feed almost immediately. Furthermore, the two inches of sand forming the floor of the roach container was liberally sprinkled with third-stage K. parvus larvae in

water, Dissection and examination of the roaches after two weeks yielded entirely negative results.

Other invertebrates (earthworms, dung beetles, snails): Earthworms[1] and dung beetles were exposed by addition of larvae to the medium in which these animals were being kept. Snails, both land and aquatic, were placed in contact with larvae by confining them for two to three hours to small Petri dishes in which 150 larvae were contained in a shallow layer of water. All these animals were killed after a period of two weeks, but none was found to harbour Kalicephalus larvae.

The Parasitic Third-Stage Larva (Plates V; K,L,M,N,O,P: VII; VIII; IX; X)

The larvae introduced per os remain ensheathed and free in the stomach until about the tenth day. In measurements and morphology, these are similar to the free-living larvae.

By the fourteenth day, the larvae have penetrated the stomach wall where they encyst in the mucosa (Plates VIII, IX, X). Encysted parasitic third-stage K. parvus larvae were never recovered outside the stomach and tended to concentrate in the posterior part of that organ. The cyst when first formed contains a clear, slightly amber-coloured liquid and has an elastic wall (Plate VIII; A). As the larva becomes older, there is often marked haemorrhage in the cyst area and the cysts themselves sometimes contain blood. In heavy infections the stomach, on macroscopic examination, shows haemorrhagic plaques several millimeters in diameter (Plate X).

---

[1] Earthworms utilized for this experiment were obtained from a greenhouse into which soil from the outside had not been introduced for a number of years and in which only chemical fertilizers were used. The conditions as stated were felt to greatly minimize the chance of previous infection.

Newly encysted larvae (14-18 days): These are exsheathed, but resemble the free-living third-stage in morphology. They are longer, varying from 0.60-0.98 mm in length. The cuticle and musculature have not changed significantly. The oral opening is larger; the buccal tube remains relatively unchanged. The oesophagus measures 0.15-0.18 mm; it is still of a long, somewhat strongyliform shape, but the bulb is slightly larger in diameter. There has been a slight increase in the absolute length of the oesophagus, but relative to the total length of the worm, there has been a diminution. The intestine and rectum are similar to like structures in the free-living stage, The nerve ring encircles the oesophagus near its midpoint. Further differentiation of the nervous system has not occurred. The excretory pore opens just behind the level of the nerve ring and in the occasional living preparation is seen to open on a minute papilla . The excretory sinus is visible in living specimens about 0.02 mm posterior along the excretory duct (Plate VIII; A). The excretory glands are no longer rudimentary. They are granular and have very large elliptical nuclei. In the area of the nuclei, they are well defined, but anteriorly and posteriorly it is difficult to determine their exact termination.

The genital primordium in the female is now located close to the tail and its shape is a long ellipse. The more anteriorly situated male rudiment, oval in shape, is essentially as in the preceding stage. Four coelomocytes could not be located in any one specimen , but on the basis of their occurrence in younger larvae and since this is the usual number in related forms it is to be expected that four coelomocytes also occur in the late stages of K. parvus. The coelomocytes are seen

as long, spindle-shaped cells with a large central nucleus. One of these is usually associated with the genital rudiment.

The tail in both sexes is proportionately shorter than in the free-living third-stage, but as yet both sexes have the same overall tail shape. In the male, however, the spicular anlagen have undergone further differentiation.

At 20 days: The larvae no longer bear the close resemblance to the free-living stage that early encysted larvae exhibited. However, some systems continue to lag in development. In gross morphology this stage is considerably more robust. The worms are now readily visible with the naked eye. The cuticle and musculature show no peculiarities. The mouth and buccal capsule are slow to change. In contrast, the oesophagus is radically different. The corpus and isthmus are much reduced in length, the bulb is large, and the oesophagus viewed as a whole is clavate. The intestine, while remaining the same in cell number (32 cells), presents an entirely different aspect. The individual cells have greatly increased in size and are more clearly defined, and a much wider lumen describes a sinuous path between them.

The nervous system is just beginning further differentiation. One observes no radical structural change, but there is a noticeable divergence from the highly nucleate condition characteristic of the early stages. The nuclei are no longer closely assooiated.

The change in the excretory system is one of the most obvious advances over the earlier stages. One can now determine the size and shape of the excretory glands with certainty. They are seen to reach to the level of the excretory pore anteriorly, where they lie ventro-

lateral to the oesophagus. The excretory duct passes into the area between the glands close to the anterior margin and is lost from view. The excretory glands are assymmetrical, one being longer than the other. In males, they extend beyond the genital rudiment, but in females, the longer gland terminates a short distance anterior to the genital primordium.

The genital primordium (text Fig. 4) of both sexes, having undergone the changes described in the section on newly encysted larvae, now develops slowly. A progressive growth and differentiation occurs but this is most gradual. On the twentieth day there is merely a slight increase in the size of individual cells within it and consequently a slight increase in size of the structure as a whole.

The tail is unchanged.

At 36 days: Outstanding at this point and evident in all succeeding larvae is the gross sexual dimorphism. The sexes are now readily distinguishable at a glance. The female has a long, evenly tapering tail, while in the male the taper is abrupt (Plate V; K, L). Otherwise in shape and general morphology, this phase of the parasitic third-stage is not especially characteristic. However, the detailed anatomy is now typical of the parasitic third-stage (Plate V; K-P). Prior to this, a transition from the free-living stage is still in progress; in most systems a period of little or no change now ensues. During this period only the genital rudiment of the male undergoes a marked morphological alteration, but this is slow, and toward the end, beginnings of the formation of the provisional buccal capsule are seen. Considerable time

has been devoted to the anatomy of this stage.[1] It is, therefore, considered desirable to present an account of the fine anatomy of the larva in this stage of its development.

The cuticle: The thin, transparent cuticle is not striated. It is longitudinally ridged along the sides of the lateral lines.

The musculature: The musculature is meromyarian and platymyarian. In cross-section taken at midbody, there are two muscle cells visible in each of the four body sectors (Plate V; P). In whole mounts, the muscle cells are seen to be rhomboid and thus to fit together with the narrow end of one cell against the wider portion of the next. It is difficult to make an exact count of the nuclei of the somatic musculature, but of varying counts between 63 and 70, the author has most confidence in counts of 68 nuclei.

The hypodermis: The longitudinal chords are simple. The lateral chords each contain three rows of nuclei, the longitudinal walls between the three rows being distinct. Transverse walls between nuclei of the same row were not seen.

The alimentary tract: A simple mouth and buccal tube are present. The oesophagus has a large bulb, which is oval rather than round. Anteriorly the bulb gradually narrows into the isthmus and from here the oesophagus tapers gradually to the anterior end. Thus there is no visible demarcation of isthmus and corpus. The paired subventral oesophageal glands extend from close to the posterior end of the oesophagus to a point a short distance anterior to the nerve ring. The single dorsal

---

[1] Over 100 specimens have been studied in both living and stained preparations. Serial sections of two entire larvae were cut and studied.

gland extends anteriorly to the posterior end of the buccal tube. In the base of each sector of the bulb, a large nucleus is visible. Of these, that of the dorsal sector is the largest.

The intestine is composed of 32 cells, the most anterior of which are usually short and rectangular. The remainder are somewhat variable but in many specimens there next follow one or two pairs of intestinal cells which are longer rectangles, then three or four of about the same length which are roughly triangular, and through these the lumen zigzags. At about this level, the intestine frequently bends as the excretory cells shift from the ventral to the dorsal side. In this bend, the cells are frequently rhomboid and the lumen continues its sinuous path. Beyond this point, the now ventrally situated intestine is composed of cells becoming progressively longer and narrower. They have the shape of greatly depressed triangles. But at the level where the longest excretory gland ends, diminution in the length of the intestinal cells again occurs and the last six to seven cells are shorter rectangles. The rectum, a delicate, cuticularized tube, leads from a well-developed intestino-rectal sphincter to the anus. What appeared to be an eccentrically situated nucleus of this sphincter was seen in one specimen. This observation was not confirmed in other preparations.

The nervous system: The cephalic papillary nerves are no longer represented by obvious chains of nuclei. Laterally, close to the anterior end, the amphidial pores are seen at the level of the posterior end of the buccal tube. From each pore the amphidial canal extends posteriad to terminate in an amphidial pouch. The cephalic papillary ganglia

are located a short distance anterior to the nerve ring. They lie close to the oesophagus. The nerve ring is prominent and in its immediate vicinity the several main ganglia of the central nervous system are visible. The lateral ganglia appear as pendulous clusters of cell bodies closely applied to the oesophagus. The single dorsal and the paired subdorsal ganglia are small. The former lies close to the nerve ring and the latter lie further posterior. The subventral ganglia occur just anterior to the anterior ends of the excretory glands. The retrovesicular ganglion lies ventral to the first intestinal cell. The ventral nerve continues to be marked by a series of nuclei; these, however, are now spaced at long intervals. The ganglia of the tail (text Fig. 5, 6), studied only by the unrefined methods of staining described in the section on materials and methods, nevertheless permitted relatively detailed study. The anal ganglion is divided into two parts, the first, the antero-anal (Aa G), lying ventrally at the level of the intestino-rectal sphincter, and the paired postero-anal ganglia (Pa G) lying one on either side of the rectum shortly before the anus. The latter ganglia are distinctive in appearance; they form a compact, intensely staining, triangular body. Dorsal and lateral to each postero-anal ganglion is a larger, but more loosely associated, triangular ganglion (Lu Ga 1). The latter is paired and represents the lumbar ganglion in part. Posteriorly it is connected with a second lumbar ganglion division (Lu Ga 2) which innervates the phasmids. There is a ventral connection to the postero-anal ganglion and anteriorly the tapering out represents the connection of this ganglion with the nerves of the lateral chords. The phasmids are seen laterally about midway between the tip of the tail and the anus.

The excretory system: The excretory pore lies ventrally just anterior to the level of maximum width of the oesophageal bulb. From it, the excretory duct leads to an excretory sinus enclosed between the rounded anterior ends of the paired excretory glands. The latter, lying ventro-laterally to the oesophagus, extend posteriorly. In the area of the fifth to sixth intestinal cell, the excretory cells bend over the intestine and come to lie side by side dorso-laterally to the intestine. The nuclei are found in the area in which the crossing over occurs. Each gland possesses a large, deep-staining nucleus, the outline of which is not sharply defined. The excretory glands are unequal in length; at their posterior ends they diminish in size and their ends are relatively sharply drawn. The longer excretory gland terminates in the region of the fourth intestinal cell from the rear.

The genital primordium (text Fig.4): An account of this structure is omitted here in favour of a separate discussion in which the development of this structure can be traced through its various stages in detail.

The structure of the tail (Plate V; K,L: text Fig. 5,6): The female tail is longer and narrower than that of the male. Three anal glands, one dorsal and two subventral, are present. The phasmids have already been described (see nervous system). The male tail is now very complex in structure. The nervous system and rectum have been mentioned previously; the three anal glands are as in the female.

Immediately posterior to the end of the spicular primordium is a large cell of unknown nature which appears to be connected with several elongate cells (glands?) which extend into the tip of the tail. The

nature of these is unknown to the author, although they are reminiscent of and may be similar to the caudal glands of free-living nematodes.

As in the case of the genital rudiment, the author desires to discuss the development of the spicular rudiment separately. It is felt that this structure deserves special attention since the literature concerning its development is indeed meagre.

Late Parasitic Third-Stage Larva (Plate VII)

These larvae, now approximately 2.00 mm in length, occur in more obvious cysts. With the naked eye, the latter appear as small, glistening elevations. Observed with a hand lens, the cyst itself presents the appearance of a raised, shiny, translucent nodule in which the ivory-coloured larvae are readily visible. The largest cysts measure approximately 2.00 x 1.50 mm.

As already noted, after approximately the thirty-sixth day in the host, there ensues a long static period. In this period, other than changes in the male genital rudiment which are described separately, there is gradual increase in overall size and in the size of most organs, but these in general maintain the same structure as found in the 36-day parasitic larvae. Tables 12 and 13 provide measurements of larvae taken at 92, 109 and 130 days.

In these later larvae, however, transition to the fourth stage is beginning and the formation of the provisional buccal capsule merits discussion. At first, two vacuolations are seen, one dorsal and one ventral to the anterior end of the buccal tube. These enlarge until they extend the length of the buccal tube. At this time, the dorso-ventral diameter across both vacuolations at their base is about 0.02 mm.

Table 10. Measurements (mm) of Parasitic Third-Stage Larvae (females) of K. parvus at Various Times of Development in the Host.[1]

Character Measured	Number of Days in Host						
	27		36				
Total length	1.32	1.56	1.83	1.79	1.83	1.74	1.85
Maximum width	0.06	0.06	0.09	0.08	0.08	0.08	0.08
Length of buccal tube	0.01	0.01	0.01	0.01	0.01	0.02	0.01
Nerve ring from ant.	0.11	0.09	0.12	0.12	0.13	0.12	0.14
Excretory pore ant.	0.14	0.15	0.16	0.16	0.16	0.16	0.17
Length of oesophagus	0.20	0.20	0.23	0.21	0.23	0.23	0.23
Width of oesophagus	0.03	0.03	0.03	0.03	0.05	0.05	0.05
Length of tail	0.08	0.10	0.09	0.07	0.09	0.08	0.09
Genital primordium from anterior	1.05	1.25	1.50	1.46	1.50	1.43	1.49

Table 11. Measurements (mm) of Parasitic Third-Stage Larvae (Males) of K. parvus at Various Times of Development in the Host.[1]

Character Measured	Number of Days in Host					
	27	36				
Total length	1.43	1.50	1.67	1.62	1.76	1.65
Maximum width	0.06	0.06	0.06	0.08	0.09	0.08
Length of buccal tube	0.01	0.01	0.01	0.01	0.01	0.01
Nerve ring from ant.	0.10	0.12	0.12	0.12	0.11	0.11
Excretory pore ant.	0.13	0.17	0.16	--	0.17	0.15
Length of oesophagus	0.18	0.21	0.21	0.23	0.24	0.21
Width of oesophagus	0.03	0.03	0.03	0.03	0.05	0.03
Length of tail	0.06	0.06	0.06	0.07	0.07	0.08
Genital primordium from anterior	1.87	1.96	1.02	0.93	1.05	0.98

[1]Measurements at earlier periods of development in the host are not tabulated since they are presented in the text.

Also at this time, the teeth of the provisional buccal capsule initiate their development at the anterior end of the oesophagus and the cuticle is just beginning to loosen anteriorly. By the one hundred and thirtieth day, each vacuolation extends posteriorly from the end of the buccal tube and encompasses part of the anterior rounded-off tip of the oesophagus. The latter appears to be undergoing a change in texture in the area where it is enclosed by the vacuolations. This probably represents the onset of oesophageal dissolution where it extends into the area which will become the new buccal capsule. Finally, in a few of the most advanced larvae collected at this period, a more definite loosening of the cuticle is seen anteriorly and this is also beginning to be evident at the tail.

The Fourth-Stage Larva

No fourth-stage larvae were recovered.

The Fifth Stage - Adult

An adult was never recovered from an experimentally infected snake. However, eggs were collected from a gopher snake, Pituophis catenifer affinis, 115 days after experimental infection. The prepatent period of 115 days as compared to the previously stated condition where K. parvus had not progressed further than the third stage in 130 days may be attributable to a host difference. The latter time is based on studies in which garter snakes and Dekay's snakes were used.

Table 12. Measurements (mm) of Late Parasitic Third-Stage Larvae (Females) of K. parvus at Various Times of Development in the Host.

Character Measured	Number of Days in Host						
	92		109		130		
Total length	1.95	2.13	2.03	2.10	2.18	2.37	2.43
Maximum width	0.08	0.08	0.11	0.12	0.09	0.11	0.12
Length of buccal tube	0.01	0.01	0.01	0.01	0.01	0.02	0.02
Nerve ring from ant.	0.12	0.12	0.13	0.12	0.11	0.13	0.12
Excretory pore ant.	0.16	0.18	0.18	0.16	0.17	0.18	0.20
Length of oesophagus	0.24	0.23	0.26	0.26	0.26	0.26	0.29
Width of oesophagus	0.06	0.05	0.05	0.05	0.05	0.05	0.05
Length of tail	0.11	0.12	0.09	0.11	0.10	0.12	0.10
Genital primordium from anterior	1.58	1.59	1.64	1.71	1.71	1.92	2.01

Table 13. Measurements (mm) of Late Parasitic Third-Stage Larvae (Males) of K. parvus at Various Times of Development in the Host.

Character Measured	Number of Days in Host						
	92		109		130		
Total length	1.83	1.80	1.91	1.89	2.07	2.22	2.16
Maximum width	0.08	0.09	0.09	0.09	0.09	0.09	0.09
Length of buccal tube	0.01	0.01	0.01	0.01	0.01	0.02	0.01
Nerve ring from ant.	0.11	0.12	0.11	0.11	0.13	0.13	0.12
Excretory pore ant.	0.16	0.17	0.18	0.16	0.18	0.17	0.18
Length of oesophagus	0.23	0.24	0.23	0.24	0.24	0.24	0.24
Width of oesophagus	0.05	0.05	0.04	0.05	0.05	0.05	0.05
Length of tail	0.09	0.09	0.09	0.09	0.11	0.11	0.09
Genital primordium from anterior	1.08	1.11	1.16	1.11	1.23	1.32	1.29

The Genital Rudiment (text Fig.4)

Structure and development

In the first stage, all genital primordia appeared similar in shape and cell number. Some difference was noted in orientation to the long axis of the body, but this could not be definitely correlated with sex. It is, however, a possibility; it is also conceivable that the orientation of the genital rudiment in the first stage is related to maturation. The latter was found to be true in Hyostrongylus rubidus by Alicata (1935). He observed that in newly-hatched larvae the genital rudiment lies at a right angle to the long axis of the body, while later in the same stage the primordium comes to lie longitudinally. The author is of the opinion that the latter explanation is more likely. This conclusion seems justified when one considers the great similarity in the development of the genital rudiment between H. rubidus and K. parvus (see discussion following). As already mentioned, the posterior coelomocyte and the genital rudiment are completely variable in relative position and the sexes do not appear to be separable on this basis.

In the second stage proper, the sexes cannot be distinguished by the genital rudiment, but in the later larvae of this stage the presence or absence of the spicular rudiment is indicative as to the sex of the larva. In this manner, the genital primordia, although similar in structure, could be correlated with the sex of the specimens. After this phase in the developmental anatomy, the genital rudiment in itself exhibits sexual dimorphism. The following discussion assumes that in the first stage the genital rudiments are the same in both sexes, in the late second stage the sexes are separated as outlined above and thereafter differentiation is not a problem.

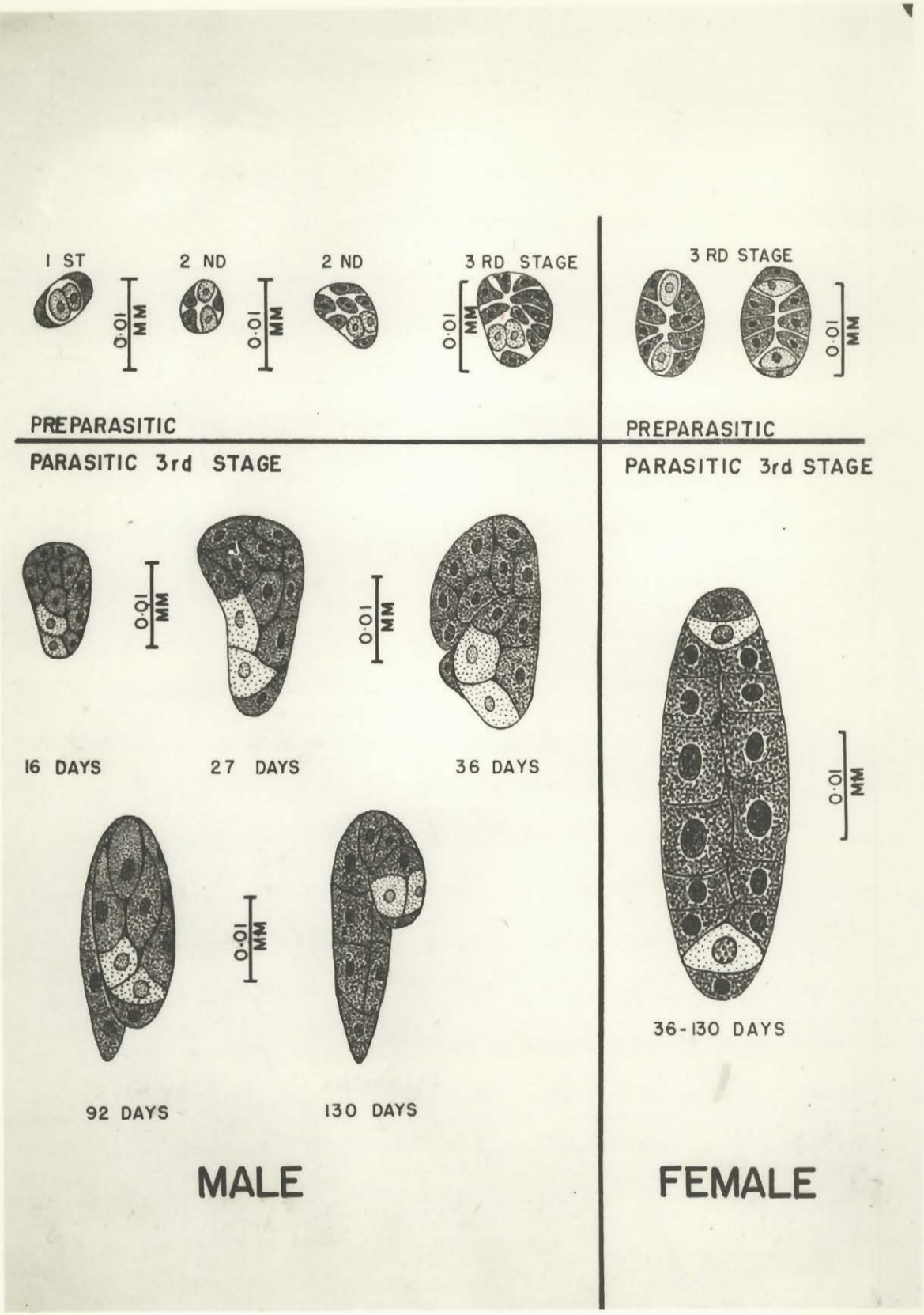


Figure 4. The Development of the Genital Rudiment of Kalicephalus parvus.

The male

First stage: The genital rudiment is elliptical in outline, and is composed of four cells. Two polar, crescent-shaped epithelial cells enclose two oval germinal cells.

Second stage: There is no change in the genital rudiment until late in this stage, at which time multiplication of the epithelial cells take place. By the time definite morphological changes in other systems indicate that the transition to the third stage is underway, the rudiment has become oval. At the narrow posterior end, an epithelial cell retains its polar position. Just anterior to it the germinal cells, having undergone no multiplication, lie side by side; in front of these in the bluntly rounded anterior end five or six epithelial cells are now situated.

Preparasitic third stage: The genital rudiment is slightly larger than in the preceding stage and the epithelial cells have increased to approximately 10 to 12. In overall shape and in the arrangement of the cells there has been no change. The epithelial cells are more crowded and hence compressed.

Parasitic third stage: During the first 27 days of parasitic life, there is no multiplication of cells. There is, however, an increase in the size of the individual cells and a consequent increase in the total size of the structure. The germinal cells remain in the narrow posterior end and the anterior end is gradually beginning to bulge to one side. After 36 days, the anterior bulge has elongated and is bent back upon the posterior part of the rudiment. The latter has become enlarged.

The germinal cells are gradually shifting into a posterior polar position and bear a single-celled epithelial cap. The epithelial cells number 12 to 14.

Gradually the tail-like, posteriorly bending portion elongates until it is as long as the wider portion containing the germ cells. It is now obvious that the structure is reversing itself and retaining the germinal cells in what will become the anterior position.

By the one hundred and thirtieth day in the host, some rudiments have almost completed the reversal. The two germinal cells are now side by side and capped by a single epithelial cell. The posterior cells in the tail-like portion are distinctly elongate. Throughout this reorientation, the number of epithelial cells has not increased beyond fourteen. From the ninety-second to one hundred and thirtieth day, there is little or no overall growth of the genital rudiment; it merely reverses itself. Later stages were not available.

The female

As already noted, the genital rudiment of the female could not be distinguished from that of the male in the first two stages. As transition to the third stage began, genital rudiments with five to eight epithelial cells in which the germinal cells remained polar were considered female. This conclusion was checked against the tail structure and found to be correct. Later in the transition, seven or eight epithelial cells are present.

In the early preparasitic third stage, the rudiment is essentially the same as described but the epithelial cell number in all specimens reaches eight and remains at that number throughout this stage. At

first, the germinal cells are polar, immediately against the margin, but slightly eccentric. Later the two epithelial cells, one at each end, which are closest to the polar position, migrate so as to cap the germinal cells.

The parasitic third stage female exhibits less alteration in the genital primordium than does the male. There is a gradual increase in number and size of the cells with a consequent elongation of the rudiment. When the 19-celled condition is attained, the rudiment becomes static in development. Female larvae at 36 days possess genital rudiments that are similar in cell number, cell arrangement and overall size to those observed in females at 130 days.

Discussion

There is some variation to be found in existing descriptions of the genital rudiment of first-stage strongyloids; e.g. Ortlepp (1923) reports two cells for K. philodryadus as does Looss (1911) for Ancylostoma duodenale. The four-celled rudiment as reported here is known for such diverse forms as Turbatrix aceti, Hyostrongylis rubidus and Crenosoma vulpis (Pai, 1928, Alicata, 1935 and Wetzel, 1941a respectively). It therefore seems probable that four cells, two epithelial enclosing two genital cells, is the usual form of the genital primordium in first-stage larvae of strongyloid nematodes and perhaps of the order Rhabditida as a whole.

As already noted, the development of the genital rudiment in K. parvus greatly resembles that of Hyostrongylis rubidus. This may indicate that the reproductive systems of the Strongylina in general

develop similarly. Possibly the similarity extends through the Rhabditida. Alicata (1935) has already called attention to the fact that the reversal of the male rudiment also occurs in Turbatrix aceti as described by Pai (1928).

Similarities between K. parvus and H. rubidus in this respect are striking indeed (and more limited observations on K. rectiphilus (Plate XII; E-I) are in agreement). In the free-living stages, the genital primordium is almost identical in individuals of like sex in both species, the only difference being that in K. parvus the maximum number of epithelial cells is less by one or two (K. parvus male 12, female 8; H. rubidus male 13, female 10). This difference may even be attributable to error. The epithelial cells are minute and an exact count is difficult. The remaining difference is in rate of development. The cellular arrangement in the rudiment of the preparasitic third stage of K. parvus is equivalent to that observed by Alicata (1935) in the early parasitic stages of H. rubidus.

In the parasitic stages, the same developmental sequence is seen in both species, but in H. rubidus the rate is much more rapid. Thus in the male, K. parvus requires 130 days to almost complete the reversal of the genital rudiment, whereas this process occurs in about five days in H. rubidus. During this reorientation, there is no increase in cell number and in K. parvus 12 to 14 cells were observed, while Alicata (1935) reports 13 for H. rubidus.

In the comparison of females of these two species, it is also true that the rate of development is greater in H. rubidus and that structurally the rudiments are similar. There appears to be a slightly

greater dissimilarity in cell number. Alicata (1935) does not mention the number of cells found in the female genital primordium of H.rubidus at this stage, but 16 cells can be counted in each of three appropriate illustrations of genital rudiments. This figure is in agreement with the author's earliest counts in K. parvus and, indeed, this number of cells is all that is apparent on superficial examination. However, in a number of excellent preparations, the author was able to count 19 cells and subsequent recounts on previously studied material agree with this number. The three extra cells lie under the longitudinal axis of the rudiment and are in a distinctly different plane. They are, therefore, easily overlooked. Considering the remarkable similarities in the structure as found in K. parvus and H. rubidus,it is suggested that 19 cells may actually also be the correct number in the case of the latter.

The Spicular Primordium (text Fig. 5,6)

Structure and development

As already noted, the later second-stage male larvae exhibit a rudimentary spicular primordium which remains the same through the preparasitic third stage. This structure was merely mentioned previously so that detailed discussion here would not be repetitious. Special mention is desirable in that it is the author's belief that the various cells observed can be homologized with the cells of the more developed spicular rudiment of the parasitic third stage.

In the late second stage, the mass of cells lying just dorsal to the rectum of the male represents the earliest structural form of the spicular primordium that can be differentiated from the various cells

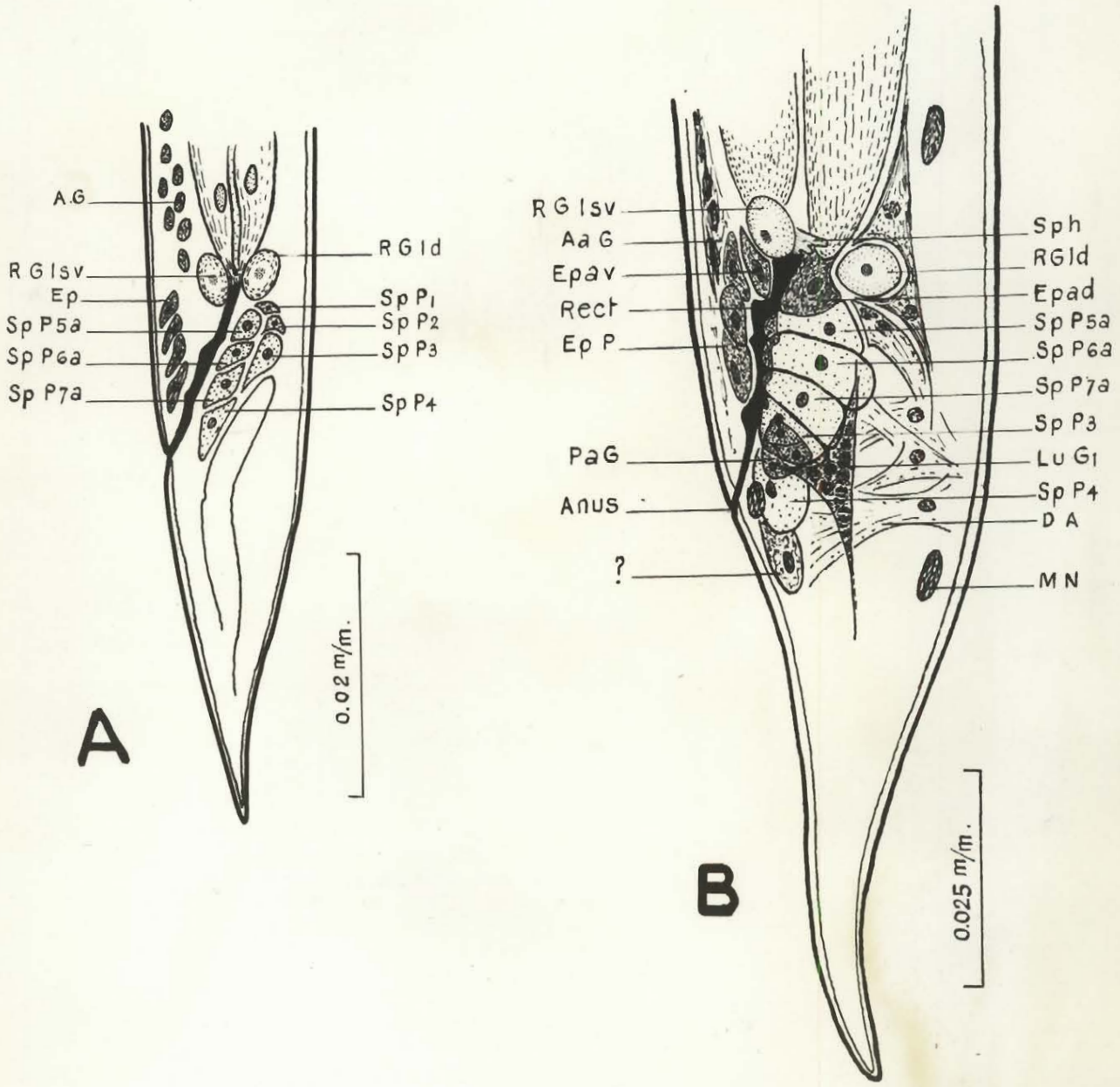


Figure 5. The Male Tail of Kalicephalus parvus in Lateral View
A. In Second Stage; B. In the Parasitic Third Stage.

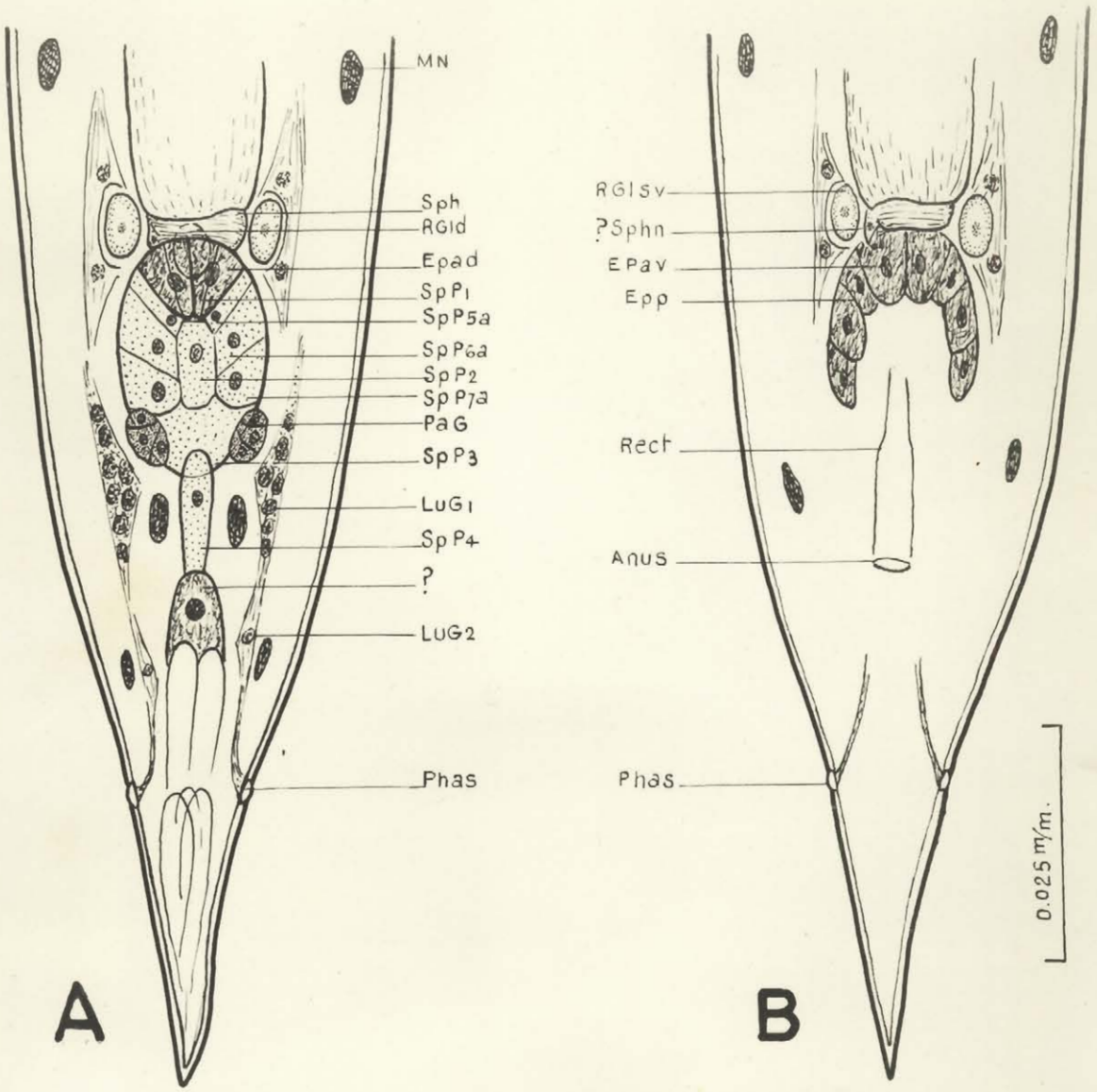


Figure 6. The Male Tail of Kalicephalus parvus in Ventral View; A. The Spicular Primordium; B. Epithelial Cells Ventral to Rectum.

and nuclei of the anal region. At this stage, it consists of 11 cells. Viewed laterally, seven cells are visible (Sp P 1-7), three of these lie along the dorsal side of the rectum (Sp P 5a-7a), and dorsal to these, four more cells are visible (Sp P 1-4). Three cells are paired with the cells lying just dorsal to the rectum and thus are hidden from view when the specimen is seen in lateral aspect. As already noted, the preparasitic male of the third stage is similar.

In the parasitic third stage, however, development resumes. Although the cell number remains the same, the cells increase greatly in size and the three anterior single cells (Sp P 1-3) move between and separate the paired cells (Sp P 5-7). Closely associated with the spicular primordium are several cells which, due to their proximity to this structure, must be discussed with it. Immediately posterior to the intestino-anal sphincter (Sph) and subventral to the rectum, two epithelial cells (Ep a v) partially surround the origin of the rectum. From these, three pairs of epithelial cells (Ep p) extend posteriad along the course of the rectum and lie latero-ventral to it. Viewed laterally, these are small flattened cells lying in close association. Viewed ventrally, they form a high arc

---

Figures 5 and 6: Aa G - Antero-anal ganglion; AG - Anal ganglion; DA - Depressor ani; Ep - Epithelial cell; Ep a d - Anterior dorsal epithelial cell; Ep a v - Anterior ventral epithelial cell; Ep p - Posterior epithelial cell; Lu G 1 - First division of lumbar ganglion; Lu G 2 - Second division of lumbar ganglion; MN - Muscle nucleus; Phas - Phasmid; Pa G - Postero-anal ganglion; Rect - Rectum; R Gl d - Dorsal rectal gland; R Gl sv - Subventral rectal gland; Sph - Sphincter; ?Sph N - ? Sphincter nucleus; Sp P 1-4 - Single cells of the spicular primordium; Sp P 5a-7a - Paired cells of the spicular primordium; ? - Cell of unknown nature.

the open ends of which lie toward the anus. The closed end is formed by the ventral anterior pair of epithelial cells (Ep a v).

Dorsal to the origin of the rectum, another pair of epithelial cells (Ep a d) complete the encirclement of the origin of the rectum. Posterior and partially dorsal to these lie the three anterior cells (Sp P 1, Sp P 5a and b) of the spicular primordium, which is a hollow ovoid mass with a posterior projection when viewed in dorso-ventral optical section. The three cells already mentioned form the anterior broad end of the oval. Next, posteriorly, two pairs of cells (Sp P 6a and b; Sp P 7a and b) along each lateral margin form the long sides of the oval and are separated medially by an elongate rectangular cell (Sp P 2). Posterior to these, a single large cell (Sp P 3) forms the narrow part of the oval. Finally, originating ventral to the latter and extending posteriorly just dorsal to the distal portion of the rectum, is the single elongate cell (Sp P 4) forming the posterior projection of the spicular rudiment.

It is readily seen that in both stages, three pairs of cells (Sp P 5-7) lie dorso-lateral to the rectum, while medially four single cells (Sp P 1-4) extend the length of the rectum.

Discussion

Chitwood and Chitwood (1950) comment as follows on the development of the spicules of nematodes in general:

> They develop in a pair of cell masses, the spicular primordia, which develop as proliferations of the dorsal wall of the cloaca, first described correctly by Seurat (1920) in Falcaustra lambdiensis. Schneider assumed the presence of a single primordium in nematodes with two spicules but this is incorrect.[1]

Of the papers referred to in the quotation, the author has seen Seurat (1920). Schneider's (1866) monograph was not obtainable. The author is not aware of any other detailed discussions of the developing spicular rudiment. Hyman (1951) merely repeats the conclusions of the Chitwoods and Seurat.

It is difficult to equate the statement of Chitwood and Chitwood with the author's observations on the second- and third-stage larvae of K. parvus. Seurat's (1920) figure of the spicular primordia of Falcaustra is based upon that of a fourth-stage larva and it is therefore possible that this structure begins as a single mass and divides so that it is double in the fourth stage. The objection could be raised that two spicules are considered more primitive than one, and unless it is assumed that one spicule was entirely lost and secondarily regained from the remaining single primordium, one would expect the rudiment to originate as two distinct bodies. While the latter condition is possible, it is beyond one's ability to prove in the light of present day knowledge, and, in fact, is not very probable. That duplex structures frequently arise from the splitting of an originally single anlagen is commonplace and, indeed, the primordia

---

[1] No year cited for Schneider. However A. Schneider (1866) is the reference according to the bibliography supplied.

of Falcaustra as figured are only partially separate; they join in a single common cell posteriorly.

It is also possible that the two single anterior cells are not actually part of the rudiment of K. parvus but merely extraneous cells occurring between the anterior horns of a double structure joined near the anus. This is the morphology of the spicular rudiment figured by Seurat (1920). Such an explanation raises more problems than it solves. The structure interpreted as the spicular rudiment by the author is a discreet body; its limits are clearly defined and all the cells attributed to it are homogeneous in their cytoplasmic and nuclear character. The author must, therefore, consider the single cells, medially located, as related to the remaining cells and as combining with these to form the entire structure.

It is unfortunate that later stages were not available so as to follow the development of this cell mass into whatever structure it is indeed primordial to, but under the prevailing conditions it is advisable to consider the two spicules of K. parvus as arising from a single mass of cells rather than a duplex structure.

Kalicephalus agkistrodontis Harwood, 1932 (Plates IV; D,E,F: XI)

The Egg (Plate XI; A, B, C, D)

The eggs of Kalicephalus agkistrodontis measure 0.07-0.08 x 0.04-0.05 mm. The eggs are oval and one side is slightly flattened. Ova laid by the female immediately after removal from a recently killed host are 32-celled; at room temperature in six to seven hours gastrulation has begun, in twelve hours the early tadpole stage is seen, during the sixteenth to nineteenth hours the fully developed embryo can be observed actively wriggling within the egg shell and the earliest hatching occurs. Hatching is at its height shortly thereafter, at about 20 hours. Twenty-four hours after incubation has begun, hatching is virtually complete.

The Preparasitic Larvae (Plate XI; E, F, G)

The free-living larvae of K. agkistrodontis are essentially the same as those of K. parvus and therefore are not discussed in detail. The measurements of the three preparasitic stages are given in the tables below:

Table 14. Measurements (mm) of K. agkistrodontis First-Stage Larvae.

Number of specimens measured	14
Total length	0.31-0.36
Maximum width	0.01-0.02
Length of buccal tube	to 0.01
Length of oesophagus	0.09-0.11
Nerve ring from anterior end	0.07-0.08
Excretory pore from anterior end	0.08-0.09
Genital primordium from anterior end	0.19-0.21
Length of tail	0.06-0.07

Table 15. Measurements (mm) of K. agkistrodontis Second-Stage Larvae.

Number of specimens measured	19
Total length	0.40-0.49
Maximum width	0.02-0.03
Length of buccal tube	0.01-0.02
Length of oesophagus	0.11-0.12
Nerve ring from anterior end	0.08-0.09
Excretory pore from anterior end	0.09-0.10
Genital primordium from anterior end	0.23-0.28
Length of tail	0.06-0.08

Table 16. Measurements (mm) of K. agkistrodontis Third-Stage Larvae.

Number of specimens measured	18
Total length	0.49-0.57
Maximum width	0.02-0.03
Length of buccal tube	0.01-0.02
Length of oesophagus	0.11-0.14
Nerve ring from anterior end	0.08-0.09
Excretory pore from anterior end	0.09-0.12
Genital primordium from anterior end	0.29-0.34
Length of tail	0.04-0.07

Table 17. Summary of the Rate of Development of K. agkistrodontis in Tap Water at Room Temperature.

Hours	Stage
0	32-celled
6-7	gastrula
12	early tadpole
16	first fully developed embryos
19	fully developed embryos, hatching beginning
20-22	hatching at height
24	hatching almost complete
48	some first ecdysis; mostly second stage
72	all in second stage
96	transition to third stage
120	all in third stage

The Parasitic Stages of K. agkistrodontis (Plates IV; D,E,F: XI; H)

Introduction

K. agkistrodontis differs markedly from K. parvus in its parasitic life history. The differences are two, the first being in time of development. As already noted, K. parvus is still in the third stage 130 days after infection. K. agkistrodontis was found in the adult or fifth stage, although immature, in 23 days. Secondly, K. agkistrodontis does not encyst. All parasitic stages occur in the lumen of the digestive tract.

Unfortunately, the detailed anatomical studies carried out on K. parvus were not possible on this species due to lack of material.

The Parasitic Third-Stage Larva (Plate XI; H)

Two days after administration of infective larvae per os, numerous individuals, still ensheathed, were recovered from the lumen of the stomach. These resembled the preparasitic larvae in all observed particulars, including overall dimensions and size of individual structures.

By the seventeenth day the larvae, free in the duodenum, have undergone considerable development. One specimen had attained the fourth stage. Most individuals were in a state of transition and a few still displayed the third-stage characteristics distinctly.

The third-stage larvae at 17 days in the host are about twice the size they were at the time of infection. They measure 0.86-1.14 mm in length by 0.03-0.06 mm in width. The genital rudiment has enlarged and in females it is a spindle-shaped mass of cells. As yet, it is not connected with the vulva, but the primordium of the latter is seen

as several cells proliferating from the body wall. In the males, the genital rudiment has bent back upon itself with both sides of the bend about equal in length. The genital primordium lies 0.53-0.69 mm from the anterior. The most slowly developing individuals show no development of the buccal capsules whereas the larvae which have progressed furthest have already a completely formed provisional buccal capsule with three small teeth forming in its base. The buccal capsule in the specimens studied varied in size from 0.06-0.07 mm by 0.05-0.08 mm. The old buccal tube is seen attached to the loosened cuticle. The nerve ring is located about 0.13-0.15 mm from the anterior; the excretory pore about 0.15-0.16 mm from the anterior. The oesophagus, proportionately shorter and more bulbed, is 0.15-0.20 mm long. The anus is situated 0.08-0.09 mm from the posterior.

The Fourth-Stage Larva

Other than the single individual found in the small intestine after 17 days and which had apparently just entered the fourth stage, two well-developed fourth-stage larvae were found after 23 days. One of these was recovered from the duodenum and the other from the stomach. Examination alive revealed a large provisional buccal capsule behind which the developing adult buccal capsule was in evidence. At this point it was decided to fix the larvae preparatory to staining etc. and in this process they were lost to further study. Additional material could not be obtained. The meagre observations described above indicated that these larvae were essentially like those fourth-stage larvae described for other bursate nematodes and like those described

by the author for K. rectiphilus. The latter had been studied shortly before this loss and it is improbable that any outstanding dissimilarity would have gone unnoticed.

The Fifth Stage Adult (Plate IV; D,E, F)

Adults, not yet mature, were recovered as early as the twenty-third day. In the most slowly developing males, the spicules were as yet completely unformed. Only thin-walled, unsclerotized, tube-like canals marked their future location. Most male specimens recovered at this time possessed spicules whose dimensions and structure had already been established, i.e. the proximal and distal ends were well-defined, the shafts were clearly outlined throughout their lengths and the alae were coming into evidence. However, mature adult cuticularization had not been attained.

The bursa is partially developed, the dorsal ray being more advanced toward its final structure than either the ventral or lateral rays. The genital cone is short. As regards the reproductive system proper, it was observed that, although all the final structures were present, they were weakly developed. In the female the vulva is present and open, and the ovejector is outlined but only weakly muscularized. The uteri are represented by thin-walled, wide tubes leading to the solid ovaries, which at this time do not extend far into either the anterior or posterior of the body. The latter are not complexly wound as in the adult, rather they are in the form of a simple reflexed tube. In the male, the reproductive structures extend as a simple tube to about half the length of the body.

This condition is much simpler and shorter than that as seen in the adult. Although not markedly set off, the ejaculatory gland, the seminal vesicle and the testes are all clearly discernible.

By the twenty-seventh day, the spicules are definite in form in all specimens studied. They are more heavily sclerotized. The bursa is only slightly more advanced than that seen earlier. The testis now ends in the anterior end of the body but still does not exhibit its definitive form. Females have a more muscular ovejector and the ovaries, while still only partially developed, are beginning to form a complex series of loops characterizing the adult.

In 58 days two mature, adult specimens, one male and one female, were recovered from an experimentally infected snake. The female was gravid; her eggs measured 0.08 x 0.05 mm. Further description is unnecessary since the adult K.agkistrodontis is already described in the taxonomic section of this thesis.

Table 18. Measurements (mm) of Fifth-Stage K. agkistrodontis (Females) at Various Times of Development in the Host.

Character Measured	Subadult						Adult
	23 days		27 days		29 days		58 days
Total length	2.64	3.26	4.11	5.12	4.29	3.54	8.57
Maximum width	0.14	0.17	0.21	0.23	0.29	0.23	0.42
Head diameter	0.11	0.14	0.15	0.17	0.21	0.18	0.20
Depth buccal capsule	0.08	0.08	0.11	0.09	0.12	0.11	0.12
Nerve ring from ant.	0.17	0.18	0.18	0.18	0.23	0.20	0.21
Excretory pore ant.	0.26	0.24	0.32	0.26	0.30	0.28	0.30
Length of oesophagus	0.23	0.24	0.26	0.24	0.27	0.27	0.26
Width of oesophagus	0.09	0.09	0.11	0.12	0.15	0.15	0.15
Vulva from anterior	1.73	2.21	2.66	3.23	2.90	3.30	5.40
Vulvar ratio	1.9:1	2.1:1	1.8:1	1.7:1	2.1:1	1.8:1	1.7:1
Length of tail	0.12	0.11	0.12	0.14	0.14	0.12	0.30

Table 19. Measurements (mm) of Fifth-Stage K. agkistrodontis (Males) at Various Times of Development in the Host.

Character Measured	Subadult					Adult
	23 days		27 days	29 days		58 days
Total length	2.27	2.48	4.05	2.75	3.83	6.78
Maximum width	0.14	0.14	0.18	0.18	0.23	0.32
Head diameter	0.14	0.14	0.14	0.15	0.15	0.18
Depth buccal capsule	0.08	0.08	0.09	0.09	0.09	0.11
Nerve ring from ant.	0.15	0.17	0.15	0.17	0.17	0.20
Excretory pore ant.	0.23	0.24	0.21	0.27	0.26	0.23
Length of oesophagus	0.20	0.23	0.21	0.24	0.23	0.24
Width of oesophagus	0.09	0.08	0.11	0.12	0.11	0.12
Length of spicule	*	0.40**	0.45	0.51	0.48	0.48

* Spicules not completely formed.

** Measured approximately; spicules incompletely sclerotized, sinuous and difficult to measure exactly.

Kalicephalus Rectiphilus Harwood, 1932 (Plates XII; XIII; XIV)

Introduction

Kalicephalus rectiphilus was not as common in the available snakes as the preceding species and this is reflected in the results obtained. Although all major stages in the life history have been observed, only few specimens were available at the various parasitic stages. Parasitic third-stage larvae were recovered but only after encystation had occurred.

The Preparasitic Stages

The egg and the free-living larvae of K. rectiphilus are essentially like those of K. parvus in development, measurements and structure. Therefore, measurements and development are reported in tabular form only (Tables 20-23).

Table 20. Measurements (mm) of K. rectiphilus First-Stage Larvae

Number of specimens measured	5
Total length	0.31-0.34
Maximum width	0.01-0.02
Length of buccal tube	to 0.01
Length of oesophagus	0.09-0.10
Nerve ring from anterior end	0.07-0.08
Excretory pore from anterior end	0.08-0.09
Genital primordium from anterior end	0.18-0.19
Length of tail	0.05-0.06

Table 21. Measurements (mm) of K. rectiphilus Second-Stage Larvae

Number of specimens measured	5
Total length	0.41-0.56
Maximum width	0.02-0.03
Length of buccal tube	0.01-0.02
Length of oesophagus	0.11-0.13
Nerve ring from the anterior end	0.08-0.09
Genital primordium from anterior end	0.30-0.31
Length of tail	0.06.0.08

Table 22. Measurements (mm) of K. rectiphilus Preparasitic Third-Stage Larvae

Number of specimens measured	10
Total length	0.52-0.70
Maximum width	0.02-0.03
Length of buccal tube	0.01-0.02
Length of oesophagus	0.12-0.19
Nerve ring from anterior end	0.08-0.11
Excretory pore from anterior end	0.09-0.12
Genital primordium from anterior end	0.30-0.37
Length of tail	0.04-0.10

Table 23. Summary of the Rate of Development of K. rectiphilus in Tap Water at Room Temperature

Hours	Stage
0	morula
6-9	tadpole stage
18	embryos fully developed
20	hatching beginning
24	hatching at its height
48	some second-stage larvae; most larvae in moult
60	majority second-stage larvae
72	some third-stage larvae
96	majority third-stage larvae
108	all third-stage larvae

The Parasitic Stages (Plates XII; XIII; XIV)

Introduction

This species differs from K. agkistrodontis in that the early parasitic stages are encysted. It differs from K. parvus, in which histotropic stages also occur, in the site of encystation and in rate of development. In K. rectiphilus, adults, although immature, are found at 33 days after infection.

The Parasitic Third-Stage Larva (Plate XII)

The parasitic third-stage larvae were recovered from cysts in the mucosa of the posterior part of the duodenum. Larvae of the third stage from this area were found 26, 28, and 33 days after infection. Sex differentiation is possible on the basis of the genital primordium and the shape of the tail.

In general, these larvae resemble the parasitic third stage of K. parvus.

Shape and size: The larvae are four or five times as long as preparasitic individuals of the same stage. Larvae of both sexes are of the same general shape, although, in the male, the taper of the tail is steeper.

The cuticle: As in K. parvus.

The musculature: As in K. parvus.

The alimentary tract: The mouth opening leads to a simple buccal tube. The oesophagus is narrower and more elongate than it is in K. parvus. The intestine is composed of 30 cells.

The nervous system: With the exception of a more posteriorly situated retrovesicular ganglion located at about the level of the third intestinal cell, the nervous system is essentially like that of K. parvus.

The excretory system: As in K. parvus but the excretory glands are slimmer.

The coelomocytes: The coelomocytes, four in number, are long, spindle-shaped cells. They are spaced at approximately equal distances between the end of the oesophagus and the genital rudiment. Their nuclei are large and centrally located.

The genital rudiment (Plate XII; E-I): In the male, the genital rudiment is located near the tenth intestinal cell. In the female it is situated near the ninth intestinal cell and, in this character, K. rectiphilus differs markedly from K. parvus where the female genital rudiment is located at the level of the thirteenth intestinal cell. Thus, in female K. parvus the genital primordium is near the tail, whereas in female K. rectiphilus, it is just a short distance behind the midbody. At this stage, the beginning of the formation of the vulva could be seen in the onset of epithelial prdiferation in the body wall at the level of the genital rudiment (Plate XII; E).

It is interesting to note that in K. rectiphilus the genital rudiments of each sex closely resemble those of like sex at the same degree of development in K. parvus. Thus, for example, in the male, at that phase where the genital rudiment is beginning its reversal, the shape of the genital primordium and the number of contained cells are similar for both species. Each has 12 to 14 cells at this stage. The females show analagous similarities.

The developing provisional buccal capsule (Plate XII; J): The provisional buccal capsule develops from vacuolations lying dorsal and ventral to the buccal tube. The teeth which will occupy the base

of the buccal capsule develop from primordia at the anterior tip of the oesophagus. The oesophagus undergoes dissolution where it extends into the vacuolated area.

Table 24. Measurements (mm) of the Parasitic Third Stage of K. rectiphilus at Various Times of Development in the Host.

Character Measured	26 days		28 days			33 days
	female	male	male	male	male	Female
Total length	2.55	2.70	2.19	3.06	2.45	2.20
Maximum width	0.12	0.11	0.09	0.11	0.11	0.09
Length of buccal tube	0.01	0.01	0.01	0.01	0.01	0.01
Length of oesophagus	0.23	0.20	0.21	0.21	0.22	0.24
Nerve ring from ant.	0.11	0.11	0.12	0.13	0.13	0.12
Excretory pore ant.	0.20	0.22	0.21	0.22	0.21	0.21
Genital primordium from anterior	1.50	1.74	1.29	1.94	1.58	1.48
Length of tail	0.11	0.07	0.07	0.07	0.07	0.06

The Fourth-Stage Larva (Plates XIII; A, B: XIV; B)

Two female fourth-stage larvae were recovered at 33 days along with one third stage female and nine subadults. These larvae were encysted in the mucosa of the posterior part of the duodenum.

In these fourth-stage larvae, the transition to the adult was advanced. The definitive buccal capsule was well differentiated, the provisional buccal capsule of one specimen being partially detached and both specimens showing a loosening of the cuticle. The development of the reproductive system had progressed as far as that of the female subadults recovered at the same time.

The two female fourth-stage larvae measure 3.82 and 4.00 mm in length and 0.18 mm in width. The provisional buccal capsule is

0.04 mm high and 0.05 mm in greatest diameter. In its base there are three teeth which connect to the oesophagus by a cuticularized duct. Two small pits, whose function is unknown, open into the anterior part of the provisional buccal capsule. The additional measurements taken are as follows: depth of definitive buccal capsule; 0.10 mm, oesophagus, 0.23 and 0.24 mm in length; oesophagus 0.07 and 0.10 mm in maximum width; nerve ring and excretory pore 0.16 and 0.25 mm from the anterior end respectively. The vulva divides the body in the ratio 1.7:1. The tail is 0.22 mm long.

The Fifth Stage

Subadults (Plates XIII; C-E: XIV; A): As already noted, subadults, having just completed the transition from the fourth stage, were found encysted in the small intestine at 33 days. These are delicate nematodes 2.94-4.05 mm in length and 0.16-0.19 mm in width. All systems are feebly developed as compared to those of the adult and little progress beyond the structural characteristics of the late members of the preceding stage has occurred.

The buccal capsule is not completely sclerotized, nevertheless its kalicephalid character is apparent. It is 0.10-0.13 mm deep.

The oesophagus is slightly longer than that of the later adult but appears less muscular. It measures 0.21-0.23 mm in length. The intestine and rectum are without peculiarities.

The reproductive system is just beginning to display its adult characteristics. All the various structures are present, but only in a very underdeveloped state. The bursa of the male is short and stumpy. Although all rays are present, they have not reached adult

proportions. In some specimens the spicules are as yet unformed, while in others cuticularization has progressed to a point where the definitive spicular dimensions are visible but hardening is obviously still incomplete. In the latter, the spicules measure 0.22-0.25 mm in length. The testis and tubes of the male reproductive system are all indicated in the rudimentary system seen, but these are small in size and poorly differentiated. The anterior tip of the testis remains in the posterior two-thirds of the body.

In the female, the opening of the vulva is indicated but does not appear to be open. The ovejector is not as yet muscularized; its general shape and proportions are merely outlined. The uteri are present as wide tubes and each of the solid ovaries extends only a short distance from its origin before bending back on itself and extending to the area of the uterus.

Adults: Forty-three days after infection, adult K. rectiphilus were recovered from the rectum of an experimentally infected snake. Only males were recovered and therefore information on the prepatent period in this species cannot be presented. Eggs were recovered from the faeces of an experimentally infected snake 92 days after infection, but it is doubtful that this represents the earliest date on which eggs could have been recovered.[1]

---

[1] It was impossible to check the faeces of this snake in the period in which eggs might have been expected to first appear since, at that time, the author was en route from the Biological Research Institute, San Diego, to the Institute of Parasitology, Macdonald College, Quebec, Canada.

Table 25. Measurements (mm) of K. rectiphilus Subadults (33 days in Host)

Character Measured	Males					Females	
Total length	3.53	3.68	3.09	2.94	3.53	4.05	3.90
Maximum width	0.18	0.16	0.19	0.18	0.16	0.19	0.18
Head diameter	0.14	0.16	0.15	0.14	0.16	0.18	0.17
Depth buccal capsule	0.12	0.12	0.10	0.12	0.10	0.13	0.13
Nerve ring from ant.	0.20	0.21	0.18	0.20	0.20	0.23	0.26
Excretory pore ant.	0.30	0.28	0.28	0.26	0.28	0.30	----
Length of oesophagus	0.21	0.22	0.24	0.21	0.25	0.23	0.24
Width of oesophagus	0.07	0.10	0.11	0.10	0.11	0.11	0.11
Length of spicule	0.25	0.23	---*	0.22	---*		
Length of tail						0.14	0.20

* unsclerotized.

Experiments on Skin Penetration with Snakes

The results of these experiments, shown in Table 26, are inconclusive, but they indicate that skin penetration may occur. Only a brief expansion of this table is given here; the possible implications of this work are brought out in the general discussion.

The snakes referred to in the table were all exposed to larvae exactly as described in the section on materials and methods. Of 13 snakes used, 10 were negative on post-mortem examination while three were positive. Of the three positives, one was exposed to 10 larvae, the prevention of drinking was successful and 40% of the larvae were recovered as later stages in the host. In the case of the remaining infected snakes, one had shed its tape and therefore results obtained from it are of doubtful value. On the third snake, the tape held and 2% of the larvae placed in contact with the snake were

subsequently recovered as parasites. All other snakes used in these experiments were negative, in spite of their exposure to greater numbers of vigorous larvae.

The author is uncertain whether taping as described can be said to definitely rule out infection per os. While it certainly did prevent drinking whenever it held, it seems possible that, after the tape had become wet and lost some of its adhesive properties, the larvae could perhaps have entered the mouth by crawling between the skin and the tape and finally between the closed lips.

The only consistent difference between those snakes which became infected and those which did not was that the former were fed one laboratory-reared newborn mouse[1] the day preceding contact with the larvae. The possible significance of this difference in technique went unnoticed until after the completion of Series 26 (see Table 26). The two snakes used subsequently would not accept food. Thereafter, snakes suitable for these experiments were not available or would not feed.

---

[1] These mice could not have been harbouring kalicephalid larvae in that they were reared in an animal room well removed from any source of contamination.

TABLE 26. Summary of Experiments on Skin Penetration with Snakes

Series Number	Snake Number	Number of Larvae Used	Number of Larvae or Adults Recovered	Success in Preventing Drinking	Ingestion of Food
I	2	5 K. parvus **	2 K. parvus		
		5 K. rectiphilus	2 K. rectiphilus	tape held	fed
II	NO	100 K. agkistrodontis	8 K. agkistrodontis	tape shed	fed
III	21	100 K. agkistrodontis	2 K. agkistrodontis	tape held	fed
V	1	150 K. rectiphilus	none	tape held	not fed
	2	150 K. rectiphilus	none	tape held	not fed
	3	150 K. rectiphilus	none	tape held	not fed
	4	150 K. rectiphilus	none	tape held	not fed
26	a *	500 K. agkistrodontis	not examined	tape held	not fed
	b	500 K. agkistrodontis	none	tape shed	not fed
	c	500 K. agkistrodontis	none	tape held	not fed
	d	500 K. agkistrodontis	none	tape held	not fed
X	1	150 K. agkistrodontis	none	tape held	would not feed
	2	150 K. agkistrodontis	none	tape shed	would not feed

* Died immediately after being placed in contact with larvae; probably injured in handling.

** The larvae which were to be used for this experiment failed to survive. Therefore the author was forced to resort to the few larvae here recorded.

DISCUSSION AND CONCLUSIONS

Mode of Infection in Nature

In the section on life history, the author has mentioned that experimental infection can occur *per os*. It was also indicated that skin penetration may occur. The question then arises as to how entry into the host is accomplished in nature. The experimental data allow no definite conclusions, but a number of possibilities are eliminated.

In the author's opinion, it is certain that a true intermediate host is not involved in the life histories of *K. parvus*, *K. rectiphilus* and *K. agkistrodontis*. A biological intermediate host, one in which stages in the development occur, cannot be omitted since these stages will not occur elsewhere and the definitive stage can only be derived from them. This still leaves the possibility of a transport host being utilized in nature. However, the writer is inclined to doubt that this is prevalent, even if it does occur. In the strongyloid, *Syngamus trachea*, which does utilize transport hosts, it is found that these hosts are not specific. Thus *Syngamus trachea* may survive in annelids, insect larvae, adult insects and centipedes (Taylor, 1935, Clapham, 1939a, b). Even in the Protostrongylinae, where an intermediate is obligatory, host specificity is not marked and most species can use a number of snails and slugs (Chandler, Alicata and Chitwood, 1941). The author, however, was unsuccessful in his attempts to infect earthworms, snails, insects and mice. Therefore, he doubts the usual existence of an intermediate host in the life history of *Kalicephalus*.

There remain the two modes of entry found in direct life histories, namely entrance through the mouth and entrance through the skin.

It has been noted that K. parvus third-stage larvae are rapidly killed by drying. This is also true for K. rectiphilus and K. agkistrodontis larvae. It has also been shown that the three species develop in both aqueous and moist faeces-sand-charcoal cultures. K. parvus larvae reared in the latter attain the infective stage in greater numbers and survive longer than those reared in aqueous cultures. Harwood (1936) has reported Kalicephalus larvae from various soil types in nature.

The results obtained with K. parvus would indicate that the conditions necessary for the survival of larvae are essentially those which are required by the ancylostomes and other species in which the larvae are rapidly killed by desiccation. The optimum conditions for these larvae are well-known; a damp area exposed to little or no sunlight is the ideal environment. Under these conditions, too, kalicephalids would survive and remain viable.

The author's work shows that oral entry results in an establishment of an infection. However, the occurrence of this process in nature does not seem too likely. Infection per os is successful when the host is a grazer or grubs in the earth for its food. This route of infection has also evolved in the oxyurids, for example, where the life history is extremely intimate. Development occurs rapidly and the larvae remaining in the egg are highly resistant to adverse environmental effects. Often the host is sedentary or regularly returns to the same

den or nest. The kalicephalids studied and snakes in general do not meet these conditions.[1]

Could larvae gain entrance to the host as a contaminant of its food? In this case one must bear in mind that snakes are strict carnivores and thus the larvae would of necessity have to be adherent to the outside of the prey. This, then, would approach ectoparasitism and to the extent of the author's knowledge, true ectoparasitism does not occur in nematodes. Furthermore, if the contaminated food animal was essentially dry-skinned as, for instance, rodents, birds, and many insects, the larvae would be killed by desiccation. If the prey is one which has a moist skin and/or lives in damp earth or rotting wood etc., as, for instance, earthworms, snails and amphibia, then the larvae could survive in some way adherent to the outside of these animals. However, on the basis of present evolutionary theory of nematode parasitism, such a close association should lead to the penetration of the carrier. This is especially true in such soft-skinned animals as snails, frogs, etc. Bearing in mind the widespread occurrence of kalicephalids in snakes today, it is difficult to believe that, given sufficient time, a successful group of parasitic organisms could be associated with a soft-skinned carrier and not have penetrated. Dougherty (1951) states:

> Most strikingly the DIAPHANOCEPHALIDAE, being specialized and at the same time restricted to snakes and lizards, suggest an antiquity of the suborder at least as great as that of the early reptiles.

---

[1]Denning in snakes is not regular in the sense that it occurs daily; it is only an annual occurrence in temperate and cold climates.

This would seem too early as there are no diaphanocephalids or kalicephalids in crocodilians or turtles. However, since species of Kalicephalus have been reported from most families of snakes including some of the most primitive families, it is indicated that the kalicephalids arose no later than with the early snakes. The author, therefore doubts that kalicephalids would normally enter their serpent hosts as a contaminant of prey.

Oral entrance of larvae as contaminants of water is more likely. It has been shown that larvae will develop in water and that these larvae are infective. In nature, it would seem that such conditions would arise as to permit kalicephalids to complete their life histories by being ingested with water, but the superior development of K. parvus larvae in the solid medium and the greater success of these larvae in the host indicates that the major route is another.

There remains the question of skin penetration. As already noted, the most likely site of successful development and survival of Kalicephalus larvae is in a damp location shaded from the sun. If Kalicephalus larvae penetrate the skin and if the stimulus which causes the larvae to penetrate is heat as it is in many known life histories of nematodes parasitic in mammals, then how is penetration possible into a cold-blooded snake? This problem can be resolved when one takes into account that, under certain conditions, a snake can indeed be at a higher temperature than its environment, as, for instance, when a snake ceases its basking in the sun and enters a shaded area. Benedict (1932) has shown that digesting snakes maintain a skin temperature which is higher than that of the environment.

He claims also that the skin of an incubating python registers a higher temperature than the air several inches away from the snake.

It is apparent that a combination of circumstances can frequently arise in which a snake enters an area contaminated by larvae and is at a higher temperature than the immediate environment. This temperature difference would presumably be sufficient to stimulate the larvae to penetrate. An example of such a situation can be found in a rocky, cavernous hillside. In such an environment, favourable conditions for the development of the larvae would be found in crevices, caverns and shaded areas between rocks. It is well-known that in such sites some snakes emerge and bask on the rocks during the warm periods of the day. If these snakes are disturbed or the temperature increases too greatly, the snakes retreat into the crevices etc. These snakes would temporarily be at a higher temperature than the soil over which they move and in which larvae would find optimum conditions for development. In this manner, skin penetration is explainable without postulating different stimuli from those active in the case of the more thoroughly investigated life histories of bursate nematodes of mammals.

In support of this largely speculative explanation of skin penetration is the case of the two (possibly three) snakes that were apparently infected percutaneously. As has already been noted, these snakes had been fed 12 to 24 hours previous to being placed in contact with the larvae. Then, if Benedict's (1932) conclusion that digesting snakes maintain a skin temperature higher than the temperature of the environment is true, this would explain why larvae penetrated these snakes and not the ten subsequently exposed.

Life History in the Host and its Comparison with Other Species of Strongylina

The life histories here reported resemble in many respects those of other bursate nematodes. Like the oesophagostomes, K. parvus and K. rectiphilus encyst and form nodules in the walls of the digestive tract, and, as in different species of nodular worms,[1] the different species of Kalicephalus were found to encyst in different areas of the digestive tract.

On the other hand, K. agkistrodontis was shown not to encyst. However, in the case of other bursate nematodes, marked differences in life history within the same genus are also known. The three species of Strongylus parasitizing the horse offer an excellent example of this.

K. rectiphilus and K. agkistrodontis mature in the host relatively rapidly, but K. parvus is slower in parasitic development. Indeed, it far exceeds the time required by most Strongyloidea for which the life histories are known. However, such slow development is found in the genus Strongylus. Ershov (1949) recovered larvae of Strongylus vulgaris in the third stage after two months, and only after three and one-half to four months was a provisional buccal capsule present and was sex differentiation possible. Sommerville (1954) reports a stasis in the development of Ostertagia sp. Larvae remained unchanged up to three months.

In the case of K. rectiphilus, both the third and fourth moults occur in the cyst. The worms do not re-enter the lumen of the digestive tract until they are adult. This is not prevalent among bursate nematodes in general, where usually the fourth stage as well as the adult occur in

---

[1] Oesophagostomes of swine encyst in the caecum and colon; oesophagostomes of ruminants in the distal half of the small intestine, the caecum and colon.

the lumen, but it is known to occur among some genera and species. Spindler (1933b) noted that Oesophagostomum longicaudum frequently remains encysted until adult. Ershov (1949) found that Strongylus vulgaris does not return to the lumen of the bowel until after the fourth ecdysis.

It is, then, readily seen in the life history studies that distinct species differences in life history occur. As has already been mentioned in this discussion, such differences have been noted in related nematode groups. The three North American species of Kalicephalus are separable on the basis of life history as follows: K. agistrodontis does not encyst; parasitic larval stages in its life history occur free in the lumen of the stomach and small intestine; as an adult this species inhabits the stomach and the oesophagus. K. parvus and K. rectiphilus both encyst but are clearly separable as parasitic larvae on the basis of the site of encystation. K. rectiphilus larvae invade the walls of the small intestine while K. parvus larvae are confined to the stomach. As adults these species move down the digestive tract, K. parvus establishing itself in the small intestine while K. rectiphilus finally settles in the rectum.

It has long been obvious that problems of identification in taxonomically difficult groups are often readily resolved by life history and ecological studies. An outstanding and well-known example of this is the Anopheles maculipennis complex in which the adults are difficult to distinguish but the various species within this group are easily separable by characters of the egg or on the basis of various ecological characteristics (Mayr, Linsley and Usinger 1953).

True, the species of Kalicephalus on which these life history studies were carried out are not difficult to separate on morphological characters alone, and it is indeed preferable that a classification be based on easily observed adult morphological characters. However, when these fail or are difficult to interpret, then it is desirable to resort to ecological and life history studies to elucidate systematic problems. The author believes that the results of his life history experiments on the three species, K. rectiphilus, K. agkistrodontis, and K. parvus, indicate that it is feasible and advisable to conduct life history experiments as an aid to the adequate identification of species in the genus Kalicephalus. Only then can a satisfactory classification be devised and, as pointed out by Mayr, Linsley and Usinger (1953), this inevitably leads the systematist to the study of evolution. In this field, especially where parasitic species are concerned, a knowledge of life history, which brings to light the larval stages, is essential since it is in these more often than in the adults that true relationships can be seen.

SUMMARY

A historical account of the genus Kalicephalus and its position in the Nematoda is presented.

On the basis of several personal collections and material loaned by various institutions, the taxonomic characters have been reviewed and several suggestions have been offered as to their relative merits. A partially original system for the breakdown of the genus Kalicephalus into small groups of similar species is advanced. These aggregates facilitate comparison and identification. The primary and secondary characters used are: 1. The uberi; whether divergent or convergent, and 2. The dorsal ray; the pattern of its terminal branches.

The North American species K. parvus Ortlepp, 1923, K. rectiphilus Harwood, 1932 and K. agkistrodontis Harwood, 1932 are redescribed and discussed. K. tennesseensis Harwood, 1934 and K. floridanus Reiber, Byrd and Parker, 1940 in part, are synonomized with K. parvus, Ortlepp, 1923. K. floridanus Reiber, Byrd and Parker, 1940 in part is also a synonym of K. rectiphilus. K. tennesseensis Reiber, Byrd and Parker,1940 not Harwood, 1932, K. humilus Caballero, 1938 and K. agkistrodontis flagellus Harwood, 1932 are synonomized with K. agkistrodontis Harwood, 1932. Complete bibliographical synonomies are provided. The taxonomic status of North American species in general has been reviewed and a key to these is presented.

Experimental life history studies were conducted on K. parvus, K.rectiphilus and K. agkistrodontis. K. parvus eggs cultured in tap water at room temperature hatch in 24 hours. The free-living

development is completed in five days. Ensheathed third-stage larvae are found free in the stomach as late as the tenth day. Thereafter exsheathed third-stage larvae are encysted under the mucosa of the stomach. Third-stage larvae were found so encysted in garter snakes until 130 days after infection. The fourth-stage larva was not recovered. Eggs were recovered from the faeces of an experimentally infected gopher snake after 115 days.

In tap water at room temperature, K. rectiphilus develops to the infective third-stage in approximately four days. In Pituophis spp. the parasitic third-stage was recovered from cysts in the duodenum 26 to 33 days after oral infection. At 33 days, fourth-stage larvae and subadults were recovered from the duodenal cysts of the same snake. Transition was in progress. Mature males were collected after 43 days.

The eggs of K. agkistrodontis are laid in the 32-celled stage. In tap water at room temperature these hatch in 24 hours. The parasitic third-stage larvae are found in five days. The parasitic stages occur free in the lumen of the digestive tract. In 17 days, third-stage, transitional and fourth-stage larvae are found in the small intestine. Most individuals are in a state of transition. Late fourth-stage larvae are recovered after 23 days in the host. In these, the definitive buccal capsule is developing. At the same time, immature adults are also recovered. These occur in the oesophagus. Fifty-eight days after experimental infection mature adults are recovered.

Special discussions of the genital rudiment and the spicular primordium are presented. The male genital rudiment in K. parvus was found to undergo a reversal. This structure in both sexes shows

great structural and developmental similarities to the genital rudiment of Hyostrongylus rubidus. The spicular rudiment could be recognized in the late second stage. It remains a single structure into the late parasitic third stage. Its development in later stages could not be followed.

The mode of entry into the host in nature is discussed. It is concluded that a true intermediate host does not occur and that a transport host is unlikely. Direct oral entry or as a contaminant of prey is considered improbable.

Ingestion of the infective stage with water is considered more likely and the possibility of skin penetration is strongly favoured.

The life histories of the species studied are compared with those of other Strongylina and it is suggested that further life history studies would provide a sounder classification and present a basis for studies of evolution.

PLATE I

Adult Kalicephalus parvus

A. Anterior end, lateral view.

B. Bursa, ventral view.

C. Bursa, lateral view.

D. Female tail, lateral view.

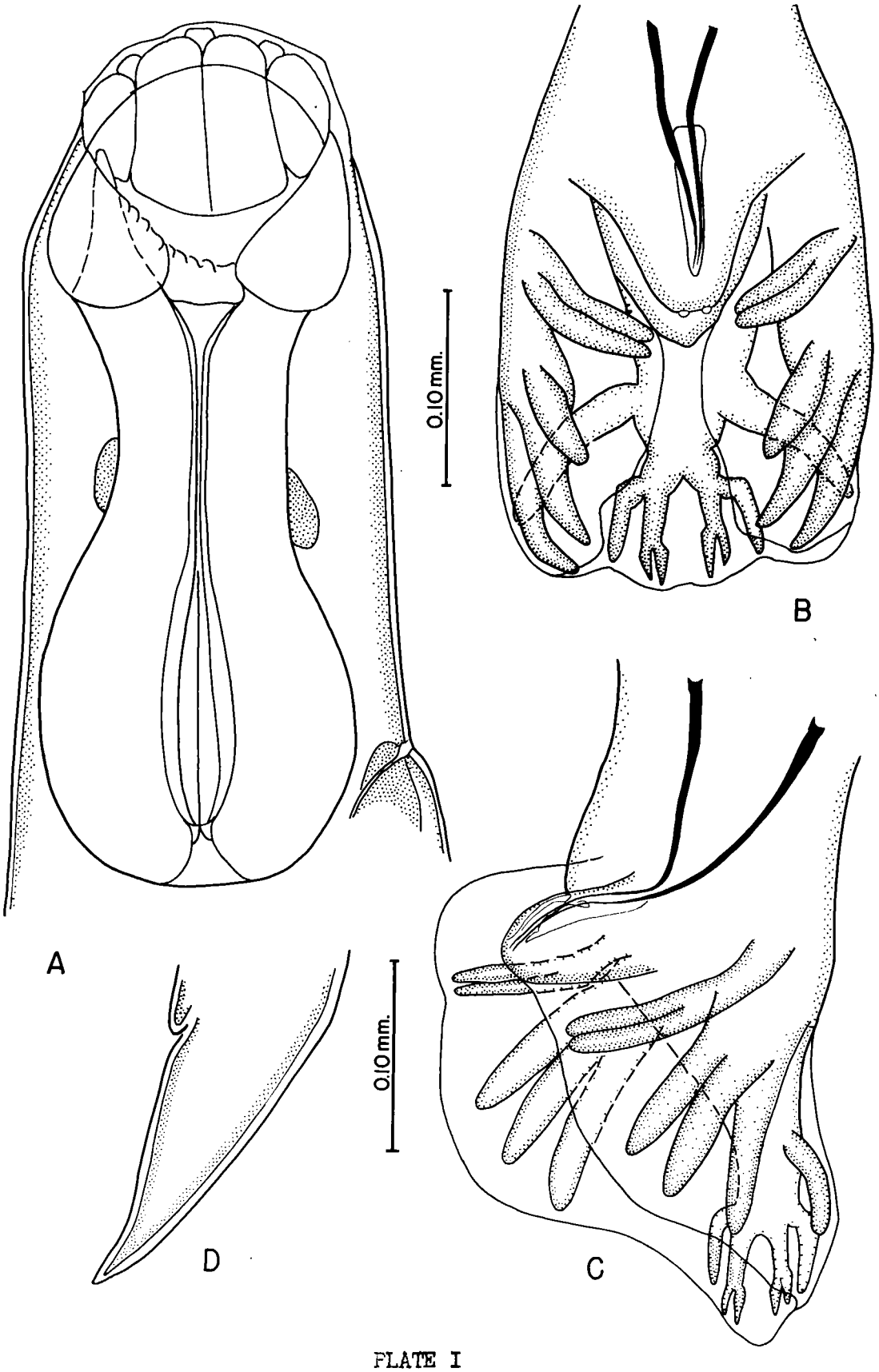


PLATE I

PLATE II

Adult Kalicephalus rectiphilus

A. Anterior end, lateral view.

B. Genital cone, ventral view.

C. Bursa, ventral view.

D. Ovejector, lateral view.

E. Genital cone, lateral view.

F. Bursa, lateral view.

G. Female tail, lateral view.

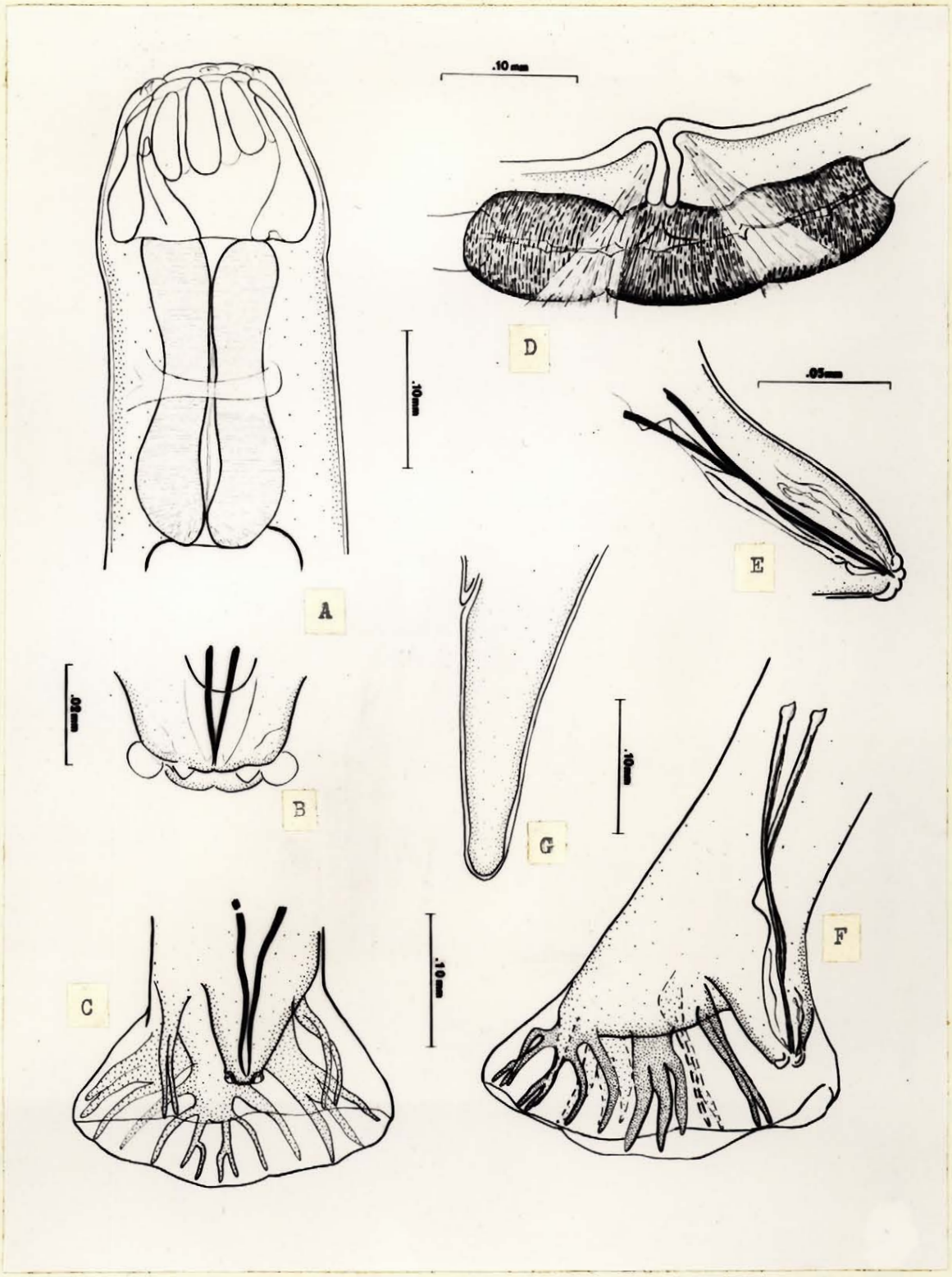


Plate II

PLATE III

Adult Kalicephalus agkistrodontis

A. Male, lateral view.

B. Anterior end, lateral view.

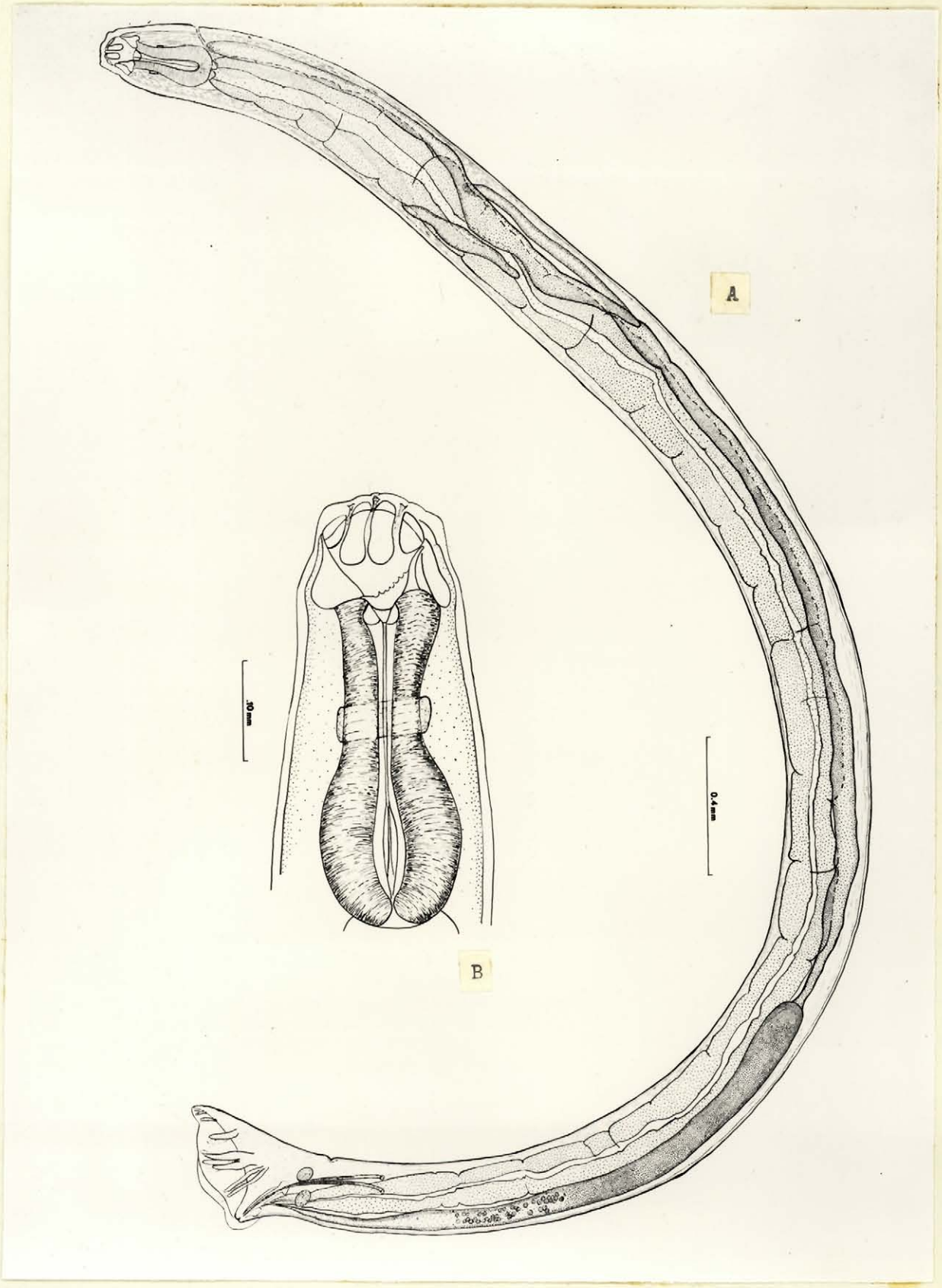


PLATE III

PLATE IV

Adult Kalicephalus agkistrodontis

A. Bursa, lateral view.

B. Bursa, ventral view.

C. Female tail, lateral view.

D. Subadult male; developing reproductive system, lateral view, 27 days.

E. Developing bursa, ventral view, 27 days.

F. Subadult female; developing reproductive system, 27 days.

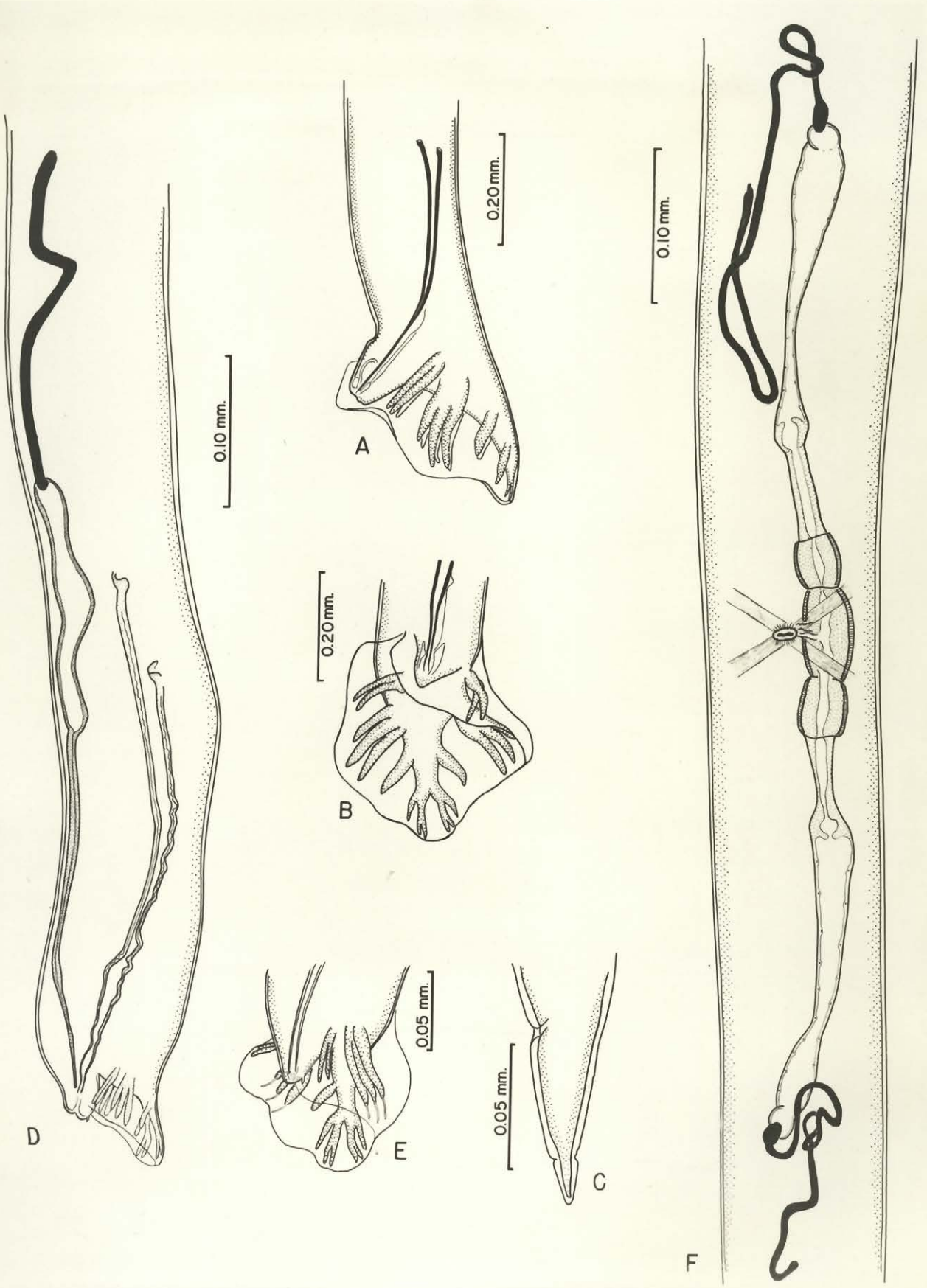


PLATE IV

PLATE V

Stages in the life history of Kalicephalus parvus

A. Egg, gastrula.

B. Egg, early tadpole.

C. Egg, late tadpole.

D. Egg, embryonated.

E. First-stage larva, lateral view.

F. First-stage larva, ventral view.

G. Second-stage larva, lateral view.

H. Preparasitic third-stage larva, ventral view.

I. Preparasitic third-stage tail, lateral view.

J. Preparasitic third-stage tail, ventral view.

K. Male parasitic third-stage larva, lateral view.

L. Posterior end female parasitic third-stage larva, lateral view.

M. Parasitic third-stage larva, en face.

N. Parasitic third-stage larva, cross-section at anterior oesphageal region.

O. Parasitic third-stage larva, cross-section at level of fourth to sixth intestinal cell.

P. Parasitic third-stage larva, cross-section at midbody.

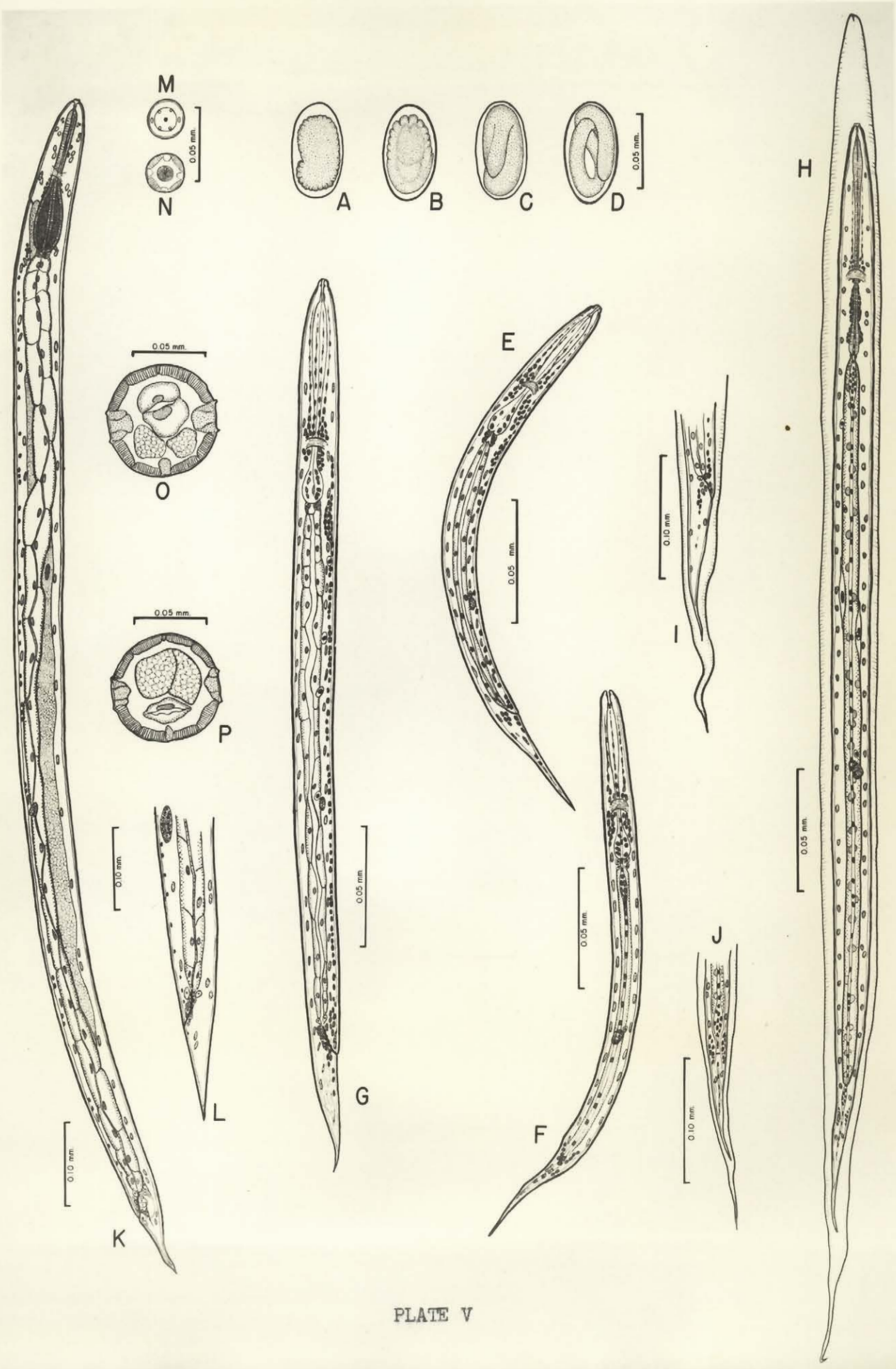

M
N
0.05 mm.
A
B
C
D
0.05 mm.
H
0.05 mm.
E
0.05 mm.
I
0.10 mm.
O
0.05 mm.
P
0.05 mm.
G
0.05 mm.
F
0.05 mm.
J
0.10 mm.
L
0.10 mm.
K
0.10 mm.

PLATE V

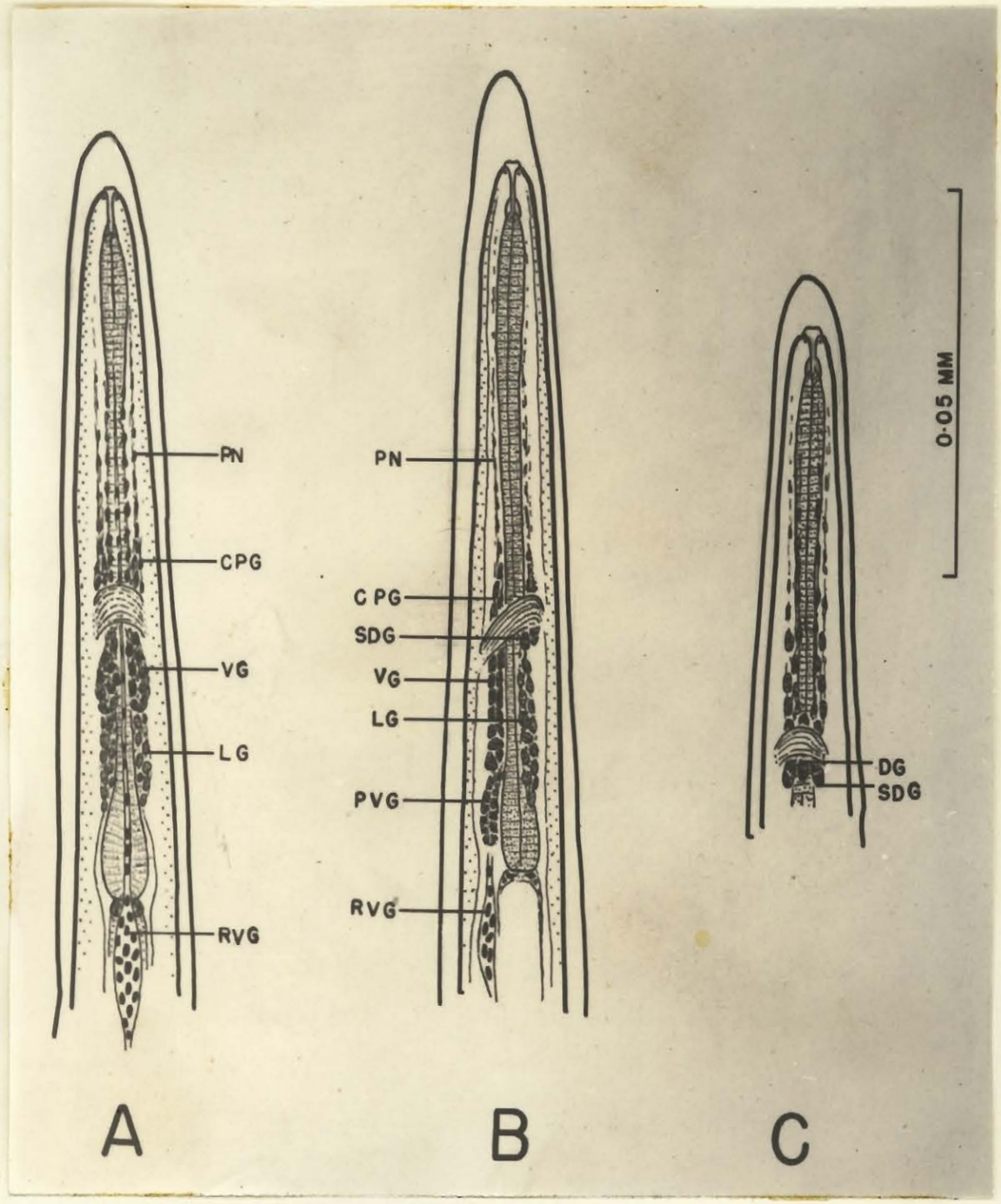
PLATE VI

Preparasitic third stage of Kalicephalus parvus

A. Anterior end, ventral view.

B. Anterior end, lateral view.

C. Anterior end, dorsal view.



CPG - Cephalic papillary ganglion; DG - Dorsal ganglion; LG - Lateral ganglion; PN - Papillary nerve; PVG - Postero-ventral ganglion; RVG - Retrovesicular ganglion; SDG - Subdorsal ganglion; VG - ventral ganglion.

PLATE VI

PLATE VII

Late parasitic third stage of Kalicephalus parvus

A. Anterior end, ventral view.

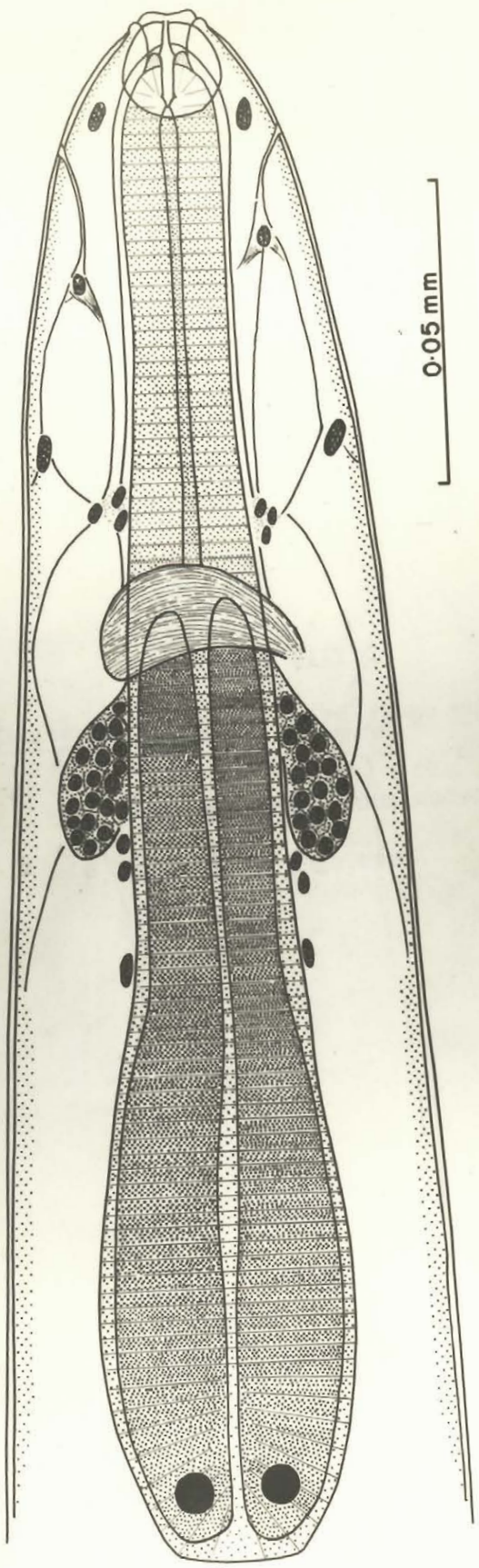


PLATE VII

PLATE VIII

Kalicephalus parvus third stage encysted

A. Cyst dissected from mucosa (live preparation).

B. Section through cyst.

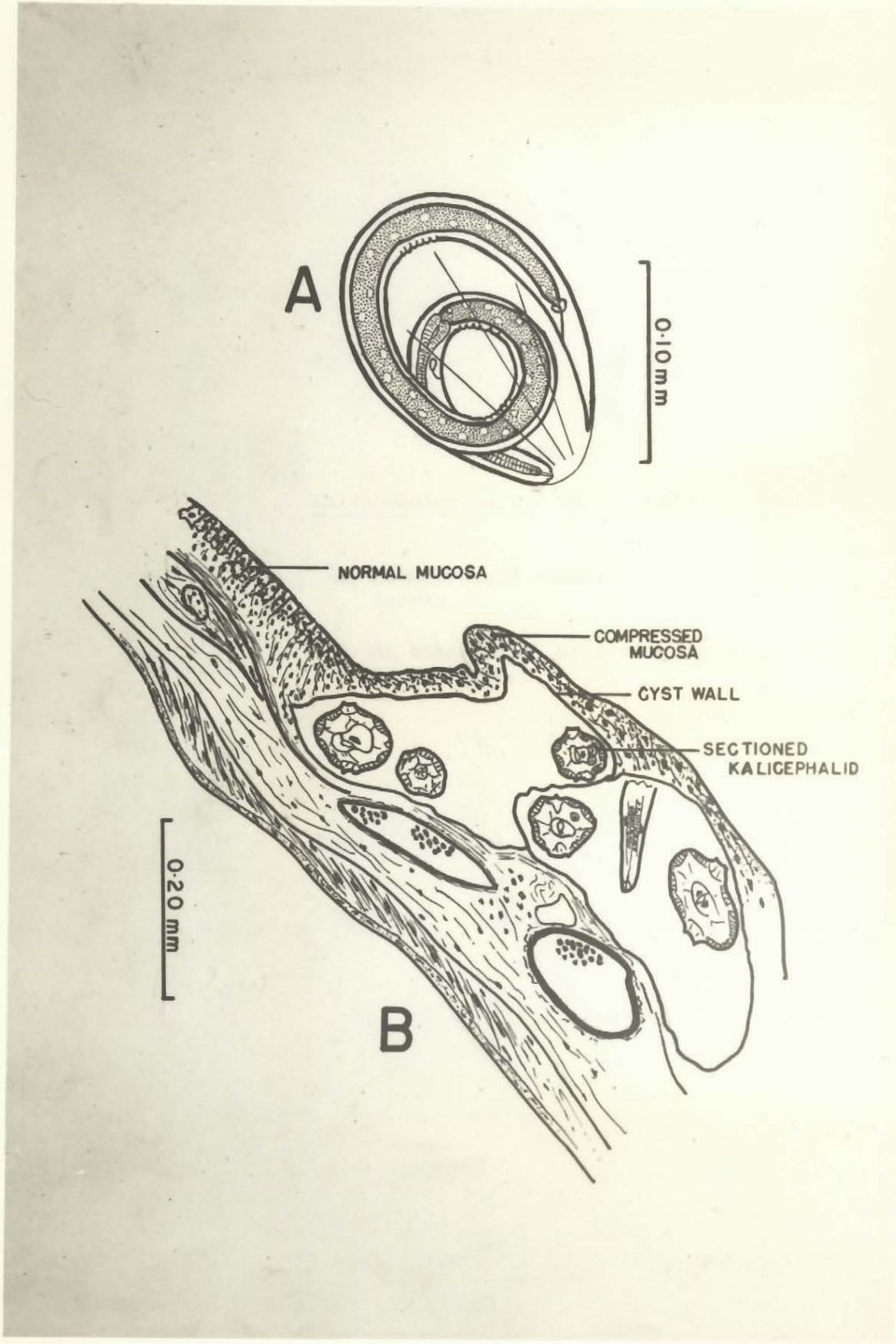

A
0·10 mm
NORMAL MUCOSA
COMPRESSED MUCOSA
CYST WALL
SECTIONED KALICEPHALID
0·20 mm
B

PLATE VIII

PLATE IX

Kalicephalus parvus third stage encysted

A. Haemorrhagic stomach showing encysted larvae.

B. An enlargement of a cyst of IX,A - male larva in cyst.

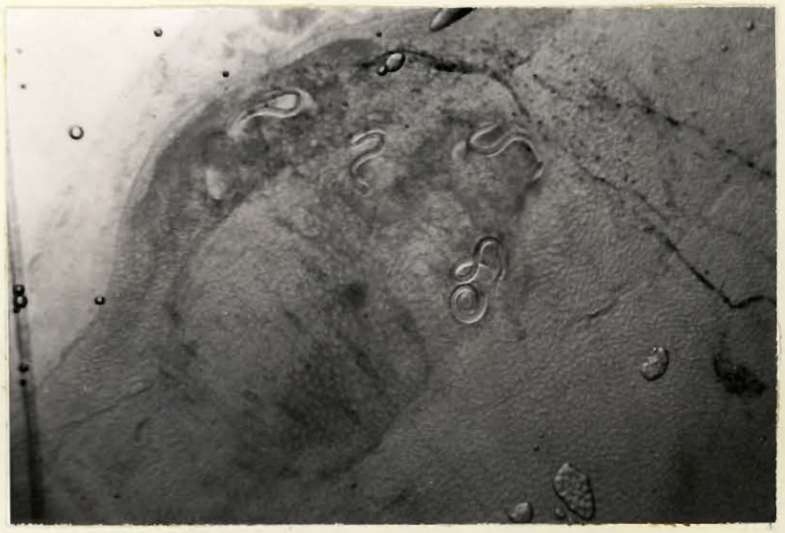


PLATE IX, Figure A
(x 13)

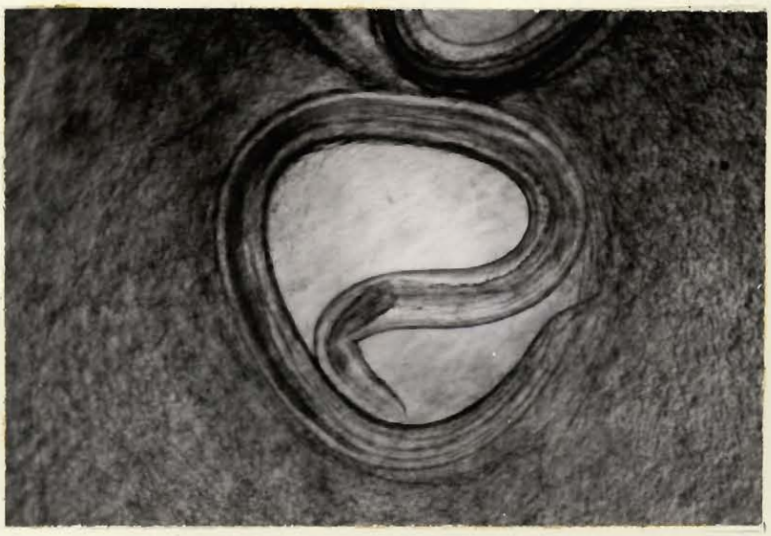


PLATE IX, Figure B
(x 108)

PLATE X

Kalicephalus parvus third stage encysted

A. Color enlargement of haemorrhagic area of IX, A.

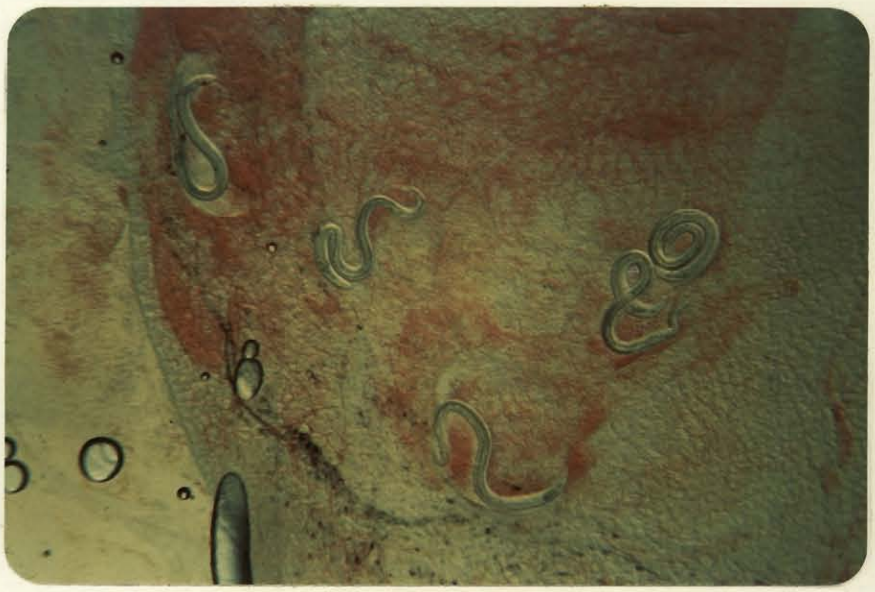


PLATE X, Figure A
(x 64)

PLATE XI

Stages in the life history of K. agkistrodontis

A. Egg, 32-celled.

B. Egg, gastrula.

C. Egg, tadpole.

D. Egg, embryonated.

E. First-stage larva, lateral view.

F. Second-stage larva, lateral view.

G. Third-stage larva, ventral view.

H. Formation of provisional buccal capsule.

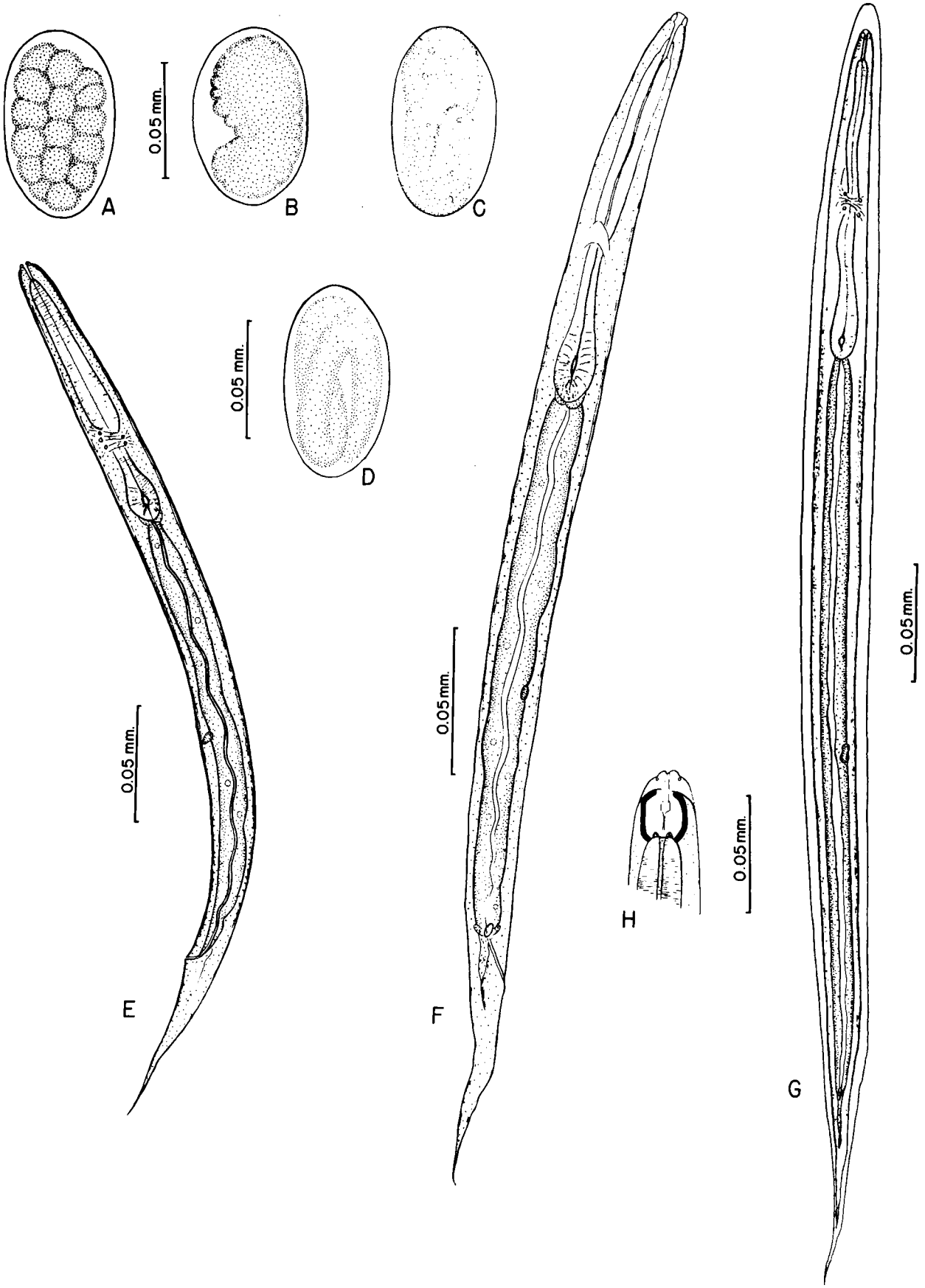


PLATE XI

PLATE XII

Parasitic third-stage larva of Kalicephalus rectiphilus

A. Anterior end, lateral view.

B. Anterior end, dorsal view.

C. Male tail, lateral view.

D. Female tail, lateral view.

E. Female genital rudiment, lateral view.

F. Female genital rudiment, ventral view.

G-I. Stages in the reversal of the male genital rudiment.

J. Late parasitic third stage showing development of the provisional buccal capsule.

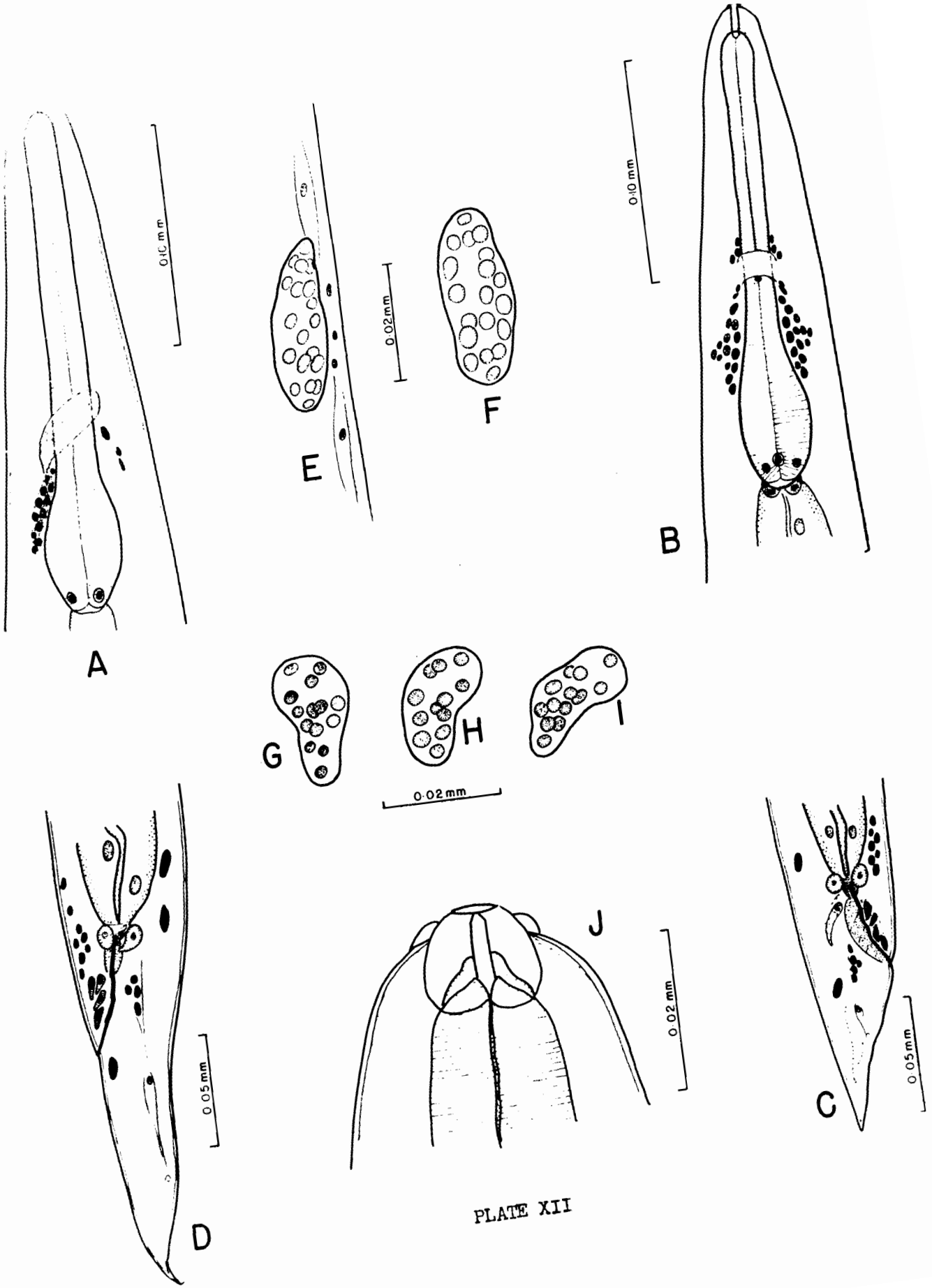


PLATE XII

PLATE XIII

Fourth stage and subadults of Kalicephalus rectiphilus

A. Fourth stage anterior end showing formation of definitive buccal capsule, dorsal view.

B. Provisional buccal capsule.

C. Encysted subadult; cast provisional buccal capsule included in cyst.

D. Subadult anterior end, dorsal view.

E. Subadult, developing bursa.

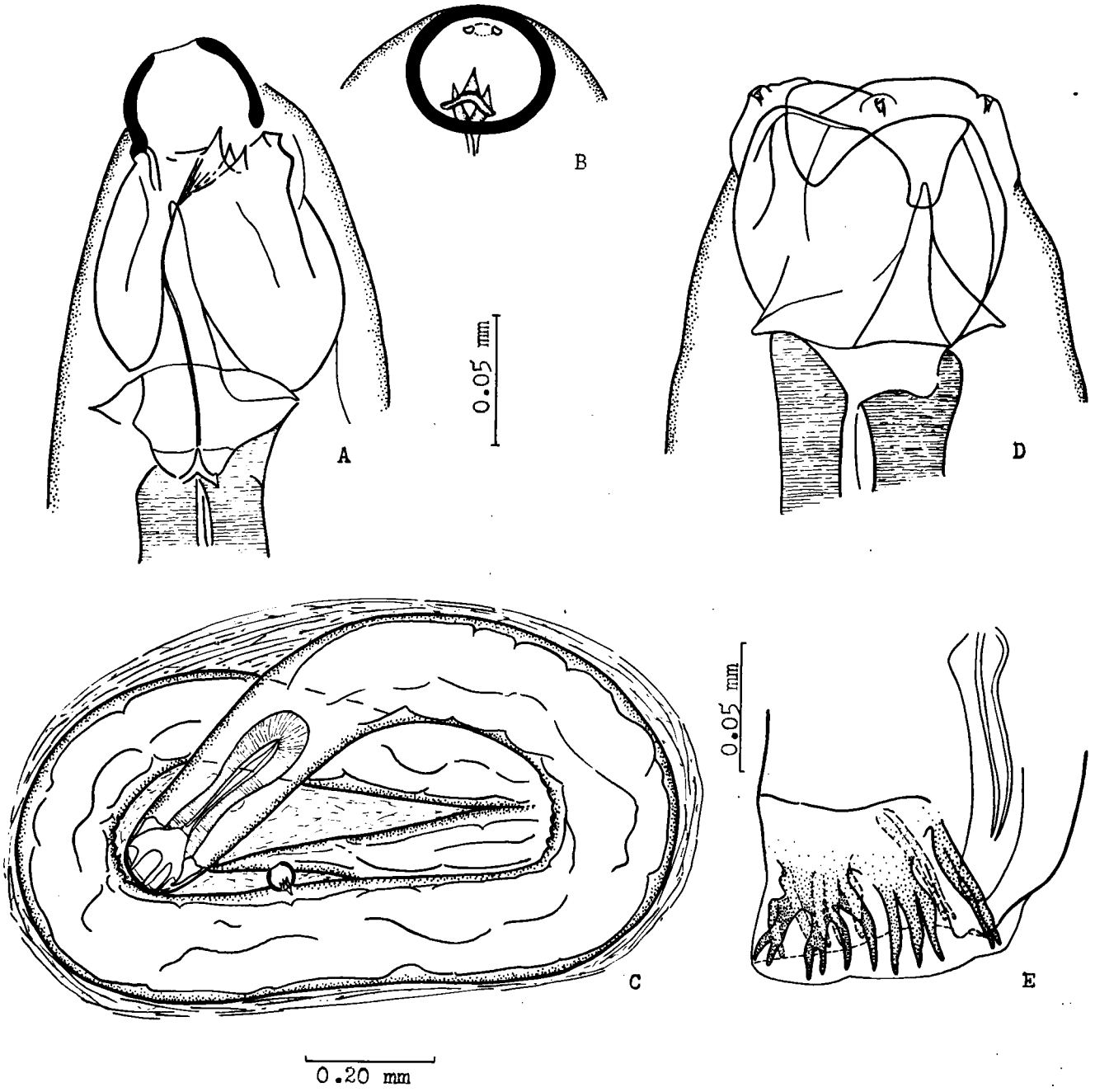


PLATE XIII

PLATE XIV

Encysted subadult of Kalicephalus rectiphilus

A. Photomicrograph of the individual figured in XIII, C.

B. Enlargement of cast provisional buccal capsule within the cyst.

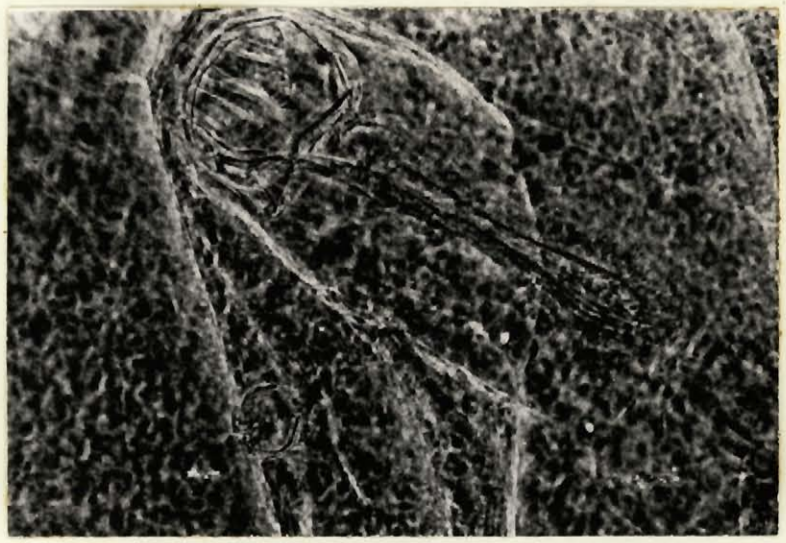


PLATE XIV, Figure A
(x 200)

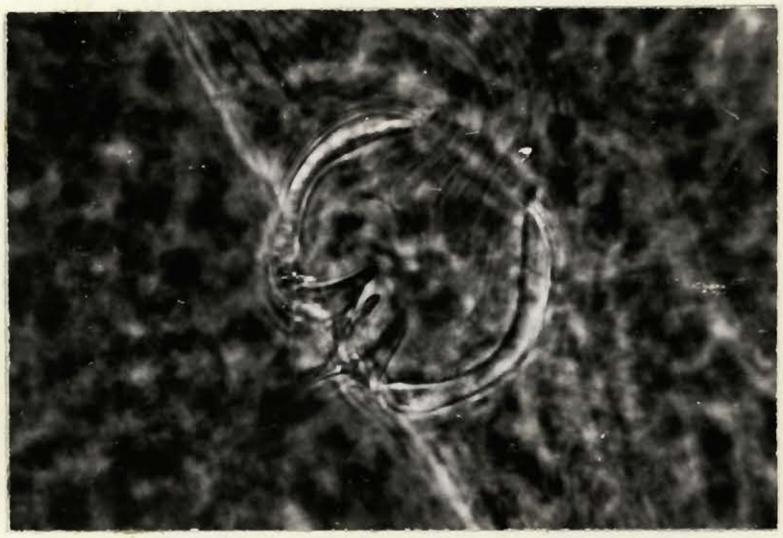


PLATE XIV, Figure B
(x 800)

HOST CATALOGUE [1,2]

SNAKES

Ablaophis rufulus whytii

Kalicephalus sp. (U.S. National Museum)

Acanthopis antarcticus

Kalicephalus sp. (U.S.National Museum)

Agkistrodon mokasen

Kalicephalus agkistrodontis Harwood 1932 (45)

Agkistrodon piscivorus

Kalicephalus agkistrodontis Harwood, 1932 (45) (*)

Agkistrodon rhodostoma

Kalicephalus sp. (U.S.National Museum)

Ahaetulla ahaetulla

Kalicephalus sp. (= Strongylus galeatus Parona, 1898) (92)

Atheris nitschei

Kalicephalus sp. (U.S. National Museum)

Bitis arietans

Kalicephalus obliquus (Daubney, 1923) (29) (39) (73) (105)
Kalicephalus rotundatus von Linstow, 1908 British Museum (Natural History)
Kalicephalus sp. ova (93)

Bitis gabonica

Kalicephalus obliquus (Daubney, 1923) (29) (6) (39) (88) (103)
Kalicephalus bitisi Campana and Chabaud, 1950 (19)
Kalicephalus sp. (U.S. National Museum)

Bitis nasicornis

Kalicephalus obliquus (Daubney, 1923) British Museum (Natural History)
Kalicephalus sp. British Museum (Natural History)
Kalicephalus sp. (U.S.National Museum)

---

1. Bracketed numbers refer to publications as numbered in the bibliography. An asterisk denotes identification of the author.
2. As far as possible all host names have been brought up to date. Several hosts, mainly those reported by Molin, Rudolfi and some of the other early authors cannot be identified with certainty.

Bitis sp.

Kalicephalus obliquus (Daubney, 1923) (109)

Boa mexicana

Kalicephalus sp. (= Strongylus boae MacCallum, 1921)(79)

Boa sp.

Kalicephalus sp. (U.S.National Museum)

Central American boa

Kalicephalus sp. (U.S. National Museum)

Boaedon lineatus

Kalicephalus colubri Ortlepp, 1923, British Museum (Natural History)
Kalicephalus sp. Sandground, 1928 (101)
Kalicephalus sp. Loveridge, 1953 (75)
Kalicephalus sp. (U.S. National Museum)

Boiga irregularis

Kalicephalus sp. (= Kalicephalus appendiculatus Stossich, 1900)
(17) (122) (72) (121)

Bothrops atrox

Kalicephalus agkistrodontis Harwood, 1932 (15)
Kalicephalus sp. (U.S. National Museum)
Kalicephalus sp. British Museum (Natural History)

Bothrops jararaca

Kalicephalus bothropis Molin, 1861 (86)
Kalicephalus inermis Molin 1861 (86)
Kalicephalus subulatus Molin, 1861 (86) (88)
Kalicephalus costatus Rudolfi, 1819 (120)

Bothrops sp.

Kalicephalus sp. (U.S.National Museum)
Kalicephalus sp. (U.S.National Museum)

Bungarus candidus

Kalicephalus bungari (MacCallum, 1918) (22) (78)

Bungaris fasciatus

Kalicephalus fimbriatus (Ortlepp, 1923) (6) (8) (67) (81) (29) (88)
Kalicephalus longior Maplestone, 1931 (5) (6) (81)
Kalicephalus minutus (Baylis and Daubney, 1922) (6) (81) (88)

Causus rhombeatus

Kalicephalus obliquus (Daubney, 1923) (29) (39)
Kalicephalus sp. British Museum (Natural History)

Cerastes cornutus

Kalicephalus (?) obliquus (Daubney, 1923) (85)

Chironius carinatus

Kalicephalus sp. (U.S.National Museum)
Kalicephalus costatus (Rudolfi, 1819) (30) (86)

Chironius sexcarinatus (see also Erymnus macrolepidotus)
Kalicephalus costatus (Rudolfi, 1819) (86)

Clelia clelia

Kalicephalus appendiculatus Molin, 1861 (86) (122)

Coluber constrictor constrictor

Kalicephalus agkistrodontis Harwood, 1932 (45) (95) (*)
Kalicephalus rectiphilus Harwood, 1932 (97) (*)
Kalicephalus parvus Ortlepp, 1923 (47) (97) (*)
Kalicephalus sp. (U.S. National Museum)

Coluber constrictor flaviventris

Kalicephalus agkistrodontis Harwood, 1932 (45)
Kalicephalus rectiphilus Harwood, 1932 (45)

Coluber viridiflavus

Kalicephalus colubri Ortlepp, 1923 (33) (72)

Coluber sp.

Kalicephalus costatus (Rudolfi, 1819) (98)

Constrictor c. constrictor

Kalicephalus boae (Blanchard, 1886) (2) (13) (14) (63) (115)
Kalicephalus boae (MacCallum, 1921) Chitwood, 1932 (79)
Kalicephalus subulatus Molin, 1861 (49) (86) (88)
Kalicephalus sp. (U.S.National Museum)

Crotalus durissus

Kalicephalus inermis Molin, 1861 (86)
Kalicephalus mucronatus Molin, 1861 (86)
Kalicephalus implicatus Kreis, 1938 (58)

Crotalus triseriatus

Kalicephalus conoidus Comroe, 1948 (28)

Crotaphopeltis hotamboeia tornieri

Kalicephalus sp. Sandground, 1928 (101)

Dendraspis angusticeps

Kalicephalus simus (Daubney, 1923) (39) (88)

Dendraspis sp.

Kalicephalus sp. (U.S.National Museum)

Dendrophidion bivittatus

Kalicephalus appendiculatus Molin, 1861 (64) (86) (121) (122)

Dinodon r. rufozonatum

Kalicephalus indicus Ortlepp, 1923 (52)
Kalicephalus nankingensis Hsü, 1934 (52)

Drymarchon corais

Kalicephalus agkistrodontis Harwood, 1932 (17)
Kalicephalus sp. Hamerton, 1935 (44)
Kalicephalus sp. (U.S.National Museum)

Dryophis mycterizans

Kalicephalus indicus Ortlepp, 1923 (6) (81)

Elaphe flavolineata

Kalicephalus longior Maplestone, 1931 (5) (6)
Kalicephalus obesus Baylis, 1933 (5) (47)

Elaphe helena

Kalicephalus willeyi von Linstow, 1904 (64) (6) (8) (29) (88)

Elaphe longissima

Kalicephalus viperae (Rudolfi, 1819) (33) (118) (119)

Elaphe obsoleta deckerti

Kalicephalus agkistrodontis Harwood, 1932 (*)
Kalicephalus parvus Ortlepp, 1923 (*)

Elaphe porphyracea

Kalicephalus sinensis Hsü, 1934 (52)

Elaphe quadrivirgata

Kalicephalus natricis Yamaguti, 1935 (133)

Elaphe r. rufodorsata

Kalicephalus indicus Ortlepp, 1923 (52)
Kalicephalus nankingensis Hsü, 1934 (52)

Elaphe scalaris

Kalicephalus viperae (Rudolfi, 1819) (33)

Elaphe taeniurus

Kalicephalus chunkingensis Hsü, 1934 (52)
Kalicephalus sinensis Hsü, 1934 (52)

Elaphe vulpina

Kalicephalus parvus Ortlepp, 1923 (*)

Elaps sp.

Kalicephalus sp. (U.S. Museum National History)

Enygrus asper

Kalicephalus enygri Kreis, 1938 (59)

Erymnus macrolepidotus[1]

Kalicephalus costatus (Rudolfi, 1819) (86)

---

[1]This species is probably Chironius sexcarinatus

Eryx conicus

Kalicephalus sp. Sambon,1907 (99) (100)
Kalicephalus longior Maplestone, 1931 (6) (81)

Eudryas b. bifossatus

Kalicephalus appendiculatus Molin, 1861 (86) (122)

Furina occipitalis

Kalicephalus sp. Johnston and Mawson, 1948 (57)
Kalicephalus sp. Johnston, 1912 (see footnote p.178) (55)

Grayia tholloni

Kalicephalus sp. Sandground, 1933 (102)

Heterodon platyrhinos

Kalicephalus agkistrodontis Harwood, 1932 (45)
Kalicephalus parvus Ortlepp, 1923 (U.S.National Museum) (*)
Kalicephalus boae (MacCallum, 1921) (79)

Lachesis muta

Kalicephalus subulatus Molin, 1861 (86) (88)
Kalicephalus sp. (Wucherer, 1872) (132)
Kalicephalus costatus (Rudolfi, 1819) (30)

Lampropeltis getulus

Kalicephalus rectiphilus Harwood, 1932 (*)
Kalicephalus parvus Ortlepp, 1923 (88)

Lampropeltis getulus holbrooki

Kalicephalus agkistrodontis Harwood, 1932 (45)

Lampropeltis getulus nigra

Kalicephalus parvus Ortlepp, 1923 (97)

Lampropeltis triangulum

Kalicephalus coronellae Ortlepp, 1923 (88)

Laticauda laticauda

Kalicephalus laticaudae Yamaguti, 1935 (133)

Leimadophis reginae

Kalicephalus appendiculatus Molin, 1861 (86)

Leptocephalus abaetulla

Kalicephalus sp. (U.S. National Museum)

Leptodira duchesnii

Kalicephalus obliquus (Daubney, 1923) (105)

Leptotyphlops sp.

Kalicephalus colubri Ortlepp, 1923 (*)

Liophis cinerascens[1]

Kalicephalus appendiculatus Molin, 1861 (86)

Liophis miliaris

Kalicephalus appendiculatus Molin, 1861 (86) (122)

Lystrophis semicinctus

Kalicephalus sp. (*)

Macrelaps microlepidotus

Kalicephalus micrurus Daubney, 1923 (29)

Masticophis flagellum flagellum

Kalicephalus agkistrodontis Harwood, 1932 (45)
Kalicephalus parvus Ortlepp, 1923 (97) (*)

Micrurus fulvius

Kalicephalus agkistrodontis Harwood, 1932 (45)

Naja haje

Kalicephalus minutus (Baylis and Daubney, 1922) (15)
Kalicephalus colubri (U.S.National Museum)
Kalicephalus sp. (U.S.National Museum)

---

[1]This species may be Duberria cinerascens Fitz, 1826

Naja melanoleuca

Kalicephalus minutus (Baylis and Daubney, 1922) (39)
Kalicephalus simus Daubney, 1923 (11)
Kalicephalus sp. Sandground, 1933 (102)
Kalicephalus sp. Loveridge, 1936 (74)
Kalicephalus sp. (U.S.National Museum)

Naja naja

Kalicephalus elongatus Maplestone, 1931 (6) (81)
Kalicephalus indicus Ortlepp, 1923 (6) (81) (82)
Kalicephalus longior Maplestone, 1931 (6) (81)
Kalicephalus minutus (Baylis and Daubney, 1922) (6) (8) (81) (88)
Kalicephalus minutus (Baylis and Daubney, 1922) (U.S.National Museum)
Kalicephalus sp. Baylis and Daubney, 1922 (6) (8)
Kalicephalus sp. Tubangui and Masilungen, 1937 (125)
Kalicephalus sp. (U.S. National Museum)

Naja nigricollis

Kalicephalus simus (Daubney, 1923) (7) (11) (29) (39) (109)

Naja sp.

Kalicephalus sp. (U.S.National Museum)
Kalicephalus sp. (U.S.National Museum)

Natriciteres olivacea uluguruensis

Kalicephalus micrurus (Daubney, 1923) British Museum (Natural History)

Natrix percarinata

Kalicephalus indicus Ortlepp, 1923 (52)
Kalicephalus nankingensis Hsü, 1934 (52)

Natrix piscator

Kalicephalus indicus Ortlepp, 1923 (6) (88)

Natrix rhombifera

Kalicephalus agkistrodontis Harwood, 1932 (45)

Natrix sipedon fasciata

Kalicephalus agkistrodontis Harwood, 1932 (45)

Natrix tigrina

Kalicephalus nankingensis Hsü, 1934 (52)
Kalicephalus natricis Yamaguti, 1935 (see footnote p.178) (133)

Natrix tigrina lateralis

Kalicephalus indicus Ortlepp, 1923 (52)

Ophiophagus hannah

Kalicephalus longior Maplestone, 1931 (5) (6) (12)
Kalicephalus indicus Ortlepp, 1923 (6) (81)

Ophis coeruleus

Kalicephalus appendiculatus Molin, 1861 (86) (122)

Ophis rhodogaster

Kalicephalus brevipenis Molin, 1861 (86)

Oxybelis fulgidus

Kalicephalus brevipenis Molin, 1861 (86)

Philodryas serra

Kalicephalus philodryadus Ortlepp, 1923 (47) (88)

Pituophis sayi

Kalicephalus agkistrodontis, Harwood, 1932 (45)

Polyodontophis subpunctatus

Kalicephalus sp. British Museum (Natural History)

Psammophis sibilans

Kalicephalus simus (Daubney, 1923) (39)
Kalicephalus sp. Sandground, 1933 (102)
Kalicephalus sp. Leiper, 1909 (61)
Kalicephalus sp. Sambon, 1907 (99)

Pseudaspis cana

Kalicephalus rotundatus von Linstow, 1908 (67)

Pseudechis porphyriacus

Kalicephalus sp. Johnston, 1912 (55)
Kalicephalus sp. Johnston, 1918 (56)

Ptyas mucosus

Kalicephalus indicus Ortlepp, 1923 (6) (80) (81) (88)
Kalicephalus elongatus Maplestone, 1931 (6) (81)
Kalicephalus brachycephalus Maplestone, 1931 (6) (81) (82)
Kalicephalus sp. Parona, 1893 (91)

Python curtus curtus

Kalicephalus sp. (U.S. National Museum)

Python molurus

Kalicephalus ersillae (Stossich, 1896) (6) (64) (117)
Kalicephalus sp. (= K. subulatus Parona, 1893 not Molin) (91)

Python regius

Kalicephalus sp. Herman, 1939 (49)
Kalicephalus sp. Hamerton, 1933 (44)
Kalicephalus sp. (U.S. National Museum)

Python reticulatus

Kalicephalus sp. (U.S. National Museum)

Python sebae

Kalicephalus boae (MacCallum, 1921) (79)

Sistrurus sp.

Kalicephalus agkistrodontis (U.S. National Museum) (*)

Spilotes pullatus

Kalicephalus appendiculatus Molin, 1861 (86) (122)

Spilotes sp.

Kalicephalus appendiculatus Molin, 1861 (86)

Thalerophis ahaetulla

Kalicephalus appendiculatus Molin, 1861 (86) (122)

Thalerophis occidentalis

Kalicephalus sp. (U.S.National Museum)

Thamnophis sirtalis proximus

Kalicephalus agkistrodontis Harwood, 1932 (45)

Thamnophis sirtalis sirtalis

Kalicephalus agkistrodontis Harwood, 1932 (95)

Trimerorhinus tritaeniatus

Kalicephalus obliquus (Daubney, 1923) (39)
Kalicephalus sp. Sandground, 1933 (102)

Trimeresurus flavamaculatus

Kalicephalus sp. (U.S.National Museum)

Trimeresurus jerdonii

Kalicephalus longior Maplestone, 1931 (52)

Trimeresurus mucrosquamatus

Kalicephalus chunkingensis Hsü, 1934 (52)
Kalicephalus longior Maplestone, 1931 (52)

Typhlops braminus

Kalicephalus willeyi von Linstow, 1904 (6) (8) (29) (65)

Typhlops lettensis obtusus

Kalicephalus sp. Loveridge, 1953 (75)

Typhlops p. punctatus

Kalicephalus sp. Sandground, 1933 (102)

Vipera ammodytes

Kalicephalus viperae (Rudolfi, 1819) (94) (98) (115)

Vipera redii

Kalicephalus viperae (Rudolfi, 1819) (30) (31) (33) (86) (98) (115) (118)

Vipera russelli

Kalicephalus willeyi von Linstow, 1904 (6) (8) (29) (65) (81) (88)
Kalicephalus sp. (U.S.National Museum)

Xenedon merremii

Kalicephalus appendiculatus Molin, 1861 (86) (122)

Xenedon severus

Kalicephalus appendiculatus Molin, 1861 (86)(122)

Zaocys d'humnades

Kalicephalus indicus Ortlepp, 1923 (52)
Kalicephalus nankingensis Hsu, 1934 (52)
Kalicephalus sp. Hoeppli and Hsü, 1934 (51)

Zaocys nigromarginatus

Kalicephalus indicus Ortlepp, 1923 (52)

UNIDENTIFIED SNAKE

"Snake"

Kalicephalus obesus Baylis, 1933 British Museum (Natural History)

Hainan Snake

Kalicephalus sinensis Hsü, 1934 (130) (131)
Kalicephalus minutus (Baylis and Daubney, 1922) (130) (131)
Kalicephalus assimilis Wu and Hu, 1938 (130) (138)

"Snake" - Hainan Province

Kalicephalus minutus (Baylis and Daubney, 1922) (52)

Australian Snake

Kalicephalus novae-britannae Baylis, 1933 (4)

Colubrine Snake

Kalicephalus colubri Ortlepp,1923 (88)

Nigerian Snake

Kalicephalus nigeriensis Ortlepp, 1923 (88)

Serpent "A"

Kalicephalus (?) *nigeriensis* Ortlepp, 1923 (7)

Tree Snake (Nigeria)

Kalicephalus (?) nigeriensis Ortlepp, 1923 (84)

Snake

Kalicephalus longior Maplestone, 1931 British Museum (Natural History)

Rat Snake

Kalicephalus sp. (U.S. National Museum)

Sumatra Green Snake

Kalicephalus sp. (U.S. National Museum)

Black Snake

Kalicephalus sp. (U.S. National Museum)

OTHER REPTILES [1]

Ceratophora stoddarti

Kalicephalus sp. British Museum (Natural History)

Phrynosoma sulphuroceus

Kalicephalus sp. (U.S. National Museum)

Tupinambis nigropunctatus

Kalicephalus sp. (U.S. National Museum)

Turtle

Kalicephalus sp. (U.S. National Museum)

---

[1]These are considered cases of accidental parasitism.

Varanus bengalensis

Kalicephalus indicus Ortlepp, 1923 (81)

Varanus salvator

Kalicephalus sp. British Museum (Natural History)

MAMMALS[1]

Cercacebus callaris

Kalicephalus sp. (U.S. National Museum)

Erithizon dorsatum

Kalicephalus simplex (Leidy, 1856) (60)

Wildcat

Kalicephalus indicus Ortlepp, 1923 (81)

---

[1]These are considered cases of accidental parasitism.

SPECIES OF KALICEPHALUS BY GEOGRAPHICAL AREA

From North America

K. agkistrodontis Harwood, 1932

K. conoidus, Comroe, 1948

K. coronellae Ortlepp, 1923

K. rectiphilus Harwood, 1932

K. simplex (Leidy, 1856) Walton, 1927

K. parvus, Ortlepp, 1923

Kalicephalus sp. Leiper, 1935

From South America

K. costatus (Rudolfi, 1819)

K. subulatus Molin, 1861

K. inermis Molin, 1861

K. implicatus Kreis, 1938

K. philodryadus Ortlepp, 1923

K. appendiculatus Molin, 1861

K. bothropis Molin, 1861

K. brevipenis Molin, 1861

K. mucronatus Molin, 1861

K. strumosus, Molin, 1861

K. boae (Blanchard, 1886)

K. boae (MacCallum, 1921) Chitwood, 1932

Kalicephalus sp. (Wücherer, 1872)

Indo-Australian

K. appendiculatus Stossich, 1900 nec Molin, 1861

K. enygri Kreis, 1938

K. novae-britannae Baylis, 1933

Kalicephalus sp. Johnston, 1912[1]

Kalicephalus sp. Johnston and Mawson, 1948[1]

Kalicephalus sp. Johnson, 1912, 1918

Asia

K. assimilis Wu and Hu, 1938

K. brachycephalus Maplestone, 1931

K. bungari (MacCallum, 1918)

K. chunkingensis Hsü, 1934

K. ersillae (Stossich, 1896) Yorke and Maplestone, 1926

K. fimbriatus (Ortlepp, 1923)

K. laticaudae Yamaguti, 1935

K. longior Maplestone, 1931
  K. radicus Bhalerao, 1931
  K. gongylophis Maplestone, 1931

K. minutus (Baylis and Daubney, 1922)
  K. naiae Maplestone, 1931

K. nankingensis Hsü, 1934

K. natricis Yamaguti, 1935[2]

---

[1]Miss Mawson is of the opinion that these are probably the same specimens (personal communication).

[2]K. natricis is certainly a synonym of K. nankingensis, but to introduce this new synonym is not within the scope of this thesis.

Asia (continued)

K. sinensis Hsü, 1934

K. willeyi von Linstow, 1904 [1]

K. obesus Baylis, 1933

K. elongatus Maplestone, 1931

K. indicus Ortlepp, 1923
- K. bengalensis Maplestone, 1929
- K. parvus Maplestone, 1932 nec Ortlepp, 1923
- K. maplestonei Chatterji, 1935

Kalicephalus spp. (Baylis and Daubney, 1922)

Kalicephalus sp. Tubangui and Masilungen, 1937

Kalicephalus sp. Sambon, 1909

Kalicephalus sp. Hoeppli and Hsü, 1934

Africa

K. costatus Skrjabin (not Rudolfi, 1819)

K. micrurus (Daubney, 1923)

K. nigeriensis Ortlepp, 1923

K. simus (Daubney, 1923)

K. rotundatus von Linstow, 1908

K. bitisi Campana and Chabaud, 1950

K. colubri Ortlepp, 1923

K. obliquus (Daubney, 1923)

Kalicephalus spp. Loveridge, 1953

Kalicephalus spp. Sandground, 1933

Kalicephalus sp. Porter, 1954

Kalicephalus sp. Loveridge, 1936

Kalicephalus sp. Hamerton, 1933

---

[1] It is very probable that two and perhaps more species have been recorded under this name in the several papers by von Linstow (for discussion see Baylis, 1936).

Africa (continued)

Kalicephalus sp. Herman, 1939

Kalicephalus sp. Leiper, 1908

Kalicephalus sp. Sambon, 1907

Kalicephalus sp. Sandground, 1933

Europe

K. viperae (Rudolfi, 1819)
K. vallei (Stossich, 1895)

K. colubri, Ortlepp, 1923

BIBLIOGRAPHY

1. ALICATA, J. E., 1935. Early developmental stages of nematodes occurring in swine. Tech. Bull. 489, U. S. Dept. Agric., 96 pp.

2. ALLESSANDRINI, G., 1905. Su di alcune uncinariae parassite dell' uomo e di altri vertebrati. Boll. Soc. Zool. Ital., 6: 23-48.

3. ANDREWS, J. S. and J. F. MALDONADO, 1941. The life history of Oesophagostomum radiatum, the common nodular worm of cattle. Research Bull. (2), Puerto Rico Agric. Exper. Station, 14 pp.

4. BAYLIS, H. A., 1927. Some new parasitic nematodes from Australia. Ann. and Mag. Nat. Hist. Series 9, 20: 214-225.

5. BAYLIS, H. A., 1933. On a collection of nematodes from Mayalan reptiles. Ann. and Mag. Nat. Hist. Series 10, 11: 615-633.

6. BAYLIS, H. A., 1936. Fauna of British India, including Ceylon and Burma. Nematoda Vol. 1 (Ascaroidea and Strongyloidea) 408 pp. London.

7. BAYLIS, H. A., 1940. On a further collection of parasitic worms from the Belgian Congo. Ann. and Mag. Nat. Hist. Series 11, 5: 401-416.

8. BAYLIS, H. A. and R. DAUBNEY, 1922. Report on the parasitic nematodes in the collection of the Zoological Survey of India. Mem. Indian Mus., 7: 263-347.

9. BAYLIS, H. A. and R. DAUBNEY, 1926. A synopsis of the families and genera of Nematoda. 277 pp. London.

10. BENEDICT, F. G., 1932. The physiology of large reptiles. Carnegie Inst. Washington. Pub. 425.

11. VAN DEN BERGHE, L., 1943. Enquete parasitologique. II. Helminths parasites. Fasc. (2) Mission (van den Berghe) (1936) Explor. Parc Nat. Albert p. 3.

12. BHALERAO, G. D., 1931. Two new parasites from the king cobra (Naja hannah). Ann. and Mag. Nat. Hist. Series 10, 8: 102-109.

13. BLANCHARD, R., 1886. Notices helminthologiques. Bull. Soc. Zool. France. 11: 294-304.

14. BLANCHARD, R., 1889. Traité de zoologie médicale. Vol. 1 Protozoaires, histoire de l'oeuf, coelentérés, échinodermes, vers (aneuriens, plathelminthes, némathelminthes). 808 pp. Paris.

15. BOULENGER, C. L., 1926. Report on a collection of parasitic nematodes, mainly from Egypt. Pt. 4. Trichostrongylidae and Strongylidae. Parasitology 18: 86-100.

16. CABALLERO y C., Eduardo, 1938. Nématodes parasites des reptiles du Mexique. Ann. Parasitol. 16: 327-333.

17. CABALLERO y C., Eduardo, 1939. Nematodos de los reptiles de Mexico. III. An. Inst. Biol. Univ. Nac. México. 10: 73-82.

18. CAMERON, T. W. M., 1927. On the parasitic development of Monodontus trigonocephalus, the sheep hookworm. J. Helminth. 5: 149-162.

19. CAMPANA, Y. and A. G. Chabaud, 1950. Note sur quelques nématodes africains collection Camille Desportes. Ann. Parasitol. 25: 308-324.

20. CHANDLER, A. C., J. E. ALICATA and M. B. CHITWOOD, 1941. Life history (zooparasitica). II. Parasites of vertebrates. An Introduction to Nematology (Chitwood et al) Sect. II Pt. II 267-301.

21. CHATTERJI, R. C., 1935. Nematodes from a common Indian lizard (Uromastix hardwicki), with remarks on Kalicephalus parvus Maplestone, 1932. Rec. Indian Mus. 37: 29-36.

22. CHITWOOD, B. G., 1932. A note on the genus Camallanus. J. Parasitol. 19:88.

23. CHITWOOD, M. B., 1940. Postembryonic development. An Introduction to Nematology (Chitwood et al) Sect. II Pt I, 227-240.

24. CHITWOOD, B. G. and M. B. CHITWOOD, 1937. An Introduction to Nematology (1st Ed.) Sect. I, Pt. I, 53 pp. Baltimore.

25. CHITWOOD, B. G. and M. B. CHITWOOD, 1950. An Introduction to Nematology. (2nd Ed.) Sect. I, Anatomy. 213 pp. Baltimore.

26. CLAPHAM, P. A., 1939a. On flies as intermediate hosts of Syngamus trachea. J. Helminth. 17: 61-64.

27. CLAPHAM, P. A., 1939b. Three new intermediary vectors for Syngamus trachea. J. Helminth. 17: 191-192.

28. COMROE, D. B., 1948. Kalicephalus conoidus, n. sp. (Strongylata) a nematode from the rattlesnake Crotalus triseriatus. Tr. Am. Micr. Soc. 67: 280-284.

29. DAUBNEY, R., 1923. Note on the genus Diaphanocephalus (Nematoda: Strongylidae), parasitic in reptiles, with a description of three new species. Parasitology 15: 67-74.

30. DIESING, K. M., 1851. Systema Helminthum Vol.2, vi + 588 pp. Vindobonae.

31. DIESING, K. M., 1855. Sechzehn Gattungen von Binnenwürmern und ihre Arten. Denkschr. K. Akad. Wissensch., Wien, Math.-Naturw. Kl., 9: 171-185.

32. DIESING, K. M., 1861. Revision der Nematoden. Sitzungsb. K. Akad. Wissensch. Wien, Math.-Naturw. Cl. 42: 595-736.

33. DOLLFUS, R. P. and A. G. CHABAUD, 1949. K. viperae (Rudolfi, 1819) (Nematoda: Strongyloidea) Un parasite de serpents à ajouter à la faune de France.

34. DOUGHERTY, E. C., 1946. A revised classification of the nematoda suborder Strongylina. J. Parasitol. 32 (suppl.): 15-16.

35. DOUGHERTY, E. C., 1951. Evolution of zooparasitic groups in the phylum Nematoda with special reference to host-distribution. J. Parasitol. 37: 353-378.

36. DUJARDIN, F., 1845. Histoire naturelle des helminthes ou vers intestinaux. xvi + 654 + 15 pp. Paris.

37. EISMA, M., 1932. De differentiate van het derde stadium van de larven der Ancylostomidae van mensch, hond en kat. Proefschrift (Leidin, 1932). 152 pp. Haarlem.

38. ERSHOV, V. S., 1947. [Developmental cycle of Strongylus vulgaris in the horse (in Russian)] Veterinariya 26: 26-28. Abstracted in Helminth. Abstracts 18: 190-192.

39. FANTHAM, H. B. and A. PORTER, 1950. The endoparasites of certain South African snakes, together with some remarks on their structure and effects on their hosts. Proc. Zool. Soc. London 120: 599-647.

40. FANTHAM, H. B. and A. PORTER, 1954. The endoparasites of some North American snakes and their effects on the Ophidia. Proc. Zool. Soc. London 123: 867-898.

41. GOODEY, T., 1922. A simple method of experimentation for skin infection with hook-worm larvae. Proc. Roy. Soc. Med. Sect. Trop. Dis. and Parasitol. 15: 19-20.

42. HALL, M. C., 1916. Nematode parasites of mammals of the orders Rodentia, Lagomorpha, and Hyracoidea. Proc. U.S. Nat. Mus. (2131) 50: 1-258.

43. HAMERTON, H. E., 1933. Report on deaths occuring in the Society's garden during the year 1932. Proc. Zool. Soc. London 103: 451-482.

44. HAMERTON, H. E., 1935. Report on deaths occuring in the Society's garden during the year 1934. Proc. Zool. Soc. London 105: 443-474.

45. HARWOOD, P. D., 1932. The helminths parasitic in the Amphibia and Reptilia of Houston, Texas and vicinity. Proc. U. S. Nat. Mus. (2940) 81: 1-71.

46. HARWOOD, P. D., 1933. The helminths parasitic in a water moccasin (snake) with a discussion of the characters of the Proteocephalidae. Parasitology 25: 130-142.

47. HARWOOD, P. D., 1934. Notes on Tennessee helminths. I. Kalicephalus tennesseensis n. sp. (nematode). J. Tennessee Acad. Sc. 9: 192-194.

48. HARWOOD, P. D., 1936. The effect of soil types on the helminths parasitic in the ground lizard, Leiolopisma laterale (Say). Ecology 17: 694-698.

49. HERMAN, C. M., 1939. Parasites obtained from animals in the collection of the New York Zoological Park during 1938. Zoologica 24: 481-485.

50. HETHERINGTON, D. C., 1923. Comparative studies on certain features of nematodes and their significance. Illinois Biol. Monogr., 8: 1-62.

51. HOEPPLI, R. J. and H. HSÜ, 1931. Histological changes in the digestive tract of vertebrates due to parasitic worms. National Med. J. China 17: 557-566.

52. HSÜ, H. F., 1934. On some Kalicephalus species from China with a discussion of certain systematic characters of the genus. Peking Nat. Hist. Bull. 8: 375-389.

53. HYMAN, L. H., 1951. The Invertebrates. Vol. 3 Acanthocephala, Aschelminthes and Entoprocta. 572 pp. McGraw-Hill, New York.

54. IHLE, J. E. W. and G. J. VAN OORDT, 1924. On the development of the larva of the fourth stage of Strongylus vulgaris (Looss). Proc. K. Akak. Wetensch., Amsterdam. 27: 194-200.

55. JOHNSTON, T. H., 1912. A census of Australian reptilian Entozoa. Proc. Roy. Soc. Queensland 23: 233-249.

56. JOHNSTON, T. H., 1918. Notes on miscellaneous endoparasites. Proc. Roy. Soc. Queensland 30: 209-218.

57. JOHNSTON, T. H. and P. MAWSON, 1948. Some new records of nematodes from Australian snakes. Rec. South Australia Mus. 9: 101-106.

58. KREIS, H. A., 1938. Beiträge zur kenntnis parasitischer Nematoden. VIII. Neue parasitische Nematoden aus dem Naturhistorischen Museum Basel. Zentralbl. Bakteriol. 1 Abt., Orig., 142: 329-352.

59. KREIS, H. A., 1940. Beiträge zur kenntnis parasitischer Nematoden. IX. Parasitische Nematoden aus dem Naturhistorischen Museum Basel. Zentralbl. Bakteriol. 1 Abt., Orig., 145: 163-208.

60. LEIDY, J., 1856. A synopsis of Entozoa and some of their ecto-congeners observed by the author. Proc. Acad. Nat. Sc. Phila. 8: 42-58.

61. LEIPER, R. T., 1908. An account of some helminthes contained in Dr. Wenyon's collection from the Sudan. Rep. Wellcome Res. Lab. 3: 187-199.

62. VON LINSTOW, O., 1878. Compendium der Helminthologie. xxii + 382 pp. Hannover.

63. VON LINSTOW, O., 1889. Compendium der Helminthologie. Nachtrag. Die Litteratur der Jahre 1878-1889. xvi + 151 pp. Hannover.

64. VON LINSTOW, O., 1904. Nematoda in the collection of the Colombo Museum. Spolia Zeylanica 1: 91-104.

65. VON LINSTOW, O., 1906. Helminthes from the collection of the Colombo Museum. Spolia Zeylanica 3: 163-188.

66. VON LINSTOW, O., 1908a. Helminthes. Nematoden und Acanthocephalen. (In Schultze, Leonhard. Zoologische und anthropologische Ergebnisse einer Forschungreise im westlichen und zentralen Südafrika ausgeführt in den Jahren 1903-1905 ... 1. Band ....1. Lieferung) Denkschr. Med.-Naturw. Gesellsch. Jena, 13: 19-28.

67. VON LINSTOW, O., 1908b. Recent additions to the collection of Entozoa in the Indian Museum. Rec. Indian Mus. 2: 108-109.

68. LOOSS, A., 1897. Notizen zur Helminthologie Egyptens. Centralbl. Bakteriol. 21: 913-926.

69. LOOSS, A., 1902. The Sclerostomidae of horses and donkeys in Egypt. Rec. Egypt Govt. School Med. 1: 25-139.

70. LOOSS, A., 1905. The anatomy and life history of Agchylostoma duodenale Dub. A Monograph. Pt. I, Anatomy of the adult worm. Rec. Egypt Govt. School Med., 3: 1-158 (+1).

71. LOOSS, A., 1911. The anatomy and life history of Agchylostoma duodenale Dub. A Monograph. Pt. II, The development in the free state. Rec. Egypt Govt. School Med., 4: 159-613.

72. LOPEZ-NEYRA, C. R., 1947. Helmintos de los vertebrados Ibericos. 1212 pp. Granada.

73. LOVERIDGE, A., 1928. (no title). Bull. Antivenom Inst. America. 2:1.

74. LOVERIDGE, A., 1936. Scientific results of an expedition to rain forest regions in Eastern Africa. V. Reptiles. Bull. Mus. Comp. Zool. Harvard Coll. 79: 207-337.

75. LOVERIDGE, A., 1953. Zoological results of a fifth expedition to East Africa. III. Reptiles from Nyasaland and Tete. Bull. Mus. Comp. Zool. Harvard Coll. 110: 143-322.

76. LUCKER, J. T., 1936. Comparative morphology and development of infective larvae of some horse strongyles. Proc. Helminth Soc. Washington 3: 22-25.

77. LUCKER, J. T., 1938. Description and differentiation of infective larvae of three species of horse strongyles. Proc. Helminth Soc. Washington 5: 1-5.

78. MACCALLUM, G. A., 1918. Notes on the genus Camallanus and other nematodes from various hosts. Zoopathologica 1: 121-134.

79. MACCALLUM, G. A., 1921. Studies in Helminthology. Pt. I, Trematodes Pt. II Cestodes Pt. III Nematodes. Zoopathologica 1: 135-284.

80. MAPLESTONE, P. A., 1929. Two new species of nematodes from Indian hosts. Rec. Indian Mus., 31: 87-92.

81. MAPLESTONE, P. A., 1931. Parasitic nematodes obtained from animals dying in the Calcutta Zoological gardens. Pts. 4-8. Rec. Indian Mus. 33: 71-171.

82. MAPLESTONE, P. A., 1932. Parasitic nematodes obtained from animals dying in the Calcutta zoological gardens. Pts. 9-11. Rec. Indian Mus. 34: 229-261.

83. MAYR, E., E. G. LINSLEY and R. L. USINGER, 1953. Methods and principles of systematic zoology. vii + 328 pp. McGraw-Hill, New York.

84. MCCULLOCH, W. E., 1930. Annual report on the Pathological Laboratory, Kaduna, 1929. Ann. Med. and San. Rep. Nigeria (1929) App. D: 63-76.

85. METTAM, R. W. M., 1935. Annual report of the veterinary pathologist, Entebbe, for the year 1934. Ann. Rep. Vet. Dept. Uganda Protect., (1934), 21-30.

86. MOLIN, R., 1861. Il sottordine degli acrofalli ordinato scientificamente secondo i risultamenti delle indagini anatomiche ed embriogeniche. Mem. R. Ist. Veneto Sc., Lett. ed Arti 9: 427-633.

87. MÖNNIG, H. O., 1926. The life-histories of Trichostrongylus instabilis and T. rugatus of sheep in South Africa. 11-12 Rep. Director Vet. Educ. and Research, Dept. Agric. Union South Africa (1) 231-251.

88. ORTLEPP, R. J., 1923. Observations on the nematode genera Kalicephalus, Diaphanocephalus, and Occipitodontus g. n., and on the larval development of Kalicephalus philodryadus sp. n. J. Helminth. 1: 165-189.

89. ORTLEPP, R. J., 1937. Observations on the morphology and life history of Gaigeria pachyscelis Raill. and Henry 1910: A hookworm parasite of sheep and goats. Onderstepoort J. Vet. Sc. and Animal Indust., 8: 183-212.

90. PAI, S., 1928. Die Phasen des Lebenscyclus der Anguillula aceti Ehrbg. und ihre experimentell-morphologische Beeinflussung. Ztschr. Wissensch. Zool., 131: 293-344.

91. PARONA, C., 1893. Catalogo della collezione elmintologica del Prof. Corrado Parona. 12 pp. (Genève) (Lib. Stiles).

92. PARONA, C., 1898. Elminti raccolti dal Dott. Elio Modigliani alle isole Mentawei, Engano e Sumatra. Ann. Mus. Civ. Storia Genova (1898-99) 19: 102-124.

93. PORTER, A., 1954. Report of the honorary parasitologist for the year 1953. Proc. Zool. Soc. London 124: 313-316.

94. RAILLIET, A. and A. HENRY, 1909. Sur la classification des Strongylidae: II. Ankylstominae. Compt. Rend. Soc. Biol., Paris 66: 168-171.

95. RANKIN, J. S., 1945. An ecological study of the helminth parasites of amphibians and reptiles of western Massachusetts and vicinity. J. Parasitol. 31: 142-150.

96. RAUTHER, R., 1930. Vierte Klasse des Cladus Nemathelminthes. Nematodes. Nematoidea=Fadenwürmer. Handb. Zool. (Kükenthal u. Krumbach) Vol. 2, 8 Lief., Teil 4, Bogen 23-32, 249-402.

97. REIBER, R. J., E. E. BYRD and M. V. PARKER, 1940. Certain new and already known nematodes from amphibia and reptilia. Lloydia 3: 125-144.

98. RUDOLFI, C. A., 1819. Entozoorum synopsis cui accedunt mantissa duplex et indices locupletissimi. x + 811 pp. Berolini.

99. SAMBON, L. W., 1907. The haemogregarines of snakes. Tr. Path. Soc. London 58: 310-370.

100. SAMBON, L. W., 1909. The haemogregarines of snakes. J. Trop. Med. and Hyg. London 12: 48-55.

101. SANDGROUND, J. H., 1928. Some new cestode and nematode parasites from Tanganyika Territory. Proc. Boston Soc. Nat. Hist. 39: 131-150.

102. SANDGROUND, J. H., 1933. Reports on the scientific results of an expedition to the southwestern highlands of Tanganyika Territory. VI. Parasitic nematodes from East Africa and Southern Rhodesia. Bull. Mus. Comp. Zool. Harvard Coll. 75: 263-293.

103. SANDGROUND, J. H., 1936. (Important infestation with parasites). In Fox, Herbert; Mortality and Matters of pathological interest. Rep. Penrose Research Lab., Zool. Soc. Phila. p. 17.

104. SCHMIDT, K. P., 1950. Modes of evolution in the taxonomy of snakes. Evolution 4: 79-86.

105. SCHUURMANS STEKHOVEN, J. H., 1937. Parasitic Nematoda. Fasc. (4) Mission (de Witte) (1933-35) Explor. Parc Nat. Albert 40 pp.

106. SCHUURMANS STEKHOVEN, J. H., 1939. Nematodes. Bronn's Klass. u. Ordung. Tierreichs, Vol. 4, Abt. 2, Buch 3, Lief. 6, 499-660.

107. SEURAT, L. G., 1920. Histoire naturelle des nématodes de la Berbérie. Première partie. Morphologie, développement, éthologie et affinités des nématodes. 221 + vi pp. Alger.

108. SKRJABIN, K. I., 1916. Parasitic trematodes and nematodes collected by the expedition of Prof. V. Dogiel and I. Sokolov in British East Africa. Nauch. Rezul't. Zool. Eksped. (V. A. Dogiel i I. I. Sokolov) Brit. Vost. Afriku i Uganda, 1914. 1: 99-157.

109. SOLOMAN, S. G., 1932. On a collection of parasitic worms from East Africa. J. Helminth. 10: 209-230.

110. SOMMERVILLE, R. I., 1954. The histotropic phase of the nematode parasite, Ostertagia circumcinta. Australian J. Agric. Research 5: 130-140.

111. SPINDLER, L. A., 1933a. Skin penetration tests with infective larvae of the swine kidney worm, Stephanurus dentatus. J. Parasitol. 20: 76-77.

112. SPINDLER, L. A., 1933b. Development of the nodular worm Oesophagostomum longicaudum in the pig. J. Agric. Research 46: 531-542.

113. STILES, C. W. and A. HASSALL, 1905. The determination of generic types, and a list of roundworm genera, with their original and type species. Bull. (79) Bureau Animal Indust., U. S. Dept. Agric. 1-150.

114. STILES, C. W. and A. HASSALL, 1920. Index-catalogue of medical and veterinary zoology. Subjects: Roundworms (Nematoda, Gordiacea, Acanthocephali). Bull. (114) Hyg. Lab., U. S. Pub. Health Serv., 886 pp.

115. STOSSICH, M., 1895a. Il genere Ankylostomum Dubini. Boll. Soc. Adriat. Sc. Nat. Trieste 16: 21-25.

116. STOSSICH, M., 1895b. Notizie Elmintologiche. Boll. Soc. Adriat. Sc. Nat. Trieste 16: 33-46.

117. STOSSICH, M., 1896. Ricerche elmintologiche. Boll. Soc. Adriat. Sc. Nat. Trieste 17: 121-136.

118. STOSSICH, M., 1898a. Note parassitologiche. Boll. Soc. Adriat. Sc. Nat. Trieste 18: 1-10.

119. STOSSICH, M., 1898b. Saggio di una fauna elmintologica di Trieste e provincie contermini. Program. Civ. Scuola R. Sup., Trieste, 162 pp.

120. STOSSICH, M., 1899. Strongylidae. Lavoro monografico. Boll. Soc. Adriat. Sc. Nat. Trieste 19: 55-152.

121. STOSSICH, M., 1900a. Contributo allo studio degli elminti. Boll. Soc. Adriat. Sc. Nat. Trieste 20: 1-9.

122. STOSSICH, M., 1900b. In A. Shipley, A description of the Entozoa collected by Dr. Willey during his sojurn in the Western Pacific. In Willey, A., Zool. Results Pt. 5. Cambridge University Press. 531-568.

123. TAYLOR, E. L., 1935. Syngamus trachea. The longevity of the infective larvae in the earthworm. Slugs and snails as intermediate hosts. J. Comp. Path. and Therap. 48: 149-156.

124. TRAVASSOS, L., 1920. Esboço de uma chave geral dos nematodes parasitos. Rev. Vet. e Zootech., Rio de Janeiro 10: 59-70.

125. TUBANGUI, M. A. and G. MASILUNGAN, 1937. Nematodes in the collection of the Philippine bureau of science, III. Philippine J. Sc., 64: 257-267.

126. VEGLIA, F., 1915. The anatomy and life-history of the Haemonchus contortus (Rud.) 3. and 4. Rep. Director Vet. Research, Dept. Agric. Union South Africa, 347-500.

127. WALTON, A. C., 1927. A revision of the nematodes of the Leidy collections. Proc. Acad. Nat. Sc. Phila. (1927) 79: 49-163.

128. WETZEL, R., 1940a. Zur Biologie des Fuchslungenwurmes Crenosoma vulpis. I. Mitteilung. Arch Wissensch. u. Prakt. Tierh., 75: 445-460.

129. WETZEL, R., 1940b. Zur Entwicklung des grossen Palisadenwurmes (Strongylus equinus) im Pferd. Arch. Wissensch. u. Prakt. Tierh. 76: 81-118.

130. WU, H. W. and Y. T. HU, 1938. Parasitic nematodes from Hainan. Sinensia, Nanking, China 9: 275-297.

131. WU, H. W. and Y. T. HU, 1940. Some parasitic nematodes from Hainan. Proc. 6 Pacific Sc. Cong 4: 253.

132. WÜCHERER, O., 1872. Ueber due Anchylostomenkrankheit, tropische Chlorose oder tropische Hypoämie. Deutsches Arch. Klin. Med. 10: 379-400.

133. YAMAGUTI, S., 1935. Studies on the helminth fauna of Japan. Pt. 11. Reptilian Nematodes. Japan J. Zool. 6: 393-402.

134. YORKE, W., and P. A. MAPLESTONE, 1926. The nematode parasites of vertebrates. Churchill, London. 536 pp.