Reprinted from THE JOURNAL OF PARASITOLOGY, October, 1936, Vol. 22, No. 5, pages 479–510

A QUANTITATIVE STUDY OF THE NEMATODES FROM A SELECTED GROUP OF EQUINES IN PANAMA[1]

A. O. FOSTER

Helminthologist to the Gorgas Memorial Laboratory, Panama, R. P.

INTRODUCTION

During June, July and August, 1935, an opportunity was provided to examine at autopsy for the recovery of parasitic worms, a total of 48 horses and mules owned by the Panama Canal Department of the U. S. Army. As the infestation of each animal was studied quantitatively, in so far as possible, as well as qualitatively, it has been felt that the findings upon this group of equines, as outlined in the following pages, contribute to our knowledge of the occurrence and relative abundance of helminthic species in equines, particularly those of this locality. In addition, these data augment materially the limited information which is at present available upon the localization of Strongylid species within the large bowel and upon the adaptation of the several species to different kinds of equines (horses or mules). At the same time, it has seemed that these data present a reasonably accurate picture, both quantitatively and qualitatively, of the verminous infestations of Army equines in the Panama Canal Zone.

Selectiveness of Animals and Miscellaneous Information

From the helminthological viewpoint, it must be emphasized that the present series of equines is a highly selected group. In the first place, all were imported into the Canal Zone, and, although the periods of residence in the Zone were not less than 5 years in any case, it cannot be concluded, on the basis of these data alone, that the species encountered in these animals are indigenous to equines of Panama. In the second place, the equines of this series presented, in contrast to other animals which we have studied, a condition of extremely light worm-infestation. Much of this may perhaps be attributed to their excellent general condition and to the fact that, for the most part, they were stabled rather than pastured. Another factor of some significance is the care which is given to Army animals, a consideration of which suggests that the worm burdens of these animals probably represent about the minimum practical level which can be attained by the intelligent application of such

[1] The author wishes to acknowledge his indebtedness to Lt. Col. C. W. Greenlee, V.C., U. S. A., whose constant cooperation and interest made this survey possible. It is a pleasure to acknowledge also the able technical assistance of Sr. Pedro Ortiz Orsini.

measures of prevention and treatment as are now known. It was, of course, these low-grade infestations which permitted, under the conditions of these autopsies, a reasonably accurate quantitative study of the various species.

In this series were 17 horses and 31 mules, ranging in age from 9 to more than 24 years, and having resided in the Canal Zone for from 5 to 19 years at the time of autopsy. They were sacrificed because of a condition of incipient lameness, the cause of which, although not thoroughly understood and perhaps of a nutritional nature, may be definitely regarded, at least, as non-verminous. It may be said, then, that the animals of this series, except for the early articular lesions responsible for their lameness (a condition which was being studied by the Veterinary Corps of the Army, under Lt. Col. C. W. Greenlee) enjoyed the same generally good physical condition which one observes regularly in Army animals.

Methods of autopsy and worm-collection.

In the handling and identification of parasites a number of routine technics were used which need not be reviewed here, although a brief statement upon the conduct of the autopsies and worm-collections has seemed advisable. The animals were killed by gun-shot and opened immediately. The Great Colon was drawn out and the dorsal and ventral portions separated by ligature of the pelvic flexure. The cecum was not ligated from the ventral colon as it had been noted in earlier autopsies that nothing was gained by so doing, a technic which has been further justified by the data upon the differential distribution of species obtained during these studies. At this point, the body cavity was completely emptied of its organs, including the aorta. Although portions of the Ligamenta Nuchae, Bursati, and of the so-called Dhobie Itch lesions were occasionally taken to the laboratory for examination, it is to be admitted that no systematic search was made for certain of the filarial worms which have been encountered now and then in intimate association with ligaments and tissues of the neck and legs. With this exception, the search for verminous lesions and parasites was rather complete. The colon and cecum was rapidly freed of attachments, which could be done easily without rupture in most cases, and then divided into three portions, viz.: the cecum, ventral colon, and dorsal colon. These portions were laid out on a smooth concrete floor, apart from each other, and opened by cutting lengthwise along the surface to which the mesocolon had been attached. The content of each portion was rolled out upon the floor and the intestine was placed for examination, lining uppermost, upon a very convenient table of large wooden boxes. A laboratory helper, who understood considerable about the

various species of equine helminths, was assigned to the examination of each portion. Usually the intestine was being examined in from fifteen minutes to a half-hour after the animal was shot. First the mucosa was rapidly examined for the attachment of worms, and notes were recorded upon this and any other interesting phenomena which were observed. Then the worms were collected from the surface of the contents, afterwards from the intestinal mucosa. At intervals during the collection, the contents were again examined, since, by observation, it was learned that the Strongylid species tend to come to the surface of the intestinal contents. After all of the visible parasites had been collected by this method, the contents were examined in small portions. Afterwards, the contents usually were pressed out on the floor, using either the hand or the sole of one's boot, and allowed to remain on the wet surface for a short interval during which the portion of the intestine was examined further. In this way worms were frequently recovered from the surface of the flattened-out contents. Then the contents were carefully pushed to one side, and any worms which were on the wet floor were collected. After further cursory examinations both of the contents and of the intestinal wall, which in many instances failed to yield any more worms, the collections were regarded as satisfactory.

This procedure has been outlined in some detail, because it has seemed to be the most practicable method for a quantitative approach to the study of equine parasites. This technic takes advantage of the readily observable fact that the Cylicostomes live in intimate association with the mucosa[2] and on the surface of the content-mass, and obviates the necessity of screening, a method of worm-collecting which gives very unsatisfactory results when applied to the intestinal contents of equines. This latter method is impracticable because of the large size of the particles of debris compared to the relatively small size of many of the Cylicostomes.

The stomach and small intestine were also examined for parasites and verminous lesions.

Summarily, it may be stated that worm-collections routinely were made into five separate bottles used for the following regions; cecum, ventral colon, dorsal colon, stomach and mesenteric arteries, and body cavity, etc. These bottles, and inked labels for putting in them, were prepared in advance. Other smaller bottles, for special uses, such for example as determining specifically a helminth of conspicuous color or one found attached, were carried regularly in the autopsy kit. The

[2] In making this statement, it is not desired to enter into the discussion of the extent to which the Cylicostomes are *normally attached* to the lining of the colon and cecum.

worms were collected into normal salt solution and later, in the laboratory, were fixed, cleared, identified, and counted. Among other equipment, there was also included a note-book in which rather complete notes were kept upon each autopsy.

Thoroughness of worm-collections

From the above discussion, it is not to be supposed that our technic is regarded as having been completely adequate for the recovery of all of the parasites. In each instance, a notation was made after finishing an autopsy, upon the degree of completeness of the helminthic collections. Our records show that there were 18 autopsies at which it was felt that "practically all" of the worms were taken, 9 cases where it was known that only a portion of the total number of smaller Cylicostomes were taken, and 21 cases, for which it was recorded that practically all of the worms were taken, *except* some of the smaller Cylicostome species from either the ventral colon or the dorsal colon. In these cases it is considered that the specimens missed from the dorsal colon were mainly of the species *Cylicostephanus longibursatus*, and from the ventral colon *Cylicocyclus nassatus*. Since these are among the most abundant species of *Strongylidae*, it has been felt that the relative proportions of Strongylid species as calculated from our data, are approximately correct. Moreover, for the larger species of *Strongylidae* it is felt that the collections were as nearly complete as possible. In spite of this, the smaller species were the most abundant, a consideration which encourages our feeling that these studies, in general, are fairly reliable from the quantitative, as well as from the qualitative, viewpoints.

Qualitative nature of the infestations

It may be permissible to point out at this time that no Trematodes were encountered in these autopsies, and that, of the Cestodes (genus *Anoplocephala*) which were so abundantly represented in the native equines which we have studied, only a single specimen (*A. perfoliata*) was present in this whole series of 48 animals. It might also be remarked that no "bots" (*Gastrophilus* larvae) were present in these animals. The nematodes, however, were found to represent 5 families, 17 genera, and 39 species.[3]

OBSERVATIONS AND DATA

Order *Myosyringata* Ward, 1917

Suborder *Strongylata* Railliet and Henry, 1913

[3] In the following pages, we have followed, in general, the nomenclature which is at present in use by the Zoological Division, Bureau of Animal Industry, U. S. Department of Agriculture.

Superfamily *Strongyloidea* Weinland, 1858; Hall, 1913
Family *Strongylidae* Baird, 1853

Within this family are included nearly all of the Nematode species which infest the large bowel of equines. From the present series of animals there were taken 32 different species belonging to 12 genera and 2 subfamilies within this family.

Although desirable, it has been found impracticable to present in tabular form the data upon the localization and quantitative occurrence of each of the species in the individual animals. It is felt, however, that the more interesting analyses and interpretations are presented in the zoologically-arranged discussions which follow.

Subfamily *Strongylinae* Railliet, 1893

This subfamily was represented by 3 genera and 8 species. It includes most of the larger Strongylid species, and particularly those which can be readily observed, for the most part, to be firmly attached to the wall of the cecum or colon. Morphologically, the species of this subfamily are distinct from the other equine species mainly by their conspicuously large, subglobular buccal capsules. In this report, about one-seventh of the total Strongylid fauna has been assigned to this subfamily and it includes some of the commonest and most frequently occurring species.

Genus *Strongylus* Mueller, 1780

The three species of this genus known to parasitize horses and mules were among the commonest of parasites from this series of animals. For what they lacked in abundance, compared to some of the smaller Strongylid species, they were compensated by their high incidence and conspicuousness. All three species were encountered together in 36 (75 per cent) of these equines; while of the other animals, 10 harbored two species, one of which was, in each case, *S. vulgaris*, and, in two instances the latter species occurred as the sole representative of the genus. Horses and mules alike appeared to be good natural hosts for all three species. It may be permissible to remark that these worms are not red or blood-colored as is often stated; rather they are distinctly dark blue, except the very young specimens, with frequently a more sanguineous aspect over the anterior fifth of the worm.

Strongylus equinus Mueller, 1780

This species occurred in 41 animals (85 per cent), of which 26 (84 per cent) were mules and 15 (88 per cent) were horses. Infestations were light, averaging 8 to 9 worms per animal, while the largest

single infestation was only 39 worms, of which number 37 were taken from the cecum. That this region is the slightly preferred habitat of *S. equinus* is further evidenced by the fact that 72 per cent of the specimens were taken from the cecum, 27 per cent from the ventral colon, and less than 1 per cent from the dorsal colon. It is felt that our data are sufficiently accurate to say also that this was the 15th commonest Strongylid species, being the 5th commonest of the cecum, the 14th of the ventral colon, and the 21st of the dorsal colon. Although only slightly less abundant than the species which follows it may be said to have been the least common species of the genus. In length, female specimens averaged about 41.5 mm. and males about 28.7 mm.

S. edentatus (Looss, 1900)

The incidence of this species paralleled closely that of *S. equinus*. It also was found in 41 animals, of which 25 were mules and 16 horses. Infestations averaged 10 to 11 worms, the largest number from one animal being 59, all of which, in this case, were taken from the ventral colon. As in the case of *S. equinus*, this species was encountered throughout the large bowel, although it differs from both the other species of the genus in its preferred localization, as evidenced by the fact that 84 per cent of the specimens were taken from the ventral colon. Only 15 per cent occurred in the cecum and less than 1 per cent in the dorsal colon. It was, however, the 6th most abundant species of the cecum, the 9th of the ventral colon, and the 17th of the dorsal colon. Its rank among the Strongylid species was next above that of *S. equinus*. Female specimens averaged about 36.5 mm. long, and males about 24.7 mm.

S. vulgaris (Looss, 1900)

This species was by far the commonest of the genus and was the only helminth encountered at every autopsy. It accounted for about 82 per cent of the total number of specimens belonging to the genus *Strongylus*. The infestations varied from 1 to 287 worms per animal, averaging about 87. It was the characteristic Strongylid species of the cecum,where about 96 per cent of the specimens occurred. It was infrequently met with in either the ventral colon (3 per cent) or the dorsal colon (1 per cent). Of the 32 Strongylid species, *S. vulgaris* was the 4th most abundant. This species, the smallest of the palisade worms, averaged 22.8 mm. in length for the females, and 16.7 mm. for the males.

Larvae of *S. vulgaris*, in various transitional stages, were recovered from either the right or the anterior branch of the Great Mesenteric Artery in 36 cases (75 per cent). Twenty animals harbored over 5

larvae each in those vessels, while 16 harbored less than this number. Compared to our observations of verminous aneurysm in native equines, it might be remarked that this is a particularly favorable finding.

Genus *Triodontophorus* Looss, 1901

The individual species of this genus were encountered in both horses and mules, although it appears from our data that the horse is the slightly preferred host and the ventral colon the usual habitat. All 4 species were found together in the same host upon two occasions, 3 (and only 3) species occurred together in one host 11 times, 2 species occurred 12 times, and one species only (usually *T. minor*) was found in 16 animals. Although seven animals harbored no parasites of this genus, it is interesting that two or more species were present at over half of the autopsies, and that three species were found together in about one-fourth of them. It is interesting also that, from the 41 animals harboring *Triodontophorus* spp., there were recovered and identified an even 800 specimens representing this genus, whose distribution as to species was as follows: *T. minor* 668 (83.5 per cent) *T. serratus* 74 (9.2 per cent), *T. tenuicollis* 82 (5.3 per cent), *T. brevicauda* 16 (2 per cent).

Triodontophorus serratus (Looss, 1900)

This species was recovered from 22 animals (46 per cent), more than half of which were horses. Since there were many more mules than horses covered in this survey, it follows that a much higher percentage (88 per cent) of the horses harbored this species than of the mules (22 per cent). The largest number of worms taken from one animal was 11, all of which in this instance were found in the cecum. This is the only species of the genus which occurred in the cecum, and likewise the only one which did not occur in the dorsal colon. Of the limited number of specimens recovered, 63 per cent were from the ventral colon and 37 per cent from the cecum. Although these figures indicate a slight preference for the ventral colon, it might be remarked that, not infrequently, in individual cases, like that above, *T. serratus* was restricted to the cecum. There were 5 such cases, while, on the other hand 11 animals harbored this species in the ventral colon only, and 6 yielded this parasite from both regions. This was one of the rarer species, ranking 17th among the Strongylid species from these animals, although it was the 8th commonest from the cecum and the 16th from the ventral colon.

It was with some hesitancy that the parasites discussed above were assigned to the species *T. serratus*. Our specimens satisfy in every particular the description given by Boulenger (1916) for *T. intermedius*

Sweet, 1909. G. Theiler (1923), in synonymizing this with Looss' type species, has admittedly shown that these two species are more closely allied then either Sweet or Boulenger had allowed, yet there still remain the consistently smaller size and conspicuously circular mouth-collar of the "*intermedius*"-type which appear to cast a reasonable doubt upon the identity of this and Looss' species. *T. serratus* was described as having a well-developed mouth-collar "flat, rather than high," and the original figures agree with this description. More than anything else, it has seemed unlikely that Looss was viewing the same species that we have observed when he figured *T. serratus*. In the event that both species, after more thorough study, shall be accepted as valid, it will follow that the species here reported is *T. intermedius* Sweet, 1909; *partim* Boulenger, 1916.

T. minor (Looss, 1900)

This was the commonest species of the genus. It was recovered from all of the horses and from 22 (71 per cent) of the mules. The largest number recovered from one animal was 73, of which 71 were taken from the ventral colon and 2 from the dorsal colon. Looss commented that *T. minor* was remarkable for its habitat in the posterior colon, although G. Theiler (1923) observed that this species, in South Africa, was common in the ventral as well as in the dorsal colon. Of the 668 specimens taken by us, 596 (89 per cent) came from the ventral colon, while only 72 (11 per cent) were recovered from the dorsal colon. It is our opinion that this, in common with the other species of the genus, is essentially a ventral colon form. *T. minor* has been considered one of the commoner species, being the 12th commonest of the family, and ranking 7th in both the ventral and dorsal portions of the colon.

From considerations pertaining particularly to this species, it has seemed that both accuracy and simplicity require that the presence or absence of denticular serrations cease to be considered a cardinal key-character for the separation of species within this genus. Keys, such as those of Boulenger (1916), Theiler (1923), and Cram (1924), which separate these species into those with "teeth usually not denticulated" and those with "teeth usually denticulated" are of little assistance. At least, if this character be used, *T. minor* should be placed with the species having denticulated teeth rather than with those species with which it has been placed in the past. Moreover, in G. Theiler's monograph, which has contributed so significantly to our knowledge of equine helminths, it has seemed that for the plate which figures *T. minor* (p. 757, fig. A) she may have mistakenly drawn the anterior end of a male specimen of *T. brevicauda*. It is unlikely that female specimens

would permit of confusion, because of their conspicuously different posterior ends. Our specimens of *T. minor* are as figured by Ihle (1922a), the teeth, at least in most cases, being serrated, although not to so marked a degree as is usually observed in *T. tenuicollis*. These considerations are presented only with the object of minimizing the confusion which might arise among a well-standardized group of species as a result of a misleading key or a mislabeled drawing.

It appears that a simple and accurate key to these species, based upon the readily discernable characters which one familiar with these species unconsciously uses for their separation, might be constructed as follows:

Key to *Triodontophorus* species

1. Mouth-collar conspicuously circular in profile ..... *T. serratus*
   Mouth-collar not as above, but flattened marginally 2
2. Flattened edges of mouth-collar directed anteriorly; tail of female blunt; dorsal ray of bursa very long (625 microns) ..... *T. brevicauda*
   Characters not as above 3
3. Buccal capsule relatively small (124×85 microns); bursa short; body distinctly tapered anteriorly ..... *T. tenuicollis*
   Buccal capsule relatively large (160×135 microns); bursa long (525 microns); anterior end rather large and prominent ..... *T. minor*

There is only one element of difficulty which might arise in making identifications of the above species, namely, the distinction with certainty between females of *T. tenuicollis* and *T. minor*, which are very closely allied, and in this circumstance, we submit that the differences between the buccal capsules is the most reliable single criterion.

T. tenuicollis Boulenger, 1916

About one-fourth (27 per cent) of the animals of this series harbored this species. It was recovered from 9 horses (53 per cent) and 4 mules (13 per cent), a difference which may indicate a preference for the horse. Although only 42 specimens were recovered, these were taken mainly from the ventral colon (86 per cent) as opposed to the dorsal colon (14 per cent) which was considered by G. Theiler as the usual habitat of the species. Although 13 worms were (in one instance, taken at one autopsy, this species may be regarded as one of the rarer Strongylid species covered in this survey. Specimens were often encountered, 3 or 4 in a group, attached to a small ulcer, although, as was true also of *T. minor*, solitary specimens were not infrequently observed to be responsible for small ulcerations.

T. brevicauda Boulenger, 1916

This interesting species was taken upon 7 occasions (15 per cent) the proportions of horses and mules which were infested being about

equal. Although the maximum infestation was 5 worms, a total of only 16 specimens were found, 15 of which were from the ventral colon. It was not found in the cecum and was one of the least common of the Strongylid species.

Genus *Craterostomum* Boulenger, 1920

Craterostomum mucronatum (Ihle, 1920)

Two specimens of this species were taken from separate animals; one a horse, the other a mule. Both occurred in the dorsal colon.

Subfamily *Cyathostominae* Nicoll, 1927

This subfamily name became obligatory upon acceptance of the genus *Cyathostomum* Molin, 1861 (syn., *Trichonema* Cobbold, 1874, *Cylicostomum* Railliet, 1901, *Cylichnostomum* Looss, 1901). With the elevation of Ihle's (1922) subgenera [*Cylicostomum* (Railliet, 1901), *Cylicostephanus, Cylicocercus, Cylicocyclus, Cylicodontophorus, Cylicotetrapedon* (1925)] to generic rank and the addition of new genera by Cram (1924) (*Cylicotoichus, Cylicobrachytus*), the genus *Cyathostomum* becomes restricted to the *tetracanthum-coronatum* group of Looss (1901). It is then, as at present used, synonymous with the subgenus *Trichonema* (Cobbold, 1874) Yorke and Maplestone, 1926, and the subgenus *Cylicostomum* (Railliet, 1901) Ihle, 1922. The subfamily is synonymous with *Cylicostominae* Railliet, 1915, and *Trichoneminae* Railliet, 1916.

This subfamily was represented in this survey by 9 genera and 24 species, which accounted numerically for about six-sevenths of the Strongylid fauna, although many of the species, because of their relatively small size, are not particularly conspicuous. The *Cyathostominae,* except *Gyalocephalus,* are distinguished mainly by their ring-shaped or cylindrical buccal capsules and the relative proximity of anus and vulva.

Genus *Cyathostomum* Molin, 1861

Three species of this genus were found during this survey, one or more of which was encountered in 42 animals (88 per cent). Nine animals harbored only 1 species, 13 harbored 2 species, and 20 harbored all three. From 6 animals no species of this genus were recovered. No preference was indicated as to horse or mule host, except possibly in the case of *C. labratum,* the distribution of which is interesting because it appeared to favor slightly the mule host. All three species occurred in all three portions of the large bowel, although as shall be indicated, each of them demonstrated a definitely preferred habitat.

Cyathostomum coronatum Looss, 1900

This was the characteristic Cylicostome of the cecum, second only to *S. vulgaris* among the Strongylid species in its incidence and abundance in that region of the bowel. It was present in 39 cases (81 per cent), the proportions of horses and mules being about equal. The maximum infestation was 111 specimens, all from the cecum. For the animals harboring this species, the average number of worms was about 27, the minimum 1. Of a total of 1055 specimens, over 90 per cent were from the cecum, over 9 per cent from the ventral colon, and a negligible percentage from the dorsal colon. Among the Strongylid species, it was the 9th commonest.

C. labiatum (Looss, 1901)

About half of the horses and mules harbored this species. Of 1009 specimens, 99 per cent were from the ventral colon, the remainder scattered in both the cecum and dorsal colon. In its preferred localization it was the 5th commonest Strongylid species, although among all of the species it was 10th in rank of abundance. It may therefore be regarded as one of the commoner Cylicostomes.

C. labratum Looss, 1900

Although this species showed a lower average infestation (18) than *C. labiatum* (39), it was found more frequently (63 per cent) than the latter (54 per cent). The 30 animals harboring this species included 71 per cent of the mules and 47 per cent of the horses. In other respects, *C. labratum* paralleled very closely *C. labiatum*, discussed above.

Genus *Gyalocephalus* Looss, 1900

Gyalocephalus capitatus Looss, 1900

Seven specimens of this species were recovered from the ventral colon of horses upon four occasions. It was not found in mules nor in any region other than that named. The largest number recovered from one animal was 3.

Genus *Poteriostomum* Quiel, 1919

Twenty-two animals (46 per cent) harbored species of this genus. Five were positive for both species and 17 harbored either one or the other. On the whole, these parasites were rather rare, although both species were taken from both hosts. They showed a distinct preference for the dorsal colon.

Poteriostomum imparidentatum Quiel, 1919

This species, 18th in rank among the Strongylid fauna, was taken from both horses (29 per cent) and mules (16 per cent) upon 10

occasions (21 per cent). A total of 64 specimens were taken, all from the dorsal colon, where the heaviest infestation was 28 worms. It was the 8th commonest form of the dorsal colon among the specimens recovered during this survey.

P. ratzii (Kotlán, 1919)

Although this species occurred more often (35 per cent) than the above, and showed a higher incident (59 per cent) in the horse than in the mule (22 per cent), it was much less numerous. Only 35 specimens were recovered, all but one of which were from the dorsal colon, where the largest single infestation was 8 worms. It was 21st in rank among the *Strongylidae*.

It has been interesting to find that these specimens of *P. ratzii* conform closely to *P. ratzii* var. *nanum* Theiler, 1923, particularly in respect to the arrangement and structure of the bursal rays. In particular, our specimens uniformly lacked the characteristic thumb-like process of the dorso-lateral way which is ascribed to the typical species, and which we have regularly observed in *P. imparidentatum*. Males varied from 10 to 13 mm. in length, and females 10.5 to 18 mm. The diameter of the buccal capsule was 174 to 201 microns and its depth 53 to 67 microns. The mouth-collar varied greatly in height. It is apparent from these data that in respect to the bursa and the size of the specimens, there is a close approach to Theiler's variety, yet the measurements of the buccal capsule, particularly the depth, approach more clearly the typical species. Moreover, there is considerable variability among specimens of both species of this genus, a consideration which supports Skladnik's view that Theiler's variety may be best considered a synonym of *P. ratzii*. This leaves but two species within the genus, the simplest key to which is as follows:

Key to *Poteriostomum* species

1. Elements of internal leaf-crown of unequal length ..... *P. imparidentatum*
   All elements of same length ..... *P. ratzii*

Genus *Cylicobrachytus* Cram, 1924

Cylicobrachytus brevicapulatus (Ihle, 1920)

The analysis of the data upon this species as to its rank, occurrence, distribution, and other factors and even in respect to the sex of the specimens (female) has shown it to be exactly parallel, in these respects, to *Craterostomum mucronatum*, discussed above. The only possible exception to this statement is that *C. brevicapsulatus* was found only in the horse (on but 2 occasions) while the former species was taken once from each host.

Although of rare occurrence, this species seems to be sufficiently distinct from all others to be readily recognizable when found. It is conspicuous microscopically by virtue of its relatively large size, prominent external leaf-crown, short buccal capsule, and thick, characteristically-shaped, oesophagus. This worm has apparently been found only twice before, and these occasions were by workers who examined a large number of animals. It was described by Ihle (1920) who recovered it from one horse in Holland. Later G. Theiler (1923) came upon one female specimen which had been taken from the pelvic flexure of a horse in South Africa. It is unfortunate that the absence of male specimens precludes, for the present, further comment upon the status of this species.

Genus *Cylicocercus* Ihle, 1922

Three species of this genus were recovered abundantly during this survey. These did not, however, include the type species, *C. alveatus* (Looss, 1900). It has been of some interest to note that in reports of equine species from Holland (Ihle, 1922a), Porto Rico (McIntosh, 1933), and Poland (Skladnik, 1935a), this species was also absent, while the other three species of the genus were listed. Other than the relatively numerous reports of *C. alveatus* from various parts of Africa (Looss 1901, Gough 1908, Yorke and Macfie 1920, Boulenger 1920, Theiler 1923) this species is either uncommon or it does not enjoy the widespread distribution which is so characteristic of most of the equine fauna. It has been noted by others (i.e., Theiler) that *Cyathostomum tetracanthum* (of Looss) is also somewhat peculiar in these respects.

In spite of what has been said, the genus *Cylicocercus* was among the most abundantly represented of the Strongylid genera, as about 13 per cent of the specimens were assigned to this genus. Every animal harbored at least one species of this genus. Over half of them (26) harbored all three species, while 15 harbored two (and only 2) species, and 7 animals only 1 species each. There was no indication of a preference for either the horse or mule host by any of the 3 species.

Cylicocercus catinatus (Looss, 1900)

This species was recovered from 43 animals (90 per cent) which number included all of the horses and 26 (85 per cent) of the mules. The maximum infestation was 897 worms, all of which, in this instance, were from the ventral colon. Although this region is undoubtedly the preferred habitat of this species, since over 96 per cent of the specimens were recovered from it, it is also true that, during this survey, this species was recovered from all three parts of the large bowel. Roughly 4 per cent of the specimens were divided about equally between the

cecum and dorsal colon. *C. catinatus* was the commonest species of the genus, and the sixth commonest among the Strongylid species. It was, however, the 4th commonest species in its preferred habitat, the 5th commonest from the dorsal colon, and the 6th from the cecum.

We have followed Skladnik (*loc. cit.*) in his synonymy of the varieties of this species with the typical form, although it has appeared that the majority of our specimens conform to *C. catinatus* var. *pseudocatinatus* (Yorke and Macfie, 1919).

C. goldi (Boulenger, 1917)

This is a characteristic species of the dorsal colon. As in the case of *C. catinatus* this form occurred in 43 animals. Of these, 16 (94 per cent) were horses and 27 (87 per cent) were mules. Of a total of 1509 specimens, 99 per cent were from the dorsal colon and about 1 per cent from the ventral colon. It occurred infrequently in the cecum also. It is remarkable that upon two occasions, a single adult specimen of *C. goldi* was recovered from the stomach, these being the only instances in which any of the Strongylid fauna were found outside of the large bowel. On the basis of our data, this was the 8th in abundance among the Strongylid species, and the 3rd commonest in its preferred habitat.

C. pateratus (Yorke and Macfie, 1919)

Twenty-nine animals (61 per cent) harbored this species. Unlike the other species *C. pateratus* occurred more frequently in mules (68 per cent) than in horses (47 per cent), although this is probably not indicative of a host-preference, since a large proportion of both hosts were infested. The distribution of specimens within the large bowel was quantiatively the same as given above for *C. goldi* with the important difference that *C. pateratus* was almost entirely restricted to the ventral colon instead of the dorsal. It was among the least common (13th in rank) among the species from both the cecum and dorsal colon, although it was the 6th commonest of the ventral colon fauna, and the 11th among the species of *Strongylidae*.

Genus *Cylicodontophorus* Ihle, 1922

On the whole, species of this genus were of rather uniformly infrequent occurrence, since the entire genus was represented in this survey by only 48 worms, although these were assignable to three species, each showing about the same incidence. Thirty-four animals (71 per cent) were apparently negative for species of this genus. Ten were infested with only one species, although 3 had double infections, and 1 harbored all three of the species.

Cylicondontophorus euproctus (Boulenger, 1917)

Six horses harbored this species in the dorsal colon. Although 11 specimens were taken from one animal, only 30 specimens in all were recovered. Over one-third of the horses harbored *C. euproctus,* yet it was not found in mules nor was it taken from any region other than the dorsal colon. Of the fauna characterizing this habitat, this was the 11th commonest species.

C. bicoronatus (Looss, 1900)

This species, taken from the ventral colon in each case, was recovered from 7 animals (15 per cent) including both hosts. Only 9 specimens were taken, the most from one animal being 3. Six animals harbored one specimen each. This was one of the least common of the Strongylid species recovered during the survey.

C. ultrajectinus (Ihle, 1920)

Nine specimens of this species were taken from 6 animals (13 per cent) including both hosts. All were found in the dorsal colon.

This species, which often has been observed in animals other than those included in this survey, is thick and fat and readily recognized at autopsy because of its characteristic sluggishness and distinct color, which is a kind of mottled gray.

Genus *Cylicostephanus* Ihle, 1922

Five species of this genus, 3 quite common and 2 relatively rare, were recovered from the equines of this survey. One animal harbored all five species, 5 harbored 4 species, 26 harbored 3 species, 12 two species each, and 4 only one species each. None were without representatives of this genus. In these five species are contained typical species of each part of the large bowel and there was no indication of a host-preference in any case.

Cylicostephanus calicatus (Looss, 1900)

This worm was 3rd in abundance and 6th in incidence among the Strongylid fauna reported in this paper. It occurred about equally among horses (76 per cent) and mules (84 per cent), and was taken from 39 (81 per cent) animals in all. The largest number taken from one animal was 924. The total number of specimens recovered and identified from the animals of this series (5388) were distributed about as follows; from the ventral colon, 94 per cent, from the cecum 5 per cent, and dorsal colon 1 per cent. It was the 2nd commonest species of the genus, and the 2nd in rank among the *Strongylidae* of the ventral colon. It was also the 4th most abundant species of the cecum, and the 6th of the dorsal colon.

At autopsy, this species because of its delicate size and the color which it sometimes exhibits, has often appeared to resemble a short strand of black thread.

C. poculatus (Looss, 1900)

This species has apparently been reported previously only from the horse. In this locality we have several times recovered it from mules and in the present series of animals it was taken from 3 horses and 1 mule, always from the cecum. Only 11 specimens were recovered, 7 of which were from one animal.

C. minutus (Yorke and Macfie, 1918)

This delicate and appropriately named worm was among the commonest of the Cylicostomes, occurring regularly in both horses and mules. Ninety-eight per cent of the specimens were taken from the ventral colon while the rest were distributed about equally between the cecum and dorsal colon. It was the 5th commonest Strongylid species, and next in abundance to *C. calicaus* in its preferred localization.

C. longibursatus (Yorke and Macfie, 1918)

Next to *S. vulgaris* this was the most frequently occurring Strongylid species and after *C. nassatus* (to be discussed later) it was the most abundant. Although specimens were taken from all three parts of the large bowel, 98 per cent were from the dorsal colon, where it was easily the predominant species. It was taken very infrequently from the cecum. The infected animals included all of the horses and all but 2 of the mules. The largest number from one animal, although more were probably present, was 1015.

C. hybridus (Kotlán, 1920)

This species was taken from 3 horses and 2 mules. Of a total of 46 specimens, 37 were from one animal. It did not occur in the dorsal colon but 96 per cent of the specimens were from the ventral colon. According to our data, this species was the 17th commonest in the ventral colon and the 12th of the cecum. On the whole it was one of the rarer species, ranking 19th among the Strongylid fauna.

Genus *Cylicotetrapedon* Ihle, 1925

This genus was created to include *Cylicostomum bidentatum* Ihle, 1925, and *C. asymetricum* Theiler, 1923, which species are distinct from others by nature of an asymmetry in the depth of their buccal capsules and by the fact that the buccal walls are thicker anteriorly than posteriorly. It is questionable whether these differences should be given

generic significance, particularly since there is nothing to exclude these species from the genus *Cylicostephanus,* already discussed. Moreover, it is felt that Cram was perfectly correct in pointing out that the elevation of Ihle's subgenera to genera serves, in the main, only to "simplify matters." One might well contend that for this reason also the above genus should be dropped, a view which has become even more reasonable since Skladnik (1935) has synomymized Ihle's species with *C. asymetricum,* leaving only one species within the genus. Moreover, Theiler originally placed *C. asymetricum* with the *calcatum-longibursatum* group which has been considered above under the genus *Cylicostephanus.* For the present, however, we shall accept this species as a member of an independent genus.

Cylicotetrapedon asymetricum (Theiler, 1923)

There were found two specimens of this species, one from the ventral colon of a mule, the other from the dorsal colon of a horse.

Of this species G. Theiler recovered 11 specimens from the ventral colon and 26 from the dorsal (considering the pelvic flexure as a part of the dorsal colon), in consequence of which she regarded this worm as probably a predominantly dorsal colon form. It is interesting that one is inclined to accept tentatively this viewpoint because of the fact that the dorsal colon is spectacularly the habitat of most of the very rare species (i.e., *C. mucronatum, O. robustus, C. brevicapsulatus, C. euproctus, C. ultrajectinus,* etc.). It has seemed that the observation that rare forms are predominantly dorsal-colon species can scarcely be questioned, although it would, of course, be folly to reason, in the light of our present knowledge, that this is anything but a coincidence.

Genus *Cylicocyclus* Ihle, 1922

Five species of this genus were recovered. Six animals harbored no representatives and none harbored all five. Eight were infested with one species each, 13 with two species, 15 with three, and 6 with four each. There were no host-preferences indicated.

Cylicocyclus radiatus (Looss, 1900)

This species was relatively rare, only 26 specimens having been taken from 7 animals. They were mainly from the ventral colon (96 per cent), although a few occurred in the dorsal colon (4 per cent). Twelve was the largest number taken from one animal.

C. elongatus (Looss, 1900)

Seven specimens were taken from 5 animals, 2 were from the cecum, 4 from the ventral colon, and 1 from the dorsal colon.

Theiler records this species as a "characteristic form of the cecum of the donkey, rarely occurring elsewhere." It may be permissible to remark that, although this species was among the rarest covered in this survey, it has been observed to be a common parasite of native interior animals (horses and mules) of Panama. Its characteristic habitat is the cecum, although, as among the present series, it may be found in any portion of the large bowel.

Our specimens are all of the var. *kotláni* (Ihle, 1920), although we have followed Skladnik's (1935a) apparently sound synonymy of this variety with the typical form.

C. nassatus (Looss, 1900)

This was the most abundant of the Strongylid species, in itself accounting for nearly one-fifth of the total Strongylid fauna. It occurred in 40 animals (83 per cent) and in all three parts of the large bowel of both the horse and mule hosts. It did, however, show a 94 per cent concentration within the ventral colon, where it was the commonest species. It was, however, also common in both the cecum and dorsal colon, such that, in spite of its preferred habitat, this species must be regarded as typical of the fauna from each of the three regions. The largest number of worms recovered and identified from one animal was 1689, and the total 7677.

Our specimens were of the var. *parvus* (Yorke and Macfie, 1918), although we have accepted, in this case also, the synonymy of Skladnik (*loc. cit.*). Male specimens were 7.5 to 8 mm. and females 9.2 to 11 mm. in length.

C. insigne (Boulenger, 1917)

This was one of the characteristic species of the dorsal colon, although it occurred rarely in the ventral colon and very infrequently in the cecum. Thirty-one animals (65 per cent) harbored this species, the largest single infestation being 561 worms. It was the 7th commonest of the Strongylid fauna but second only to *C. longibursatus* in the dorsal colon.

This species, when present, is very conspicuous, not only because of its larger size compared to the other Cylicostomes of the dorsal colon, but also because of the brilliant red color which is so characteristic of the young adult specimens.

C. leptostomus (Kotlán, 1920)

In many respects, this was a borderline species, being neither common nor rare. Twenty animals (42 per cent) harbored this worm, although only 180 specimens, in all, were recovered. The maximum infes-

tation was 44. It was 16th in abundance and 14th in incidence of the Strongylid fauna and was encountered in all three portions of the large bowel, although 96 per cent of the specimens were from the ventral colon, where it was the 10th most abundant species.

Suborder *Oxyurata* Cram, 1927

Superfamily *Oxyuroidea* Railliet, 1916

Family *Oxyuridae* Cobbold, 1864

Two rather distantly related species of Oxyurids were recovered quite commonly from the equines of this series.

Genus *Oxyuris* Rudolphi, 1803

Oxyuris equi (Schrank, 1788)

This species was not abundant in these animals. Small numbers of adult worms, fourth-stage larvae, and transitional stages were recovered from 18 animals (38 per cent). Twelve of the positive animals were horses (71 per cent) and 6 were mules (19 per cent). It is possible that this difference in incidence between horses and mules may indicate a preference for the horse-host. The numbers of adult worms varied from 2 to 297 per animal. Male specimens were plentiful, when the parasite was present. The dorsal colon and the terminal portions of the intestinal tract were the regions normally infested. Although no attempt was made to study quantitatively the larval and transitional stages, it was noted that these were usually much more numerous than adults and that they occurred typically in the dorsal colon. All stages occurred infrequently in the ventral colon, and even in the cecum.

In an otherwise splendid study upon the biology of the fourth stage larvae, Wetzel (1930) has stated that in the 17 fresh autopsies observed by him, these larvae were "always attached to the mucous membrane" and "always restricted to the ventral colon" (p. 95). On the basis of my own observations, I am impelled to state that these larvae were sometimes or (less conservatively) often attached to the mucous membrane and nearly always most abundant in the dorsal colon.

Genus *Probstmayria* Ransom, 1907

Probstmayria vivipara (Probstmayr, 1865)

The very small size of this species precluded from the start any attempt to study its occurrence quantitatively. There was, indeed, no attempt made to examine for the presence of this species at autopsy. Our data are, however, of such a nature as to throw considerable light, conservatively, upon the occurrence, abundance, and localization of this

scarcely visible species. In the collection of Strongylid species, as described previously, it will be recalled that specimens from the cecum, ventral colon, and dorsal colon, respectively, were collected into bottles of normal salt solution. Upon returning to the laboratory the content of each bottle was emptied and rinsed into a large glass Petri dish prior to fixing the worms. After all of the helminths were removed, the solution was routinely examined under the low-power of the microscope for specimens which had escaped the eye and to determine the presence of *P. vivipara*. More often than not that part which had contained the worms from the ventral colon was abundantly supplied with specimens of *P. vivipara*. These were neither counted nor saved, except for a few hundred specimens which have been kept in our collection. In other words, specimens of *P. vivipara* were apparently so numerous, when present, as to have been collected in large numbers, probably adhering, for the most part, to larger species.

Our records show that this species was found after this manner in 27 animals (56 per cent) including 8 horses (47 per cent) and 19 mules (61 per cent). They were taken from both the cecum and dorsal colon, but were typically abundant in the collections from the ventral colon. In more than half the cases, they were observed only from this region. It may be concluded then, that this is a very common species, at least in this locality. In abundance, it can scarcely be questioned that, could quantitative studies be made on this species, it would be many times more numerous than any of the other equine species. To consider this species rare, as has been frequently indicated in the literature, is to be misled by its insignificant size.

Suborder *Ascaridata* Railliet and Henry, 1915

Superfamily *Ascaroidea* Railliet and Henry, 1915

Family *Ascaridae* Baird, 1853

Genus *Parascaris* Yorke and Maplestone, 1926

Parascaris equorum (Goeze, 1782)

This species was uncommon among the equines of this series. Three horses and six mules were infested, practically all of the worms being immature. The number per animal varied from 2 to 14. Although this species localizes mainly in the upper part of the small intestine, three specimens were, in one case, taken from the stomach.

Suborder *Spirurata* Railliet and Henry, 1915

Superfamily *Spiruroidea* Railliet and Henry, 1915

Family *Spiruridae* Oerley, 1885

Genus *Habronema* Diesing, 1861

Three species of this genus were of rather common occurrence during this survey. Thirty-five animals (73 per cent) were infested. Three harbored all three species, 18 harbored 2 species, and 14 harbored only one species. Because of the intimate association of these species with the gastric mucosa, there is in every case some doubt as to the thoroughness with which the worms were collected. It is not felt that our data approach the actual infestations of these animals, although it was apparent that, in general, the infestations were relatively light. Moreover, the data are sufficiently reliable to show roughly the incidence and relative abundance of each species.

Habronema muscae (Carter, 1861)

This species was recovered from 30 animals (63 per cent), including 12 horses (71 per cent) and 18 mules (58 per cent). The number per animal ranged from 1 to 106. It was not unusual to recover this species from the surface of the content-mass from the stomach, although more often the worms were buried in the mucous exudate of the stomach tissue.

H. megastoma (Rudolphi, 1819)

Although of lower incidence than either of the other species of the genus, *H. megastoma* is probably the most important pathogen. From 4 to 20 worms per animal were taken upon six occasions from walnut-sized gastric tumor-like abscesses, always showing a sanguinous aspect, and generally located upon the margin of the cardiac glandular region of the mucosa. In comparison with our observations upon native animals, where several hundred worms have been taken from a single abscess, it may be permissible to consider that the infestations among the animals of this series were very light.

H. microstoma (Schneider, 1866)

This was the most abundant species of the genus although it occurred less often than *H. muscae*. It was found in 22 animals (46 per cent), the number of specimens varying from 1 to 127 per animal, and was observed to be associated at times with an eroded and ulcerated mucosa. It is particularly interesting that this species was taken from 61 per cent of the mules (19) and only 18 per cent of the horses (3). Considering that these animals were raised under the same conditions, one is prompted to suggest that of the two, perhaps the mule is the more natural host for this species.

Superfamily *Filarioidea* (Weinland, 1858) Stiles, 1907

Family *Filariidae* (Cobbold, 1864) Claus, 1885

Genus *Setaria* Viborg, 1795

Setaria equina (Abildgaard, 1789)

Nine animals (19 per cent) harbored this species in the body cavity. From each of 2 horses and 7 mules, from 1 to 4 specimens were taken.

DISCUSSION

Species encountered.

From the 48 horses and mules covered by this survey there are recorded, in addition to the Cestode species, *Anoplocephala perfoliata,* which is mentioned in the introductory pages, a total of 39 different Nematode species. Of these, 32 species were of the family *Strongylidae* and their generic distribution as follows: *Strongylus* 3, *Triodontophorus* 4, *Craterostomum* 1, *Cyathostomum* 3, *Gyalocephalus* 1, *Poteriostomum* 2, *Cylicobrachytus* 1, *Cylicocercus* 3, *Cylicodontophorus* 3, *Cylicostephanus* 5, *Cylicotetrapedon* 1, *Cylicocyclus* 5. The seven other species, not closely related systematically, were *Oxyuris equi, Probstmayria vivipara, Parascaris equorum, Habronema muscae, H. megastoma, H. microstoma,* and *Setaria equina.*

Host-variations in the number of different species and their abundance.

In the animals of this series the number of different species of *Strongylidae* varied from 6 to 22 per animal, with an average of 15. In the cecum the number of different species ranged from 2 to 9, with an average of 5. For the ventral colon, the variation was from 3 to 16, averaging 11. The dorsal colon showed a range of from 1 to 14 different Strongylid species, with an average of 6.

The total number of Strongylid worms recovered from these animals varied from 36 to 4124 and averaged 849 per host. In the cecum the range was from 2 to 354, with an average of 127. The range from the ventral colon was from 9 to 3765 worms, with an average of 486. For the dorsal colon the range was from 2 to 1121 worms, with an average of 236 per animal.

Of the 7 species, other than *Strongylidae,* these animals harbored from none to 5 species each, and averaged 2 to 3 species (2.56) per animal. Considering, as a group, these extra-*Strongylidae,* it may be summarized that 1 animal harbored none of these species, 8 harbored 1 species, 17 harbored 2 species, 9 harbored 3 species, 11 harbored 4 species, and 2 harbored 5 species.

With respect to the numerical importance of these extra-*Strongylidae*, our data show an average, per animal, of about 33 worms each, exclusive of *P. vivipara* and fourth stage larvae of *O. equi*.

Relative abundance of different species of Strongylidae.

A total of 40,707 Strongylid parasites were identified from these equines, of which 40,145 or 98.62 per cent were accounted for by 15 species. These were also the more frequently occurring species, as will be indicated, and it will be recalled that 15 was also the average number of different Strrongylid species per animal. Also from what has been said above, it follows that 17 of the 32 species accounted for less than 1.5 per cent of the total Strongylid fauna. Consequently, in respect to their abundance, the Strongylid species fall readily into two groups which have been conveniently designated as the "commoner" and "rarer" species. These species and their abundance, together with a summary of data upon their localization and incidence, are presented in Table 1.

This table gives the rank, in abundance, of each species and the data from which these positions were determined. In order to facilitate comparisons, percentages have been employed to indicate the distribution of the specimens of each species although the ranks representing the relative abundance of the several species from the different regions have, of course, been determined from the actual numbers of worms.

In order to avoid unnecessary repetitions of specific names and comparative data, there have also been included in Table 1, certain information which shall be utilized in later discussions.

It may be observed, in addition to what has already been said about the abundance of species, that a large proportion of the Strongylid fauna is accounted for by relatively few of the commonest species. For example, *C. nassatus*, constituted about 1/5 of this fauna. This species and *C. longibursatus*, together, accounted for about one third. These two and *C. calicatus* represented about ½, and, proceeding further, it has been calculated that less than 1/5 of the Strongylid species (the 6 commonest) accounted for about 4/5 of the fauna.

Incidence of species

Of the *Strongylidae*, it may be observed in Table 1 that 15 species, coinciding exactly with the 15 more abundant species, were taken from more than half of the animals, while 17 were taken from less than half. Moreover, 11 of these "commoner' species occured in over three-fourths of these equines, while 13 of the "rarer" species occurred in less than one-fourth. Every species occurred at least twice, although only two specimens each were recovered of *C. mucronatum*, *C. brevicapsulatus* and *C. asymetricum*.

TABLE 1.—*An arrangement of the species of Strongylidae in the order of their abundance, giving comparative data upon their localization and incidence*

Species	Abundance		Localization						Preferred Habitat	Incidence				
			Cecum		Ventral C.		Dorsal C.							
	No. Spec.	Rank	%	Rank	%	Rank	%	Rank		No. Pos.	Rank	% Pos.	Horses Pos. (%)	Mules Pos. (%)
The "commoner" species														
Cylicocyclus nassatus	7677	1	5	3	94	1	1	4	VC	40	5	83	82	84
Cylicostephanus longibursatus	7178	2	+	12	2	12	98	1	DC	46	2	96	100	95
C. calicatus	5388	3	5	4	94	2	1	6	VC	39	6	81	76	84
Strongylus vulgaris	4200	4	96	1	3	11	1	12	C	48	1	100	100	100
Cylicostephanus minutus	3933	5	1	7	98	3	1	9	VC	37	7	77	71	81
Cylicocercus catinatus	3095	6	2	6	96	4	2	5	VC	43	3	90	100	84
Cylicocyclus insigne	2272	7	+	11	4	15	96	2	DC	31	9	65	65	64
Cylicocercus goldi	1509	8	+	13	1	22	99	3	DC	43	3	90	94	87
Cyathostomum coronatum	1055	9	91	2	9	13	+	17	C	39	6	81	82	81
C. labiatum	1009	10	+	12	99	5	1	15	VC	26	12	54	53	55
Cylicocercus pateratus	848	11	+	13	99	6	1	13	VC	29	11	61	47	68
Triodontophorus minor	668	12	..	..	89	7	11	7	VC	32	8	81	100	71
Cyathostomum labratum	543	13	1	10	97	8	2	14	VC	30	10	63	47	71
Strongylus edentatus	430	14	15	6	84	9	1	17	VC	41	4	85	94	81
S. equinus	340	15	72	5	27	14	1	21	C	41	4	85	88	84
The "rarer" species														
Cylicocyclus leptostomus	180	16	2	11	96	10	2	17	VC	20	14	42	35	46
Triodontophorus serratus	74	17	37	8	63	16	...	–	VC	22	13	46	88	22
Poteriostomum imparidentatum	64	18	...	–	...	–	100	8	DC	10	17	21	29	16
Cylicostephanus hybridus	46	19	4	12	96	17	...	–	VC	5	20	10	18	6
Triodontophorus tenuicollis	42	20	...	–	86	18	14	16	VC	13	16	27	53	13
Poteriostomum ratzii	35	21	...	–	3	25	97	10	DC	17	15	35	59	22
Cylicodontophorus euproctus	30	22	...	–	...	–	100	11	DC	6	19	13	35	...
Cylicocyclus radiatus	26	23	...	–	96	19	4	19	VC	7	18	15	24	10
Triodontophorus brevicauda	16	24	...	–	94	20	6	19	VC	7	18	15	12	16
Cylicostephanus poculatus	11	25	100	9	...	–	...	–	C	4	21	8	18	3
Cylicodontophorus bicoronatus	9	26	...	–	100	21	...	–	VC	7	18	15	18	13
C. ultrajectinus	9	26	...	–	...	–	100	15	DC	6	19	13	24	6
Gyalocephalus capitatus	7	27	...	–	100	23	...	–	VC	4	21	8	24	...
Cylicocyclus elongatus	7	27	29	12	57	24	14	19	..	5	20	10	12	10
Craterostomum mucronatum	2	28	...	–	...	–	100	18	DC	2	22	4	6	3
Cylicobrachytus brevicapsulatus	2	28	...	–	...	–	100	18	DC	2	22	4	12	...
Cylicotetrapedon asymetricum	2	28	...	–	50	25	50	19	..	2	22	4	6	3

Of the extra-*Strongylidae*, none were rare, although only the stomach worms as a group (*Habronema* spp.) and *P. vivipara* may be considered to have been common.

Host-preferences.

Our observations have indicated that, in general, both horses and mules are good natural hosts for the majority of the species encountered. There were, however, 3 species which were found only in horses; viz., *G. capitatus*, *C. brevicapsulatus*, and *C. euproctus*. Also three of the *Triodontophorus* species (excepting *T. brevicauda*) and *P. ratzii* were recovered from a significantly greater percentage of horses than mules. No species were found exclusively in mules, although *C. labratum* showed a slightly greater incidence in this host.

Of the extra-*Strongylidae*, it appears that the horse was the slightly favored host by *O. equi* while *H. microstoma* was found in a much larger percentage of mules than horses.

Host-localization of Strongylid species.

Eight species (one fourth of the total) were recovered exclusively from one region of the large bowel. *C. poculatus* was found only in the cecum, *G. capitatus* and *C. bicoronatus* only in the ventral colon, and *C. mucronatum*, *P. imparidentatum*, *C. brevicapsulatus*, *C. euproctus*, and *C. ultrajectinus* only from the dorsal colon. Eight other species (another fourth) were taken only from two adjoining portions of the large bowel. By reference to Table 1, it may be noted that *T. serratus* and *C. hybridus* were taken from both the cecum and ventral colon. Similarly, 3 *Triodontophorus* species, *P. ratzii*, *C. asymetricum*, and *C. radiatus* were each taken from both the ventral and dorsal colon, but never from the cecum. The other 16 species, exactly half, and including most of the "commoner" ones, occurred at one time or another in all three regions. These considerations, although interesting, do not, however, emphasize adequately the extent to which the several species were observed to be localized in a single region. In 25 of the 32 species, more than 90 per cent of the specimens were concentrated in a single part of the bowel. Moreover, available data indicate that for *every* species there is a preferred or normal localization. There are two instances where our data, by reason of their insufficiency, may be misleading, hence attention is called to them at this point. During this survey, *C. elongatus* occurred but rarely, and only 7 specimens were taken. Their distribution indicated that this species may occur in any part of the bowel, although, contrary to the possible implication of our data, this form, as noted by others (e.g., Theiler) and as observed by us in autopsies of native animals, is essentially a cecal form. In the

other instance, *C. asymetricum,* as mentioned earlier, is probably a dorsal colon species, although during this survey, it was taken once from the dorsal colon and once from the ventral colon.

To summarize further, Table 1 shows that a total of 19 different species occurred, at one time or another in the cecum, that 26 occurred in the ventral colon, and that 27 different species were taken from the dorsal colon. Conversely, it follows that 13 species were not found at any time in the cecum, that 6 species did not occur in the ventral colon, and that 5 never were taken from the dorsal colon. It is usually considered that the ventral colon shows the greatest variety and abundance of fauna, an observation which, in general, is further emphasized by these data, yet when one considers the chance-occurrence of the "rarer" species, it becomes apparent that the dorsal colon has potentially as great a variety of fauna as does the ventral colon. This consideration comes from the fact, mentioned earlier, that the dorsal colon seems to be the remarkable habitat of so many of the "rarer" species. Of the "commoner" species, only 3 are characteristically dorsal colon forms, while of the "rarer" species, there are 7 which enjoy this distinction. The *average* animal, however, showed about twice as many different species in the ventral colon as elsewhere.

Although the data which have been presented, by reason of their quantitative character, leave no doubt that there is a definitely preferred habitat for each of the Strongylid species, there is an additional consideration which ought to be emphasized at this point since it gives even stronger support to these data. Often it has been observed that specimens encountered in regions other than the usual habitat for the species were immature adults or transitional larvae. The counts of such specimens, although relatively few in number, have been included in our data. Frequently, also, larvae and transitional stages of such species as *S. vulgaris, C. calicatus,* and *C. insigne* have been removed from soft nodules of the mucosa and submucosa of regions other than the preferred habitats for these species. Boulenger (1921) noted that *C. insigne* was mainly confined to the posterior colon, an observation which is thoroughly confirmed by our findings, but he noted, in addition, that larvae of this species occurred in the submucosa of the cecum. In keeping with this observation, it has been interesting to find during the present study, that most of the specimens of this species taken from either the cecum or ventral colon were very young adults or transitional larvae. It is true, of course, that these younger stages were also encountered in the dorsal colon, but it has seemed that the absence of the occurrence elsewhere of a proportionate number of adult specimens is significant. It seems very likely that a condition of larval development, paralleling Boulenger's observation in the case of *C. insigne,* may

be equally true of a number of other species. Such findings suggest that the larval stages of some of these species, or possibly all, may be passed in any region of the bowel, and that, after the emergence of the young adults into the lumen of the bowel, there is a migration to that region which one conveniently may call the "preferred habitat." There is need of much investigation along this line, although it has seemed that the facts thus far point to a distinct tendency, on the part of the adult worms of many species to localize in a single region of the bowel. This probably does not apply to certain of the very common species which, in spite of their quantitative concentrations, may be considered as typical of any region of the bowel.

The hypothetical infestation.

In view of what has been said, and in keeping with a desire to present a comprehensive picture of the verminous infestations of these equines, it has seemed natural that one should construct, using average figures of the actual data, an infestation which would represent, concisely and summarily, the findings of this survey. It has been stated that the average number of Strongylid parasites per animal was 849, and that the average in the cecum was 127, in the ventral colon 486, and in the dorsal colon 236. These figures represent the numbers of worms and their distribution which must be assigned to the hypothetical infestation. Moreover, the average number of different Strongylid species per animal was 15, and the average from the cecum was 5, from the ventral colon 11, and from the dorsal colon 6. These figures represent the number and distribution of different species which must be assigned to the hypothetical animal. The selection of the actual species to be assigned to this infestation is not more difficult. One has only to select, from Table 1, the 5 commonest species of the cecum, the 11 commonest from the ventral colon, and the 6 commonest from the dorsal colon. It is apparent from the averages given above that there must be a certain amount of "overlapping" of species, but since this represents precisely the situation which one encounters at every autopsy, there is no difficulty in the selection of these species. In order to determine the quantitative occurrence of the respective species, it is necessary only to divide the total number of specimens of each, taken from the respective regions to which they are assigned in the hypothetical infestation, by the number of animals covered in this survey. In other words, these also are average figures.

In view of these considerations, and since the data from which this infestation is derived are given fully in either the table or discussion, it may be permissible to present, without further comment, this average or so-called "hypothetical" infestation.

The hypothetical infestation

1. Number and distribution of Strongylid parasites.

Total		
849		
Cecum	Ventral colon	Dorsal colon
127	486	236

2. Number and distribution of different species.

Total		
15		
Cecum	Ventral colon	Dorsal colon
5	11	6

3. Hypothetical species, abundance of each, and their localizations.

Cecum	Ventral colon	Dorsal colon
85 *Strongylus vulgaris*	151 *Cylicocylus nassatus*	147 *Cylicostephanus longibursatus*
20 *Cyathostomum coronatum*	105 *Cylicostephanus calicatus*	46 *Cylicocyclus insigne*
7 *Cylicicyclus nassatus*	81 *C. minutus*	32 *Cylicocercus goldi*
6 *Cylicostephanus calicatus*	62 *Cylicocerus catinatus*	2 *Cylicocyclus nassatus*
5 *Strongylus equinus*	21 *Cyathostomum labiatum*	2 *Cylicocerus catinatus*
123	18 *Cylicocercus pateratus*	2 *Cylicostephanus calicatus*
	13 *Triodontophorus minor*	231
	11 *Cyathostomum labratum*	
	8 *Strongylus edentatus*	
	3 *S. vulgaris*	
	3 *Cylicostephanus longibursatus*	
	476	

To make the picture complete, one must add some 33 worms representing 2 species of extra-*Strongylidae*, say, for example, *Habronema muscae* and *Oxyuris equi*, and, in addition, *Probstmayria vivipara*, which was present more often than not.

Considering the manner in which this hypothetical infestation has been derived, it is remarkable that there appears in it only one item which may possibly be considered at variance with the actual data. In Table 1, it can be noted that *Cylicocyclus leptostomus*, a "rarer" species and predominantly localized in the ventral colon when it occurs, was 10th in abundance from this region. In the hypothetical infestation this species does not appear, although the two species (*S. vulgaris* and *C. longibursatus*) which ranked 11th and 12th respectively, do appear. These ranks were, of course, determined from the actual occurrence of these species in this region, the data being as follows; *C. leptostomus* 173, *S. vulgaris* 139, and *C. longibursatus* 120. In all, however, only

180 specimens were taken of the first-named species. It has been felt that, in the first place, these actual differences are not significant (considering the number of animals) and, in the second place, that there are many other reasons, including the fact that the hypothetical infestation was limited to a total of 15 *different* Strongylid species, which, upon consideration, more than justified the selections which have been made.

Finally, there are two further considerations which should be emphasized. In the first place, the quantitative occurrence of the respective species does not equal numerically the total number of worms postulated for the hypothetical imfestation. It does, however, approximate this number within 2 per cent, which is in remarkable agreement with the actual findings, in respect to which it has been pointed out that about 98 per cent of the Strongylid fauna was contained within the 15 commonest species—precisely the species listed in the hypothetical infestation. From this it becomes apparent that an allowance of 19 worms, or 2 per cent, for the occurrence of the "rarer" species, is not only in conformity with the data but is the most accurate postulation of what one might anticipate at autopsy. In the second place, the figures given are below the *true* quantitative infestations of the equines which were studied by us, since *all* of the worms were not recovered and identified. Mentally, the above figures might be uniformly corrected by some common factor—conservatively and amply estimated, perhaps, at about 20 per cent or 30 per cent. There is no reason to believe, however, that any of these considerations or limitations, detract from the scientific usefulness of these data.

Kind of Host and Size of Infestations.

The Strongylid infestations of the 17 horses covered by this survey varied from 36 to 1725 worms each, with an average of 834 per animal. For the 31 mules the range was from 74 to 4124 worms each, with an average of 856 worms per animal. It will be noted that these averages approximate closely the average for the entire series (849), it thus being indicated that both horses and mules are equally good hosts for at least most of the Strongylidae of equines.

Age of host and size of infestations.

It has been interesting to note that the infestations of the 33 animals which were 15 years of age or under ranged from 36 to 4124 worms each and averaged 1053 per animal. On the other hand, the infestations of the 15 animals which were 16 years of age or over varied from 48 to 1659 worms per animal with an average of 396 each. Further subdivisions in these age-groups may be summarized as follows:

Age-groups (yrs.)	No. Animals	Range in Infestation	Average
10 and under	11	163 – 3878	1105
11 to 15	22	36 – 4124	1028
16 to 20	9	168 – 1659	550
over 20	6	48 – 359	164
	48	36 – 4124	849

From these data, it appears that there was a definite trend toward lighter infestations in the older animals. Considering the fact that the animals from which these data are derived were reared under the same conditions throughout, it has seemed that there is indicated, to a rather marked degree, a definite age-resistance after about 15 years of age.

SUMMARY

1. Data have been presented upon the qualitative and quantitative occurrence of the Nematode parasites recovered at autopsy from 48 horses and mules imported into the Panama Canal Zone and owned by the P. C. Dept. of the U. S. Army.

2. In all, 39 Nematode species were recovered, 32 of which were of the family *Strongylidae*. These parasites are reported for the first time from Army equines of the Panama Canal Zone.

3. A discussion of the incidence, abundance, host-localization, and host-preference (horse or mule) of each species has been presented.

4. Most of the Strongylid fauna was accounted for by relatively few of the species. Of the species recovered, 15 were considered as "common" and 17 as "rare." The "common" species accounted for over 98 per cent of the Strongylid fauna.

5. Of the 32 different species of *Strongylidae,* in spite of the fact that all were demonstrated quantitatively to have preferred localizations in the large bowel, there were taken at one time or another 19 different species from the cecum, 26 from the ventral colon, and 27 from the dorsal colon.

6. The Strongylid infestations averaged 849 worms per animal. The number from the cecum averaged 127, from the ventral colon 486, from the dorsal colon 236.

7. There was an average of 15 different Strongylid species per animal. In the cecum the average was 5, in the ventral colon 11, in the dorsal colon 6.

8. There was an average of 2 to 3 species of extra-*Strongylidae* per host, which contributed, on the average, about 33 worms to the infestations.

9. It is believed that the infestations of these animals, as summarized in 6, 7, and 8 above, represent about the minimum practical level attain-

able by the intelligent application of the known methods of prevention and treatment.

10. A hypothetical infestation has been presented which summarizes both qualitatively and quantitatively many of the results of this survey. It also gives the typical Strongylid fauna of the cecum, ventral colon, and dorsal colon, respectively.

11. Horses and mules harbored about the same average infestations, although certain of the species showed a preference for one or the other of these hosts.

12. The older animals, particularly those over 15 years of age, harbored lighter infestations than the younger ones. This was interpreted as an indication of an age-resistance of equines against Strongylid parasites.

13. Larvae of *S. vulgaris,* the agent of verminous aneurysm and arteritis in equines were taken from branches of the Great Mesenteric Artery in 75 per cent of the cases.

14. One parasite, *Cylicostephanus poculatus,* apparently reported previously only from horses, is herein recorded from the mule.

15. A few brief discussions, apart from those already summarized, have been given upon problems of systematics, biological characteristics, economic importance, etc., of some of the parasites encountered.

16. The methods of autopsy and worm-collection which were employed during this study in making a quantitative approach to the study of the equine infestations have been described in detail.

References Cited

Boulenger, Charles L. 1916.—Sclerostome parasites of the horse in England. I. The genera *Triodontophorus* and *Oesophagodontus.* Parasit., 8: 420–439.

1920.—Sclerostomes of the donkey in Zanzibar and East Africa. ibid., 12: 27–32.

1921.—Strongylid parasites of horses in the Punjab. ibid., 13: 315–326.

Cram, Eloise B. 1924.—A new Nematode, *Cylindropharynx ornata,* from the zebra, with keys to related Nematode parasites of the *Equidae.* Jour. Agri. Res., 28: 661–672.

Gough, L. H. 1908.—Notes on South African parasites. An. Rept. of the So. African Assoc. for the Adv. of Sci. (quoted from G. Theiler).

Ihle, J. E. W. 1920.—Een nieuwe *Cylicostomum*—soort (*C. brevicapsulatum*) uit den darm van het paard. Tijdschrift voor Diergeneeskunde, Deel 47, Aflevering 5, 182.

1922.—Over de verdeeling van het geslacht Cylicostomum. ibid., 49: 135–136.

1922a.—Report of the commission appointed to inquire into the sclerostomiasis in Holland. I. Zoological part. Vol. I. The adult Strongylids (Sclerostomes) inhabiting the large intestine of the horse. 118 pp. 131 figs. Nat. Printing office, The Hague.

Looss, A. 1901.—The *Sclerostomidae* of horses and donkeys in Egypt. (With 13 plates). Records of the Egyptian Gov't Faculty of Medicine, Cairo, Egypt. Vol. 1, pp. 21–114.

McIntosh, Allen. 1933.—Equine parasites from Puerto Rico. Jour. Parasit., 20: 110.

Skladnik, Jozef. 1935.—Sur la synonymie des quelques especes de la sous-famille des *Trichonemінae*. Ann. de Parasit., 13: 307–311.

1935a.—*Trichonemінae* u koni w polsce. odb. z. mies. "Wiadomosci Weterynaryjne" No. 177, 137–183. (with 25 plates and French summary).

Theiler, Gertrud. 1923.—The Strongylids and other Nematodes parasitic in the intestinal tract of South African Equines. 9th and 10th Repts. of the Director of Veterinary Education and Research, Dept. of Agri. Un. of So. Africa. April, pp. 603–773.

Wetzel, Rudolf. 1930.—On the biology of the fourth stage larva of *Oxyuris equi* (Schrank). Jour. Parasit., 17: 95–97.

Yorke, W. and J. W. S. Macfie. 1920.—*Strongylidae* in Horses. II. Species found in West Africa and Jamaica. Ann. Trop. Med. Parasit., 14: 165.