Helminths

of Domestic Equids

Illustrated Keys to Genera and Species with Emphasis on North American Forms

J. RALPH LICHTENFELS (Drawings by ROBERT B. EWING)



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Helminths of Domestic Equids

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J. RALPH LICHTENFELS (Drawings by ROBERT B. EWING)

Animal Parasitology Institute, Beltsville Agricultural Research Center, ARS, USDA, Beltsville, Maryland 20705 Dedication

To Allen McIntosh, teacher, friend, and inspiration to many helminthologists

ABSTRACT: Dichotomous keys are provided for genera and species of helminths of domestic equids. Keys to genera are illustrated with halftone drawings, usually of the type species, and they include a generic diagnosis. Keys to species are illustrated with photomicrographs of key characters, but species diagnoses are not provided. Only genera and species occurring in North America are illustrated, but all genera are included in the keys and exotic species are compared with similar illustrated species. The helminths include 75 species in 28 genera of Nematoda, four species in three genera of cestodes, and five species in two genera of trematodes. Systematic revision has been kept to a minimum in this welldefined group of helminths. A history and comparison of systematic schemes is provided. The number of genera in the group sometimes referred to as Cyathostomum, sensu lato, is reduced from seven to four. Keys to species are given for the nematode genera Cyathostomum, Cylicocyclus, Cylicodontophorus, Cylicostephanus, Poteriostomum, Triodontophorus, Strongylus, Habronema, and Onchocerca, and for the four species of cestodes. Synonyus of all species are listed along with information on geographic distribution, prevalence, and location in the host. Separate lists are provided of: (1) unusual, accidental, or occasional helminths of domestic equids; and (2) helminths from zebras that do not also occur in other equids. Illustrations of larvae and discussion of life histories are given in a separate section, but little is known of most species. A detailed index is provided of all scientific names used.

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The horse, Equus caballus, the ass, Equus asinus, and their hybrids are hosts to a great variety of helminth parasites, most of which have traveled the world with their hosts. Nematodes are represented by 28 genera and 75 species, cestodes by three genera and four species, and trematodes by two genera and five species. Many others are occasionally found in horses.

The recent increase in numbers of horses in the United States has caused in turn a resurgence of interest in the unwelcome worms that share their table, sap their energy, and sometimes kill their hosts, although usually more insidiously than infectious disease organisms. This increased attention to helminths of horses has resulted in the need for diagnostic keys to these parasites using readily recognizable characters and the most recent literature on their systematics.

This treatise is intended to serve as a basic working tool—providing easy identifications to genus and species of adult helminths of equids. Only helminths normally parasitic in the horse, the ass, and their hybrids are covered. Helminths of zebras that are not parasites of other equids are listed in a separate section as are helminths that are occasionally found in horses, mules, and asses but are normally parasitic in other animals. Some illustrations of nematode larvae are given in a section following the keys to species, but little information is available and many larvae cannot be identified (sometimes not even to genus) because of the lack of life cycle studies of most species.

This treatise consists of illustrated keys to genera and to species. The keys to genera are illustrated with halftone drawings of the type species of each genus and include a diagnosis of the genus. For genera with only a single species in equids, a diagnosis of the species is given instead of the genus. Illustrations are original unless noted otherwise.

The keys to genera include all known genera of helminths of equids anywhere in the world: however, exotic genera-not known to occur in North America—usually are not illustrated because specimens were not available. Keys to species known to occur in North America are illustrated with photomicrographs of key characters-usually buccal and cephalic characters-that will identify both males and females. Exotic species are usually not included in the keys to species, but are listed at the end of the key with a brief comparison to illustrated species. A short discussion of the systematics of the genus and species is provided. The most available diagnoses of species are cited in the keys to species, and complete species diagnoses are not given in this treatise. A synonymy of each species is provided in the Outline Classification, and authors and dates of species are given only there and in the Index. Geographic distribution, prevalence, and location in host are also given for each species in the Outline Classification.

Some workers will lament that most exotic genera and species have not been illustrated or included in the keys to species. For a host like the horse that has traveled much of the world with man this may appear to be a major shortcoming; however, species absent from North America are not commonly found in other parts of the world either, and any disadvantage attributable to the omission of the exotic and usually rare species from the keys is outweighed by their greater simplicity. It should be possible to differentiate exotic species from similar illustrated species by using the brief comparisons that follow the keys.

Although this treatise will provide no information on pathology, control, or treatment, it is hoped that progress in these areas may be spurred by facilitating identification of the helminths.

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II. Materials and Methods

The writer made no collections of helminths directly from hosts for this study. Specimens were obtained from the USDA Parasite Collection, from the USNM Helminthological Collection, and from workers currently engaged in studies of helminths of equids at various laboratories in the United States. Specimens from the USNM Helminthological Collection included many paratypes from Looss' (1900) type series. The A. O. Foster collection (Foster, 1936, 1937; Foster and Ortiz, 1937; Foster and Alicata, 1939), consisting for the most part of large numbers of accurately identified specimens, was invaluable in this study. Numerous specimens, especially larvae, were supplied by K. C. Kates and M. L. Colglazier of this institute. Other individuals and laboratories that provided specimens are listed in the Acknowledgments. Usually large numbers of specimens were available for study. *En face* mounts of a few species were studied.

Nematodes were cleared for study in temporary wet mounts in a solution of 80% melted phenol crystals and 20% absolute alcohol. Photomicrographs were taken with the aid of a 35-mm camera and a microscope equipped with a differential interference contrast attachment.

Drawings were made with the aid of a camera lucida. Final rendering of the drawings involved a pencil tone technique.

III. Outline Classification of Helminths of Domestic Equids, Their Geographic Distribution, Prevalence, Location in Host, and Synonyms

The species are listed by genus and higher categories. Each species is followed by its geographic distribution, location in host, and a list of its synonyms. Geographic distribution is given by continent or as cosmopolitan and may be abbreviated. An asterisk precedes names of species not known to occur in North America.

The classification for nematodes follows B. G. Chitwood (Chitwood and Chitwood, 1950, reprinted 1974) and M. B. Chitwood (1969) above generic level. The classification of genera and species of Nematoda is modified from previous systems and is discussed further in the introduction to the Nematoda given in this treatise. The classification system for cestodes and trematodes follows Yamaguti (1959, 1971).

> Phylum Nematoda Order Rhabditida Suborder Rhabditina Family Cephalobidae

- Micronema deletrix Anderson and Bemrick, 1965
- Rare—N. A.; Afr.—nares; brain *Rhabditis gingivalis Stefanski, 1954
 - Very Rare—Eur.—gums

Family Strongyloididae

Strongyloides westeri Ihle, 1917 Common in foals—cosmopolitan—small intestine

> Order Strongylida Suborder Strongylina Family Strongylidae Subfamily Strongylinae

Ocsophagodontus robustus (Giles, 1892) Railliet and Henry, 1902

Rare—cosmopolitan—colon

- =Sclerostoma robustum Giles, 1892
- =Pseudosclerostomum securiferum Quiel, 1919
- =Strongylus robustus (Giles, 1892) Popov, 1927
- Triodontophorus serratus (Looss, 1900) Looss, 1902

Rare—cosmopolitan—colon

- =Triodontus serratus Looss, 1900
- =Triodontophorus intermedius Sweet, 1909
- Triodontophorus minor (Looss, 1900) Looss, 1902

?Common—cosmopolitan—colon

=Triodontus minor Looss, 1900

Triodontophorus tenuicollis Boulenger, 1916 Rare—cosmopolitan—colon Triodontophorus brevicauda Boulenger, 1916 Rare-cosmopolitan-colon Triodontophorus nipponicus Yamaguti, 1943 Common-Eur., N. A., S. A., Asia-colon *Triodontophorus popovi Ershov, 1931 Rare—Asia—colon *Triodontophorus brochotribulatus Martinez Gomez, 1966 Rare—Eur.—colon Strongylus equinus Mueller, 1780 Common—cosmopolitan—cecum =Strongylus equorum Zeder, 1800 =Strongylus armatus Rudolphi, 1802, in part =Strongylus neglectus Poeppel, 1897 =Sclerostoma equinum (Mueller, 1780) Blainville, 1828 =Sclerostomum quadridentatum Sticker. 1901, not Dujardin, 1845 Strongylus edentatus (Looss, 1900) Railliet and Henry, 1909 Common-cosmopolitan-colon =Sclerostoma edentatum Looss, 1900 =Alfortia edentatus (Looss, 1900) Skrjabin, 1933 Strongylus vulgaris (Looss, 1900) Railliet and Henry, 1909 Very common—cosmopolitan—cecum =Sclerostoma vulgare Looss, 1900 =Strongylus armatus Rudolphi, 1802, in part =Sclerostomum bidentatum Sticker, 1901 =Delafondia vulgaris (Looss, 1900) Skrjabin, 1933 *Strongylus asini Boulenger, 1920 Rare—Asia, Afr., S. A.—cecum, liver =Delafondia asini (Boulenger, 1920) Skrjabin, 1933 Craterostomum acuticaudatum (Kotlan, 1919) Ihle, 1920 Rare-Afr., Asia, Eur., N. A.-colon, cecum =Cylicostomum acuticaudatum Kotlan, 1919 =Cylicostomum mucronatum Ihle, 1920 =Craterostomum mucronatum (Ihle, 1920) Ihle, 1920

*Craterostomum tenuicauda Boulenger, 1920 Very rare—Eur., Asia—colon, cecum

Subfamily Globocephalinae

- *Acheilostoma paranecator Travassos and Horta, 1915
 - Very rare—S. A.—intestine

Subfamily Cyathostominae

- Cyathostomum tetracanthum (Mehlis, 1831) Molin, 1861, in part, Looss, 1900
 - Rare-cosmopolitan-cecum, colon
 - =Strongylus tetracanthus Mehlis, 1831, in part
 - =Sclerostomum tetracanthum (Mehlis, 1831) Diesing, 1851, in part
 - =Cylichnostomum tetracanthum (Mehlis, 1831) Looss, 1902
 - =Cylicostomum tetracanthum (Mehlis, 1831) Gedoelst, 1903
 - =Cylicostoma tetracanthum (Mehlis, 1831) Looss, 1911
 - =Trichonema tetracanthum (Mehlis, 1831) Railliet, 1919
 - *=Trichonema arcuata* Cobbold, 1874, in part
 - =Trichonema aegyptiacum Railliet, 1923
 - =Cylicostomum aegyptiacum (Railliet, 1923) Cram, 1924
 - =Cylicostomias aegyptiaca (Railliet, 1923) Cram, 1925
 - *Erschowinema aegyptiacum* (Railliet, 1923) Tshoijo, 1957
 - =Sclerostoma quadridentatum Dujardin, 1845, in part

Cyathostomum coronatum Looss, 1900 Common—cosmopolitan—cecum, colon

- =Cylichnostomum coronatum (Looss, 1900) Looss, 1902
- =Cylicostomum coronatum (Looss, 1900) Gedoelst, 1903
- =Trichonema coronatum (Looss, 1900) Le-Roux, 1924
- =Cylicostomias coronata (Looss, 1900) Cram, 1925
- *Erschowinema coronatum* (Looss, 1900) Tshoijo, 1957
- =Trichonema subcoronatum Yamaguti, 1943

^{*}Species not known to occur in North America.

- Cyathostomum labiatum (Looss, 1902) Mc-Intosh, 1933
 - Common-cosmopolitan-cecum, colon
 - =Cyathostomum labratum Looss, 1900, in part
 - =Cylichnostomum labiatum Looss, 1902
 - =Cylicostomum labiatum (Looss, 1902) Gedoelst, 1903
 - =Cylicostomum labiatum digitatum Ihle, 1921
 - =Trichonema labiatum (Looss, 1902) Le-Roux, 1924
 - =Cylicostomias labiatum (Looss, 1902) Cram, 1925
 - =Schulzitrichonema labiatum (Looss, 1902) Barus, 1961
- Cyathostomum labratum Looss, 1900
 - Common—cosmopolitan—cecum, colon
 - =Cylichnostomum labratum (Looss, 1900) Looss, 1902
 - =Cylicostomum labratum (Looss, 1900) Gedoelst, 1903
 - =Trichonema labratum (Looss, 1900) Le-Roux, 1924
 - =Cylicostomias labrata (Looss, 1900) Cram, 1925
 - =Schulzitrichonema labratum (Looss, 1900) Barus, 1962
- *Cyathostomum alveatum Looss, 1900 Rare—Afr., Asia, Eur.—cecum, colon
 - =Cylichnostomum alveatum (Looss, 1900) Looss, 1902
 - =Cylicostomum alveatum (Looss, 1900) Gedoelst, 1903
 - =Cylicocercus alveatus (Looss, 1900) Cram, 1924
 - =Trichonema alveatum (Looss, 1900) Yorke and Maplestone, 1926
 - =Erschowinema alveatum (Looss, 1900) Tshoijo, 1957
- Cyathostomum pateratum (Yorke and Macfie, 1919) K'ung, 1964
 - Common-cosmopolitan-cecum, colon
 - =Cylicostomum pateratum Yorke and Macfie, 1919
 - =Trichonema pateratum (Yorke and Macfie, 1919) LeRoux, 1924
 - =Cylicocercus pateratus (Yorke and Macfie, 1919) Cram, 1924
 - =Cylicodontophorus pateratus (Yorke and Macfie, 1919) Ershov, 1939
 - =Cylicostomum cymatostomum Kotlan, 1919

Cyathostomum catinatum Looss, 1900

- Very common—cosmopolitan—cecum, colon
- =Cylichnostomum catinatum (Looss, 1900) Looss, 1902
- =Cylicostomum catinatum (Looss, 1900) Gedoelst, 1903
- =Trichonema catinatum (Looss, 1900) Le-Roux, 1924
- =Cylicocercus catinatum (Looss, 1900) Cram, 1924
- *Erschowinema catinatum* (Looss, 1900) Tshoijo, 1957
- =Cylicostomum pseudocatinatum Yorke and Macfie, 1919
- =Cylicostomum catinatum litoraureum Yorke and Macfie, 1920
- *Cyathostomum montgomeryi (Boulenger, 1920) K'ung, 1964
 - Rare-Afr.-cecum, colon
 - =Cylicostomum montgomeryi Boulenger, 1920
 - =Cylicotoichus montgomeryi (Boulenger, 1920) Cram, 1924
 - =*Trichonema montgomeryi* (Boulenger, 1920) Yorke and Maplestone, 1926
 - =Erschowinema montgomeryi (Boulenger, 1920) Tshoijo, 1957
- *Cyathostomum sagittatum (Kotlan, 1920) McIntosh, 1951
 - Rare—Eur., Asia—cecum, colon
 - =Cylicostomum sagittatum Kotlan, 1920
 - =Trichonema sagittatum (Kotlan, 1920) Le-Roux, 1924
 - =Cylicostomias sagittatum (Kotlan, 1920) Cram, 1925
 - =Cylicodontophorus sagittatum (Kotlan, 1920) Ershov, 1939
- Cylicodontophorus bicoronatus (Looss, 1900) Cram, 1924
 - Common—cosmopolitan—cecum, colon
 - =Cyathostomum bicoronatum Looss, 1900
 - =Cylichnostomum bicoronatum (Looss, 1900) Looss, 1902
 - =Cylicostomum bicornatum (Looss, 1900) Gedoelst, 1903
 - =Trichonema bicoronatum (Looss, 1900) LeRoux, 1924

*Species not known to occur in North America.

- Cylicodontophorus euproctus (Boulenger, 1917) Cram, 1924 Rare-cosmopolitan-colon, cecum =Cylichnostomum euproctus Boulenger, 1917=Cylicostomum euproctus (Boulenger, 1917) Ransom and Hadwen, 1918 =Trichonema euproctus (Boulenger, 1917) LeRoux, 1924 Cylicodontophorus mettami (Leiper, 1913) Foster, 1936 Very rare—Afr., Asia, Eur., N. A.—colon, cecum =Cylicostoma mettami Leiper, 1913 =Cylicostomum mettami (Leiper, 1913) Ransom and Hadwen, 1918 =Trichonema mettami (Leiper, 1913) Le-Roux, 1924 1913)=Cylicocercus mettami (Leiper, Cram, 1924 =Cylicostomum ihlei Kotlan, 1921 Cylicocyclus radiatus (Looss, 1900) Chaves, 1930 Rare—cosmopolitan—colon =Cyathostomum radiatum Looss, 1900 =Cylichnostomum radiatum (Looss, 1900) Looss, 1902 $=Cylicostomum \ radiatum \ (Looss, 1900)$ Gedoelst, 1903 =Trichonema radiatum (Looss, 1900) Le-Roux, 1924 =Cylicostomum prionodes Kotlan, 1921 Cylicocyclus auriculatus (Looss, 1900) Chaves, 1930Rare-Afr., Asia, N. A., S. A.-colon =Cyathostomum auriculatum Looss, 1900=Cylichnostomum auriculatum (Looss, 1900) Looss, 1902 =Cylicostomum auriculatum (Looss, 1900) Gedoelst, 1903 =Trichonema auriculatum (Looss, 1900) LeRoux, 1924 Cylicocylus elongatus (Looss, 1900) Chaves, 1930 Common—cosmopolitan—cecum =Cyathostomum elongatum Looss, 1900 =Cylichnostomum elongatum (Looss, 1900) Looss, 1902 =Cylicostomum elongatum (Looss, 1900) Gedoelst, 1903
 - =Trichonema elongatum (Looss, 1900) Le-Roux, 1924

- =Cylicostomum elongatus kotlani Ihle, 1920
- =Cylicostomum elongatus macrobursatum Kotlan, 1920
- Cylicocyclus nassatus (Looss, 1900) Chaves, 1930
 - Very common—cosmopolitan—colon
 - =Cyathostomum nassatum Looss, 1900
 - =Cylichnostomum nassatum (Looss, 1900) Looss, 1902
 - =Cylicostomum nassatum (Looss, 1900) Gedoelst, 1903
 - =Trichonema nassatum (Looss, 1900) Le-Roux, 1924
 - =Trichonema ashworthi LeRoux, 1924
 - =Cylicocyclus bulbiferus Chaves, 1930
 - =Cylicostomum nassatum parvum Yorke and Macfie, 1918
- Cylicocyclus insigne (Boulenger, 1917) Chaves, 1930

Very common—cosmopolitan—colon

- =Cylichnostomum insigne Boulenger, 1917
- =Cylicostomum insigne (Boulenger, 1917) Ransom and Hadwen, 1918
- =Trichonema insigne (Boulenger, 1917) Le-Roux, 1924
- =Trichonema insigne rosenbuschi Galofre and Rosa, 1944
- =Cylicostomum zebrae Boulenger, 1920
- Cylicocyclus leptostomus (Kotlan, 1920) Chaves, 1930
 - Common—Afr., Asia, Eur., N. A.—cecum, colon
 - =Cylicostomum leptostomum Kotlan, 1920
 - =Trichonema leptostomum (Kotlan, 1920) LeRoux, 1924
 - =Schulzitrichonema leptostomum (Kotlan, 1920) Ershov, 1943
 - =Cylicotetrapedon leptostomum (Kotlan, 1920) K'ung, 1964
 - =Cyathostomum bogoriense Smit and Notosoediro, 1923
- Cylicocyclus ultrajectinus (Ihle, 1920) Ershov, 1939

Common-cosmopolitan-colon

- =Cylicostomum ultrajectinum Ihle, 1920
- =Trichonema ultrajectinum (Ihle, 1920) LeRoux, 1924
- =Cylicodontophorus ultrajectinum (Ihle, 1920) Cram, 1924

Cylicocyclus triramosus (Yorke and Macfie, 1920) Chaves, 1930 Rare—Afr., Asia, N. A.—colon, Pstomach =Cylicostomum triramosum Yorke and Macfie, 1920 =Trichonema triramosum (Yorke and Macfie, 1920) LeRoux, 1924 Cylicocyclus brevicapsulatus (Ihle, 1920)Ershov, 1939 Very rare-Afr., Asia, Eur., N. A.-colon =Cylicostomum brevicapsulatum Ihle, 1920 =Cylicobrachytus brevicapsulatum (Ihle, 1920) Cram, 1924 =Trichonema brevicapsulatum (Ihle, 1920) Mönnig, 1926 *Cylicocyclus adersi (Boulenger, 1920) Chaves, 1930Rare—Afr., Asia—colon =Cylicostomum adersi Boulenger, 1920 =Trichonema adersi (Boulenger, 1920) Le-Roux, 1924 *Cylicocyclus largocapsulatus (Iren, 1943) n. comb. Very rare—Asia—colon =Trichonema largocapsulatus Iren, 1943 *Cylicocyclus matumurai (Yamaguti, 1942) n. comb. Very rare—Asia—colon =Trichonema maturmurai Yamaguti, 1942 Cylicostephanus calicatus (Looss, 1900) Cram, 1924Very common—cosmopolitan—colon =Cyathostomum calicatum Looss, 1900 =Cylichnostomum calicatum (Looss, 1900) Looss, 1902 $=Cylicostomum \ calicatum \ (Looss, 1900)$ Gedoelst, 1903 =Trichonema calicatum (Looss, 1900) Le-Roux, 1924 =Erschowinema calicatum (Looss, 1900) Tshoijo, 1957 =Cylicostomum barbatum Smit and Notosoediro, 1923 =Trichonema tsengi K'ung and Yang, 1963 Cylicostephanus poculatus (Looss, 1900)Cram, 1924 Rare—cosmopolitan—colon, cecum =Cyathostomum poculatum Looss, 1900 =Cylichnostomum poculatum (Looss, 1900) Looss, 1902 $=Cylicostomum \ poculatum \ (Looss, 1900)$

=Cylicostomum poculatum (Looss, 1900) Gedoelst, 1903 =Trichonema poculatum (Looss, 1900) Le-Roux, 1924

- =Petrovinema poculatum (Looss, 1900) Ershov, 1943
- Cylicostephanus minutus (Yorke and Macfie, 1918) Cram, 1924
 - Very common—cosmopolitan—colon, cecum
 - =Cylicostomum minutum Yorke and Macfie, 1918
 - =Trichonema minutum (Yorke and Macfie, 1918) LeRoux, 1924
 - =Erschowinema minutum (Yorke and Macfie, 1918) Tshoijo, 1957
- Cylicostephanus longibursatus (Yorke and Macfie, 1918) Cram, 1924
 - Very common—cosmopolitan—colon, cecum
 - =Cylicostomum longibursatum Yorke and Macfie, 1918
 - =Trichonema longibursatum (Yorke and Macfie, 1918) LeRoux, 1924
 - =Cylicostomum nanum Ihle, 1919
 - =Cylicostomum calicatiforme Kotlan, 1919
- Cylicostephanus asymetricus (Theiler, 1923) Cram, 1925
 - Very rare—Afr., Asia, Eur., N. A.—cecum, colon
 - =Cylicostomum asymetricum Theiler, 1923
 - =Cylicotetrapedon asymetricum (Theiler, 1923) Ihle, 1925
 - =Schulzitrichonema asymetricum (Theiler, 1923) Ershov, 1943
 - =Erschowinema asymetricum (Theiler, 1923) Tshoijo, 1957
- Cylicostephanus bidentatus (Ihle, 1925) n. comb.
 - Very rare—Eur., N. A.—colon
 - =Cylicostomum bidentatum Ihle, 1925
 - =Cylicotetrapedon bidentatum (Ihle, 1925) Ihle, 1925
 - *=Trichonema bidentatum* (Ihle, 1925) Yorke and Maplestone, 1926
 - =Schulzitrichonema bidentatum (Ihle, 1925) Barus, 1963

*Species not known to occur in North America.

- Cylicostephanus hybridus (Kotlan, 1920) Cram, 1924
 - Rare—Asia, Eur., N. A., S. A.—colon, cecum
 - =Cylicostomum hybridum Kotlan, 1920
 - *=Trichonema hybridum* (Kotlan, 1920) Le-Roux, 1924
 - =Erschowinema hybridum (Kotlan, 1920) Tshoijo, 1957
 - =Schulzitrichonema hybridum (Kotlan, 1920) Barus, 1963
 - =Trichonema parvibursatus Vaz, 1934
- Cylicostephanus goldi (Boulenger, 1917) n. comb.
 - Common—cosmopolitan—colon, cecum
 - =Cylichnostomum goldi Boulenger, 1917 =Culicostomum goldi (Boulenger, 1917)
 - Ransom and Hadwen, 1918
 - *=Trichonema goldi* (Boulenger, 1917), Le-Roux, 1924
 - =Cylicocercus goldi (Boulenger, 1917) Cram, 1924
 - =Schulzitrichonema goldi (Boulenger, 1917) Ershov, 1943
 - =Cylicotetrapedon goldi (Boulenger, 1917) K'ung, 1964
 - =Cylicostomum tridentatum Yorke and Macfie, 1920
- *Cylicostephanus ornatus (Kotlan, 1919) n. comb.
 - Rare—Eur., ?Asia, ?N. A.—colon, cecum =Cylicostomum ornatum Kotlan, 1919
 - =Trichonema ornatum (Kotlan, 1919) Le-Roux, 1924
 - =Cylicostomias ornatum (Kotlan, 1919) Cram, 1925
 - =Cyathostomum ornatum (Kotlan, 1919) McIntosh, 1933
 - =Cylicodontophorus ornatum (Kotlan, 1919) Ershov, 1939
- *Cylicostephanus skrjabini (Ershov, 1930) n. comb.

- =Trichonema skrjabini Ershov, 1930
- =Petrovinema skrjabini Ershov, 1943
- Poteriostomum imparidentatum Quiel, 1919 Common—cosmopolitan—colon, cecum
 - =Cylicostomum imparidentatum (Quiel, 1919) Ihle, 1920
 - =Cylichnostomum imparidentatum (Quiel, 1919) Vevers, 1920

=Poteriostomum pluridentatum Quiel, 1919

=Cylicostomum zebrae Turner, 1920

- =Hexodontostomum markusi Ihle, 1920 Poteriostomum ratzii (Kotlan, 1919) Ihle, 1920 Common—cosmopolitan—colon, cecum
 - =Cylicostomum ratzii Kotlan, 1919
 - =Cylichnostomum ratzii (Kotlan, 1919) Yorke and Macfie, 1920
 - =Craterostomum ratzii (Kotlan, 1919) Ostertag, 1932
 - =Poteriostomum ratzii nanum Theiler, 1923
- *Poteriostomum skrjabini Ershov, 1939 Rare—Asia—colon, cecum
- Gyalocephalus capitatus Looss, 1900 Rare—cosmopolitan—cecum, colon
 - =Gyalocephalus equi Yorke and Macfie, 1918
- *Caballonema longicapsulatum Abuladze, 1937 Very rare—Asia—cecum, colon
 - =Caballonema longispiculata Kopyrin and Burikova, 1940
 - =Sinostrongylus longibursatus Hsiung and Chao, 1949
- *Cylindropharynx aethiopica Roetti, 1947 Very rare—Asia—cecum, colon
- *Cylindropharynx asini Roetti, 1947 Very rare—Asia—cecum, colon

Suborder Trichostrongylina Family Trichostrongylidae Subfamily Trichostrongylinae

- Trichostrongylus axei (Cobbold, 1879) Railliet and Henry, 1909
 - Common—cosmopolitan—stomach
 - =Strongylus axei Cobbold, 1879
 - =Strongylus extenuatus Railliet, 1898
 - =Strongylus tenuissimus Mazzanti, 1891
 - =Strongylus gracilis McFadyean, 1896 (not Leuckart, 1842)
 - =Cobboldostrongylus axei (Cobbold, 1879) Sarwar, 1956

Family Dictyocaulidae Subfamily Dictyocaulinae

- Dictyocaulus arnfieldi (Cobbold, 1884) Railliet and Henry, 1907
 - Rare—cosmopolitan—lungs
 - =Strongylus arnfieldi Cobbold, 1884
 - =Arnfieldia arnfieldi (Cobbold, 1884) Sarwar, 1957

Rare—Asia—colon, cecum

^{*}Species not known to occur in North America.

Order Ascarida Suborder Ascaridina Family Ascarididae Subfamily Ascaridinae

- Parascaris equorum (Goeze, 1782) Yorke and Maplestone, 1926
 - Common in foals, rare in adults-cosmopolitan—small intestine
 - =Ascaris equorum Goeze, 1782
 - =Ascaris equi Schrank, 1788
 - =Fusaria lumbricoides equorum Zeder, 1800
 - =Ascaris gigas equi Rudolphi, 1809
 - =Ascaris megalocephala Cloquet, 1824
 - =Ascaris laevissima Baird, 1853

Suborder Oxyurina Family Oxyuridae Subfamily Oxyurinae

- Oxyuris equi (Schrank, 1788) Rudolphi, 1803 Common—cosmopolitan—colon
 - =Trichocephalus equi Schrank, 1788
 - =Oxyuris curvula Rudolphi, 1803
 - =Oxyuris mastigodes Nitzsch, 1857
- =Lepturis curvula (Rudolphi, 1803) Schlotthauber, 1860
- *Oxyuris poculum Linstow, 1904 Very rare—Ceylon—colon

Subfamily Probstmayriinae

- Probstmayria vivipara (Probstmayr, 1865) Ransom, 1907
 - Very common—cosmopolitan—colon
 - =Oxyuris vivipara Probstmayr, 1865
 - =Rhabdonema vivipara (Probstmayr, 1865) Railliet, 1887
 - =Anguillula vivipara (Probstmayr, 1865) Railliet, 1893
 - =Strongyloides vivipara (Probstmayr, 1865) Linstow, 1905

Order Spirurida Suborder Spirurina Family Spiruridae Subfamily Habronematinae

Draschia megastoma (Rudolphi, 1819) Rare-cosmopolitan-stomach =Spiroptera megastoma Rudolphi, 1819

- =Spirura megastoma (Rudolphi, 1819)Blanchard, 1849
- 1819)(Rudolphi, =Filaria megastoma Schneider, 1866
- =Habronema megastoma (Rudolphi, 1819) Railliet, 1923

Habronema muscae (Carter, 1861) Diesing, 1861Common—cosmopolitan—stomach =Filaria muscae Carter, 1861 =Filaria stomoxeos Linstow, 1875 =Dermofilaria irritans Rivolta, 1884 Habronema majus (Creplin, 1849) Ransom, 1911 Common-cosmopolitan-stomach =Spiroptera megastoma major Creplin, 1849 =Filaria microstoma Schneider, 1866 =Spiroptera microstoma (Schneider, 1866) Zurn, 1872 *Habronema tyosenense Yamaguti, 1943 Very rare—Asia—stomach Family Thelaziidae Subfamily Thelaziinae Thelazia lacrymalis (Gurlt, 1831) Railliet and Henry, 1910 Very rare—Asia, Eur., S. A.—eye =Filaria lacrymalis Gurlt, 1831 =Filaria palpebralis Wilson, 1844 Suborder Filariina Family Onchocercidae Subfamily Onchocercinae *Elaeophora boehmi Supperer, 1953 Rare-Eur.-arteries, veins Onchocerca reticulata Diesing, 1841 Rare-cosmopolitan-tendons, ligaments =Spiroptera reticulata (Diesing, 1841) Railliet, 1885 =Spiroptera cincinnata Ercolani, 1866 =Filaria reticulata (Diesing, 1841) Creplin, 1846 =Trichina reticulata (Diesing, 1841) Creplin, 1841Onchocerca cervicalis Railliet and Henry, 1910 Common—cosmopolitan—cervical ligaments Family Setariidae Subfamily Setariinae Setaria equina (Abildgaard, 1789) Railliet and Henry, 1911 Very common-cosmopolitan-body cavity, mesenteries, eye, and many other sites =Gordius equinus Abildgaard, 1789 =Filaria equi Blanchard, 1849

- =Filaria papillosa Rudolphi, 1802
- =Filaria oculi Siebold, 1839

^{*}Species not known to occur in North America.

Family Filariidae Subfamily Filariinae

- *Parafilaria multipapillosa (Condamine and Drouilly, 1878) Yorke and Maplestone, 1926
 - Rare—Asia, Eur., Afr., S. A.—subcutaneous and intermuscular connective tissue
 - =Filaria multipapillosa Condamine and Drouilly, 1878

=Filaria haemorrhagica Railliet, 1885

Nematoda of Uncertain Classification Parasitic in Horses

Cylicocyclus pekingensis K'ung and Yang, 1964—See Key to Species for discussion.

Tridentoinfundibulum gobi Tshoijo, 1957

- Bidentostomum ivaschkini Tshoijo, 1957, in Popova, 1958—This and the preceding genus and species are based on the presence of large teeth in the buccal cavity. Because of the rather unconventional system of classification devised by Tshoijo and described by Popova (1958), I prefer to await additional information before accepting these two new genera and species.
- Cylicodontophorus mongolica Tshoijo, 1957— See Key to Species for discussion.
- Schulzitrichonema schulze Ershov, 1943—So little description of this species has been published that it must be considered species inquirenda.
- Schulzitrichonema caragandicum (Funicova, 1939) Skrjabin, 1953—Sce page 13 for discussion.

Class Cestoda Family Anoplocephalidae Subfamily Anoplocephalinae

- Anoplocephala perfoliata (Goeze, 1782) Blanchard, 1848
 - Rare—cosmopolitan—intestine
 - =Taenia perfoliata Goeze, 1782
 - =Taenia equina Pallas, 1781, in part
 - =Taenia quadrilobata Mueller, 1789
 - =Alyselminthus lobatus Zeder, 1800
 - =Taenia quadriloba Gmelin, 1790

- Anoplocephala magna (Abildgaard, 1789) Spengel, 1905
 - Rare—cosmopolitan—intestine
 - =Taenia magna Abildgaard, 1789
 - =Taenia plicata Zeder, 1800
 - =Taenia plicata servei Bounhiol, 1912
 - =Taenia plicata strangulata Railliet, 1893
 - =Taenia megalocephala Cobbold, 1874
 - =Taenia zebrae Rudolphi, 1808
- Paranoplocephala mamillana (Mehlis, 1831) Baer, 1927
 - Rare—cosmopolitan—intestine
 - =Anoplocephala mamillana (Mehlis, 1831) Blanchard, 1891
 - =Taenia mamillana Mehlis, 1831

Subfamily Monieziinae

*Moniezia pallida Mönnig, 1926 Rare—Afr.—intestine

> Class Trematoda Family Paramphistomidae Subfamily Gastrodiscinae

- *Gastrodiscus aegyptiacus (Cobbold, 1876) Railliet, 1893
 - Rare—Afr., Asia—intestine
 - =Diplostoma aegyptiacum Cobbold, 1876
 - =Cotylogaster cochleariformis (Diesing, 1838)
 - =Gastrodiscus sonsinoii Cobbold, 1877
 - =Gastrodiscus polymastos Leuckart, 1880
 - =Hemistomum aegyptiacum (Cobbold, 1876)
- *Gastrodiscus equi LeRoux, 1938 Rare—Afr.—intestine
- *Gastrodiscus secundus Looss, 1907
 - Rare—Asia—intestine

Subfamily Pseudodiscinae

- *Pseudodiscus collinsii (Cobbold, 1875) Stiles and Goldberger, 1910
 - Common—India—intestine
 - =Amphistoma collinsii Cobbold, 1875
 - =Pseudodiscus stanleyii (Cobbold, 1875) Stiles and Goldberger, 1910
 - =Paramphistomum collinsii (Cobbold, 1875)
- *Pseudodiscus cobboldi Montgomery, 1906 Rare—India—intestine

*Species not known to occur in North America.

IV. Nematoda Parasitic in Domestic Equids

A. Introduction

The nematodes normally parasitic in the horse fall into seven suborders, 12 families, 28 genera, and 75 species (of which 22 genera and 53 species are known to occur in North America). The great majority (56 of 75 species) belong in a single family, the Strongylidae. The other 19 nematode species, scattered in 10 different families, are for the most part so well known and easily identified that they are discussed herein only in the keys to genera and species. The family Strongylidae, however, with many closely related species, has been a difficult group for many workers and an introductory discussion of this family follows.

The Strongylidae of horses-nematodes with a well-developed buccal capsule, a mouth collar with two leaf-crowns, and a strongyloid copulatory bursa—can be separated into two subfamilies: Strongylinae, usually large or medium-sized with a globular or funnel-shaped buccal capsule; and Cyathostominae, usually small to medium-sized with a cylindrical buccal capsule. In this treatise the Strongylinae of domestic equids are organized in four genera, Strongylus, Oesophagodontus, Triodontophorus, and Craterostomum; and 14 species (the four genera and 10 species are known to occur in North America). This four-genera system is accepted by most taxonomists except that Skrjabin and his students subdivide the genus Strongylus into three genera following Ershov (1943). The reasons I do not follow Ershov (1943) are given in the Discussion of the Key to the Species of the Genus Strongylus. The strongylins are relatively easy to identify (Figs. 34-49; 156-173).

The Cyathostominae of domestic equids consisting of eight genera and 41 species (of which six genera and 29 species are known to occur in North America) are the most difficult to identify for the inexperienced worker. However, with careful attention to the characteristics of the mouth collar, cephalic papillae, internal leaf-crown (ILC) and external leaf-crown (ELC), extra-chitinous supports of the ELC, buccal capsule, and esophageal funnel (Fig. 1), these species of small to medium-sized strongylids are readily recognizable. Characteristics of the posterior ends of males and females are also illustrated in Figure 1 to assist the inexperienced worker; however, cephalic characteristics are used almost exclusively in the keys.

Most of the cephalic characters listed above have been used by almost all previous workers, but one character needs further explanation. Extra-chitinous supports for the ELC consist of a sclerotized ring anterior to the buccal capsule. It sometimes appears to be a continuation of the buccal capsule, but it is usually connected by strands of connective tissue to the buccal capsule, the leaf crowns, and mouth collar giving support to the ELC elements that are characteristic of this genus. Extra-chitinous supports are found only in the genus Cyathostomum as defined in this treatise. Looss (1902) referred to this structure "problematic structure in substance of as mouth collar," and described and illustrated it in C. tetracanthum, C. coronatum, C. catinatum, C. labratum, and C. labiatum. This terminology was followed by Ihle (1922) and Skladnik (1935). Theiler (1923) changed the name of this structure to extra-chitinous supports of the external leaf-crown. She described this structure in C. sagittatum in addition to those mentioned by Looss (1902) above. To my knowledge, however, no workers have previously attached any systematic importance to this structure. It became apparent in the course of the present study that this structure is present in all species of the natural group first recognized by Looss (1902) as the "tetracanthum group." All species included in the genus Cyathostomum in this treatise have this structure except perhaps for C. montgomeryi which occurs only rarely in Africa and was not available for study. Thus, the presence of extra-chitinous supports of the external leaf-crown is proposed as an additional diagnostic character for the genus Cyathostomum.



Figure 1, A-D. Cyathostomum coronatum, labeled drawings showing characteristics typical of Cyathostominae. A. Head, dorsoventral view, \times 700. B. Male tail, lateral view, \times 300. C. Dorsal lobe of bursa of male tail, dorsal view, \times 300. D. Female, lateral view of posterior end, \times 300.

The eight genera of Cyathostominae of domestic equids are Cyathostomum Molin, 1861 sensu stricto; Cylicocyclus Ihle, 1922; Cylicodontophorus Ihle, 1922; Cylicostephanus Ihle, 1922; Poteriostomum Quiel, 1919; Gyalocephalus Looss, 1900; Caballonema Abuladze, 1937; and Cylindropharynx Leiper, 1911. The last four of these genera are universally accepted and no further discussion of them will be given here. The first four genera listed above, however, are more controversial. They contain all the 53 species (some now listed as synonyms) of the genus *Cyathostomum* Molin, 1861, *sensu lato* that various workers have grouped into at least 15 different genera since 1900 when Looss placed 12 new species in this genus. To aid the reader in relating the present system of four genera for *Cyathostomum*, *sensu lato* to that used by previous workers, the following brief history is given. More detailed discussion of the bases for placing various species in particular genera can be found in the Discussion following each key to species.

B. History and Comparison of Classification Schemes

The genus *Cyathostomum* was described for the small to medium-sized strongylids of horses by Molin (1861) who lumped them all in one species, C. tetracanthum (Mehlis, 1831). Cobbold (1874) later described Trichonema arcuata for a larval form of C. tetra*canthum*—in reality a group of species. Looss (1900) described 12 new species in the genus Cyathostomum, selecting C. tetracanthum, the most common species, as type of the genus. Much controversy has developed over which genus, Cyathostomum or Trichonema, is valid. Both Cobbold (1875) and Looss (1902) abandoned their genera in favor of others. American workers (Foster, 1936, 1937; Mc-Intosh, 1951) eventually accepted the validity of Cyathostomum based on the International Code of Zoological Nomenclature which clearly recognizes genera as valid even when the name differs in only one letter from another genus name. In the case of Cyathostomum, the existence of another nematode genus, Cyathostoma Blanchard, 1849, had convinced many workers that Cyathostomum was a homonym. The arguments for accepting Cyathostomum were summarized by McIntosh (1951), long after he had settled the question for himself and his co-workers and had submitted the case to the International Commission of Zoological Nomenclature in 1932. The Commission ruled (Hemming, ed., 1943) that Cyathostomum was not a homonym of Cuathostoma.

Unfortunately, many workers, especially Skrjabin and his students and co-workers, have followed the arguments of LeRoux (1924) that Cyathostomum is a nomen nudum and have recognized Trichonema as the name for this genus. According to the International Commission's Opinion, Looss' (1900) restriction of C. tetracanthum to the species most commonly found in horses and asses in Egypt could only be questioned if there was reasonable doubt as to whether this species was among those studied by Mehlis (1831). We now know that C. tetracanthum does occur in Europe so no reasonable doubt should exist that Cyathostomum is valid.

As can be seen in the lists of synonyms in the Outline Classification preceding this section, many additional genera have been coined for the species collectively known as *Cyathostomum*, *sensu lato*. Major contributions and schemes of classification for this group were made by Ihle (1922), Ershov (1943), McIntosh (1951), and K'ung (1964). In the following paragraphs the systems of these workers are briefly described and compared with that resulting from the present study.

The system of Ihle (1922) organized 20 species in seven groups-five of which he designated as subgenera-all in the genus Cylicostomum which is a synonym of Cyathostomum. Ihle's five subgenera were Cylicostomum, Cylicocercus, Cylicocyclus, Cylicostephanus, and Cylicodontophorus. His other groups were the Brevicapsulatum-group and the Montgomeryi-group. Cram (1924) raised all the subgenera of Ihle (1922) to generic rank, placed the Brevicapsulatum-group in the genus Cylicobrachytus Cram, 1924, and the Montgomeryi-group in Cylicotoichus Cram. 1924. The system of McIntosh (1951) is essentially identical to that of Ihle (1922) as modified by Cram (1924) except that Cylicotoichus is omitted (probably because C. montgomeryi was a parasite of the zebra not known from domestic equines) and Cylicotetrapedon Ihle, 1925, is added. The results of the present study differ from the scheme evolved by Ihle, Cram, and McIntosh as follows:

- 1. The genus Cylicocercus, which was distinguished primarily by the bent female tail, is eliminated by placing three species (C. alveatum, C. catinatum, and C. pateratum) in the genus Cyathostomum and one species (C. goldi) in the genus Cylicostephanus.
- 2. The species of the genus *Cylicotetrapedon*, which were distinguished by the presence of teeth in the esophageal funnel, are included in *Cylicostephanus* as suggested by Foster (1936).
- 3. The two species of Cylicobrachytus (C. prionodes and C. brevicapsulatum) are placed in Cylicocyclus following Ershov (1939) and K'ung (1964).
- 4. Cylicodontophorus ultrajectinus is moved to Cylicocyclus following Ershov (1939).
- 5. Cyathostomum ornatum is moved to Cylicostephanus.

The system of Ershov (1943) divided Cyathostomum, sensu lato into five genera including Trichonema, Cylicocyclus, Cylicodontophorus, Petrovinema Ershov, 1943, and Schulzitrichonema Ershov, 1943. The results of the present study differ from the scheme of Ershov (1943) as follows:

- 1. The species of *Trichonema* are assigned either to *Cyathostomum* or to *Cylicostephanus*.
- 2. Two species, C. pateratum and C. sagittatum, are moved from Cylicodontophorus to Cyathostomum.
- 3. The genus Schulzitrichonema Ershov, 1943, distinguished by teeth in the esophageal funnel and identical to Cylicotetrapedon Ihlc, 1925, is eliminated and the species are assigned to Cylicocyclus (C. leptostomus) or to Cylicostephanus (C. asymetricus and C. goldi).
- 4. Petrovinema is eliminated and the two
- species are included in *Cylicostephanus*.5. *Cylicodontophorus ornatum* is moved to *Cylicostephanus*.

In 1964 K'ung reorganized Cyathostomum, sensu lato. He substituted Trichonema for

Cylicostephanus and accepted Cyathostomum, Cylicocyclus, Cylicodontophorus, Cylicotetrapedon, Petrovinema, and Skrjabinodentatus Tshoijo, 1957. The results of the present study differ from the system of K'ung (1964) as follows:

- 1. Trichonema is not acceptable as a substitute for Cylicostephanus.
- 2. The species of the genus *Petrovinema* are included in *Cylicostephanus*.
- 3. The species of the genus Cylicotetrapedon are included in Cylicostephanus except for C. leptostomum which is placed in Cylicocyclus.
- 4. Skrjabinodentatus Tshoijo, 1957, is not acceptable. This genus was created for S. caragandicum (Funicova, 1939) by Tshoijo who used a very peculiar set of differential characters. I regard this species, therefore, as species inquirenda.

The nematodes of horses, except for the lack of a uniform taxonomy above the species level, are a stable well-known group. As can be seen from the Outline Classification, very few legitimate new species have been described since 1925.

C. Key to Genera

- 1A. Males lacking; females long, slender and delicate, with cylindrical esophagus about one-fifth to oneseventh as long as nematode _______ *Strongyloides*
 - B. Dioecious; females usually with relatively short esophagus _____ 2

Strongyloides westeri—only species in horses. DIAGNOSIS: Strongyloididae. Body long, 8–9 mm, slender, 80–95 μ , attenuated anteriorly. Lips indefinite; buccal capsule very small. Esophagus cylindrical, without bulb, about one-seventh as long as body. Tail short, conical. Vulva posterior to midbody, opens directly into opposed uterine branches. Ovejectors absent. Few eggs (40–50 by 30–40 μ) with those closest to vulva usually embryonated. Ovaries reflexed. Only females in parasitic generation.



Figure 2. Strongyloides westeri, parasitic female, lateral view, $\times 64$.

- 2A. Males with strongylid bursa copulatrix; intestine composed of few large multinucleate cells _____
- 3A. Parasites of respiratory system
- B. Parasites of digestive tract _____ 4

Dictyocaulus arnfieldi—only species normally occurring in horses. DIAGNOSIS: Dictyocaulinae. Body white, filiform. Mouth surrounded by six flat papillae. Buccal capsule small but distinct, about twice as broad as deep. Esophagus with slight bulbar swelling at posterior end. MALE 24 to 40 mm long, 250 μ wide. Bursa copulatrix short with short lobelike rays not lobulated; dorsal ray divided and the 2 branches slightly bidigitate. Spicules slightly curved, equal, 200-250 μ long, with brown spongy appearance. Gubernaculum of irregular ovoid shape, 50 μ long. FEMALE 43–70 mm long, 400 μ wide. Vulva slightly anterior to midbody. Anus 400 μ from bluntly pointed tail. Eggs 80-100 by 50–60 μ , embryonated.



3

Figures 3-5. Dictyocaulus arnfieldi. 3. Head, dorsal view, \times 290. 4. Male tail, dorsal view, \times 140. 5. Female tail, lateral view, \times 75.

- 4A. Filiform worms without buccal capsule ______ *Trichostrongylus*
 - B. Stouter worms with well-developed buccal capsule _____ 5

Trichostrongylus axei—only species normally occurring in horses. DIAG-NOSIS: Trichostrongylinae. Small slender nematode without buccal capsule. MALE 3.4–4.4 mm long. Bursa copulatrix wider than long, unlobulated; ventroventral ray very slender; dorsal ray slender, divided near tip and each branch further divided. Spicules unequal in size; right 89–95 μ ending in short blunt point; left spicule 110–120 mm ending in long curved slender point; slender process near middle on medial side of each spicule. Gubernaculum spindle-shaped, 50– 60 μ long. FEMALE 4.5–5.5 mm long. Vulva in posterior third of body. Muscular ovejectors opposed, vagina and ovejectors lined with thick cuticle. Tail straight, tapers gradually.



Figures 6-9. Trichostrongylus axei. 6. Head, ventral view, $\times 2,080$. 7. Male tail, dorsal bursal ray, $\times 450$. 8. Male tail, lateral view, $\times 450$. 9. Female tail, lateral view, $\times 450$.

Gyalocephalus capitatus—only species in genus. DIACNOSIS: Cyathostominae. Body relatively short and thick, about 8.5–11.0 mm long. Mouth collar high with inconspicuous papillae. External leafcrown (ELC) of many (90–95) fine-pointed elements that project from mouth collar. Internal leafcrown (ILC) consists of 30 large elements, broad, and pointed with origin at base of buccal capsule. Buccal capsule short, much wider than deep, and thick-walled, with ring of toothlike structures around posterior internal surface at origin of ILC. Dorsal gutter absent. Esophageal funnel very large, surrounded by greatly dilated anterior end of esophagus; contains 3 large sickle-shaped dentiform projections-1 dorsal, 2 subventral--each with a small tooth at its base; 3 additional small double teeth spaced among sickle-shaped projections. Esophagus flask-shaped. MALE. Bursa lobulated, large with exceptionally long prebursal papil-Genital cone of variable lae. length, long to very long, usually extends to or beyond edge of bursa. FEMALE. Vulva 300–400 μ anterior to anus. Tail 200–300 μ long, tapers gradually to conical tip. Eggs large, 120 by 50 μ .



Figures 10–13. Gyalocephalus capitatus. 10. Head, dorsal view, \times 190. 11. Male tail, dorsal bursal ray, \times 120. 12. Male tail, lateral view, \times 120. 13. Female tail, lateral view, \times 55.

- 7A. Cylindrical buccal capsule greatly elongated, about 2 or 3 times deeper than wide ______12
 - B. Buccal capsule not greatly elongated, not more than 1.5 times deeper than wide ______ 8
- 8A. Elements of internal leaf-crown (ILC) as long as or longer, broader, and usually less numerous than elements of external leaf-crown (ELC) 11
- 9A. Posterior margin of buccal capsule with ringlike hoop-shaped thickening; lateral papillae usually large, broad, and hornlike Cylicocylus

Cylicocyclus Ihle, 1922. DIAGNOSIS: Cyathostominae. Small to medium-

sized, about 10-25 mm long. Mouth collar usually high with broad lateral papillae that may be prominent. Elements of ELC much larger, broader, and fewer than those of the ILC. Elements of ILC usually short, thin rods at or near anterior edge of buccal capsule. Extra-chitinous supports of ILC absent. Buccal capsule short with thin walls tapering anteriorly; hoop-shaped thickening around posterior margin. Dorsal gutter usually not present in buccal capsule. Buccal cavity much broader than deep. MALE. Dorsal ray of bursa split to region of origin of externodorsal rays. Spicules filiform, equal, with pick-shaped tips. FEMALE. Vulva close to anus. Tail usually straight but may be bent slightly dorsally.

Type species: C. radiatus illustrated below. Key to species on pages 42–48.



Figures 14-17. Cylicocyclus radiatus. 14. Head, dorsal view, $\times 260$. 15. Male tail, dorsal bursal ray, $\times 65$. 16. Male tail, lateral view, $\times 65$. 17. Female tail, lateral view, $\times 100$.

> Cyathostomum Molin, 1861, sensu stricto. DIAGNOSIS: Cyathostominae. Small, about 5–12 mm long. Mouth collar moderately high. Cephalic papillae not prominent. Elements of ELC larger, broader, and fewer than elements of ILC but elements of both leaf-crowns of similar shape. Elements of ILC inserted at considerable depth in buccal

cavity. Sclerotized extra-chitinous supports of ILC occur at or near anterior edge of buccal capsule. Buccal capsule generally short, thick-walled. Dorsal gutter not present in buccal capsule. Buccal cavity as broad or broader than deep. MALE. Dorsal ray of bursa split to region of proximal branch or to origin of externodorsal rays. Spicules filiform, equal, with pickshaped tips. FEMALE. Vulva close to anus. Tail may be straight or bent dorsally with a ventral bulging anterior to the vulva.

Type species: *C. tetracanthum* illustrated below. Key to species on pages 38–42.



Figures 18-21. Cyathostomum tetracanthum. 18. Head, dorsal view. Extra-chitinous supports indicated (arrow), \times 340. 19. Male tail, dorsal bursal ray, \times 50. 20. Male tail lateral view, \times 90. 21. Female tail, lateral view, \times 110.

> Cylicostephanus Ihle, 1922. DIAG-NOSIS: Cyathostominae. Small, about 4–10 mm long. Mouth collar depressed. Lateral papillae (amphids) not prominent. Submedian papillae prominent. Elements of ELC longer, usually broader, and fewer than elements of ILC. Elements of ILC are short thin rods or plates inserted at or near the an

terior edge of the buccal capsule. Extra-chitinous supports for ILC absent. Buccal capsule of varying thickness, usually with dorsal gutter. Buccal cavity usually slightly narrower anteriorly. MALE. Dorsal ray of bursa split to region of proximal branch or to origin of externodorsal rays. Spicules filiform, equal, with pick-shaped tips. FE-MALE. Vulva near anus. Tail usually straight.

Type species: C. calicatus illustrated below. Key to species on pages 51–55.



Figures 22–25. Cylicostephanus calicatus. 22. Head, dorsal view, \times 425. 23. Male tail, dorsal bursal ray, \times 65. 24. Male tail, lateral view, \times 100. 25. Female tail, lateral view, \times 140.

> Cylicodontophorus Ihle, 1922. DI-AGNOSIS: Cyathostominae. Small, medium-sized, about 7–14 mm long. Mouth collar high with lateral papillae inconspicuous and submedian papillae short and conical. ELC not as salient as ILC. ILC elements usually longer, broader, and less numerous than ELC elements. ILC elements inserted near

anterior edge of buccal capsule. Extra-chitinous supports of ELC absent. Buccal capsule short, thickwalled—of nearly uniform thickness or thicker anteriorly. Dorsal gutter present or absent. Buccal cavity broader than deep. MALE. Dorsal ray split only to proximal branch. Spicules filiform, equal, with hook-shaped tips. FEMALE. Vulva near anus. Tail of female short with sharp tip. Prominent ventral bulge may be present anterior to vulva.

Type species: C. bicoronatus illustrated below. Key to species on pages 49–50.



Figures 26–29. Cylicodontophorus bicoronatus. 26. Head, dorsal view, \times 290. 27. Male tail, dorsal bursal ray, \times 50. 28. Male tail, lateral view, \times 70. 29. Female tail, lateral view, \times 95.

B. Buccal capsule walls thicker posteriorly than anteriorly; ILC inserted on anterior edge of buccal capsule; dorsal bursal ray split only to most distal branches; female tail long, tapered to blunt tip ______ *Poteriostomum*

> Poteriostomum Quiel, 1919. DIAG-NOSIS: Cyathostominae. Mediumsized, about 12–18 mm long and rather thick. Mouth collar high with short, inconspicuous submedian papillae with broad round bases; lateral papillae short and broad. ELC of numerous short, thin, pointed elements that protrude from mouth collar. ILC arises at anterior edge of buccal

capsule; consists of long, broad acutely tipped elements. Buccal capsule broader than deep; walls thicker posteriorly. Dorsal gutter usually present; broad, extends almost ¹/₂ depth of buccal cavity. Esophagus short, thick, posterior ²/₃ expanded. Esophageal funnel large, cone-shaped. MALE. Dorsal ray of bursa split only to most distal branch; branches arise at right angles. Edge of bursa with fine denticulation. FEMALE. Vulva near anus. Tail long or short.

Type species: *P. imparidentatum* illustrated below. Key to species on pages 55-56.



Figures 30-33. Poteriostomum imparidentatum. 30. Head, dorsal view, $\times 230$. 31. Male tail, dorsal bursal ray, $\times 30$. 32. Male tail, lateral view, $\times 50$. 33. Female tail, lateral view, $\times 50$.

12A. Dorsal gutter projects well into buccal cavity; esophageal funnel with 3 small teeth; ELC of 8 broad petals, ILC inconspicuous ______ *Caballonema**

> Caballonema longicapsulatumonly species in genus. DIAGNOSIS: Cyathostominae. Small to mediumsized, 6–12 mm long. Mouth collar high; submedian papillae long; lateral papillae short, inconspicuous. ELC of 8 broad petals, ILC inconspicuous. Buccal capsule cylindrical, exceptionally deep, almost 3 times as deep as wide (300 by 120 μ). Dorsal gutter well developed, about 170 μ long. Esophageal funnel with 3 conical denticles that do not project into buccal cavity. Esophagus cylindrical. MALE. Dorsal lobe of bursa markedly elongated; bifurcated to externodorsals. Edge of bursa denticulated. Gubernaculum scoopshaped. FEMALE. Vulva fairly distant from anus, about twice as distant as length of tail.

 B. Dorsal gutter does not project into buccal cavity; esophageal funnel without teeth; ELC of 6 broad petals; ILC of 12 broad petals Cylindropharynx*

> Cylindropharynx Leiper, 1911—2 species in horses (C. aethiopica and C. asini), but descriptions not available. GENERIC DIAGNOSIS: Cyathostominae. Mouth collar depressed, submedian papillae large, lateral papillae broad but not protruding. ELC of 6 large petals that may be greatly modified. ILC of 12 broad thick petals at anterior edge of buccal capsule. Buccal capsule cylindrical and extremely long. Dorsal gutter absent. Esophageal funnel without denticles. Esophagus cylindrical, thicker posteriorly. MALE. Dorsal ray with one lateral branch on each side that may be split distally; externodorsal ray arises separately from dorsal ray. Edge of bursa may be denticulated. FEMALE. Vulva fairly close to anus.

^{*} Genera not known to occur in North America but reported elsewhere in domestic equids. Specimens were not available for study and no illustrations are given.

- 13A. Buccal capsule funnel-shaped, with thickened posterior ring; dorsal gutter absent Oesophagodontus

Oesophagodontus robustus—only species in genus. DIAGNOSIS: Strongylinae. Buccal capsule shaped like a funnel or a wine glass with a thickened ring encircling its posterior margin. Esophageal funnel with 3 lancetlike teeth that do not project into buccal capsule. ILC of many long slender pointed elements at anterior edge of buccal capsule. ILC elements are bent backwards at base with free ends reflected slightly anteriorly. ELC composed of fewer, broader, thicker elements of about same length. Mouth collar depressed with sharp ridge on peripheral edge. Lateral papillae short, not prominent. Submedian papillae prominent, extend above mouth collar, consist of broad base and a long slender distal part with broad base bearing short bilobed process. Dorsal gutter absent. MALE 15-18 mm long by 1 mm wide. Bursa closed all around with no protruding dorsal lobe. Dorsal ray represented by 2 groups of 4 rays. FEMALE 19-24 mm long; tail 500-700 μ long; vulva 2.2–3.5 mm anterior to anus.



Figures 34–37. Oesophagodontus robustus. 34. Head, dorsal view, \times 70. 35. Male tail, dorsal view, \times 85. 36. Male tail, lateral view, \times 100. 37. Female tail, lateral view, \times 15.

- 14A. Leaf-crowns present; mouth directed straightforward ______ 15
 - B. Leaf-crowns absent; mouth directed slightly dorsally _____ Acheilostoma*

Acheilostoma paranecator—only species in horses. DIAGNOSIS: Globo-

* Not known to occur in North America but reported elsewhere in domestic equids. Specimens were not available for study and no illustrations are given. cephalinae. Medium-sized, 8–12 mm long. Mouth directed slightly dorsally. Mouth collar well developed, somewhat subterminal. Leaf-crowns absent. Buccal capsule spherical with 2 subventral and 2 subdorsal teeth at its bottom. Dorsal gutter extends into buccal cavity as a cone between the subdorsal teeth. MALE. Caudal bursa trilobate, dorsal lobe smaller than laterals. Rays of bursa thick. Dorsal ray bifurcated with bifid tips. Externodorsals branch from thick dorsal ray. Spicules about 1.0 mm long, thin, end in small hook. FEMALE. Vulva at midbody. Uterine branches divergent. Tail 170 μ long. Eggs oval, 63 by 43 μ .

- 15A. Buccal capsule globular, deeper than wide ______ Strongylus
 - B. Buccal capsule subglobular, wider than deep _____ 16

Strongylus Mueller, 1780. DIAG-NOSIS: Strongylinae. Large stout nematodes. Buccal capsule globular, deeper than wide with greatest diameter near middle. ELC with numerous thin-pointed elements protruding from high mouth collar. ILC similar in size and number of elements to external crown. Elements of ELC originate near tips of ILC elements so 2 crowns appear to be one. Lateral and submedian papillae not prominent. Dorsal gutter long, extends to anterior part of buccal capsule. Buccal capsule with or without teeth. MALE bursa small closed all around with dorsal lobe and slightly developed genital cone. Spicules not hook-shaped at distal ends. FEMALE with vulva near beginning of posterior third of body; uteri divergent.

Type species, S. equinus, illustrated below. Key to Species of Strongylus on pages 60-61.



Figures 38-41. Strongylus equinus. 38. Head, lateral view, \times 27. 39. Male tail, dorsal view, \times 27. 40. Male tail, lateral view, \times 40. 41. Female tail, lateral view, \times 34.

> Triodontophorus Looss, 1902. DI-AGNOSIS: Strongylinae. Mediumsized worms. Buccal capsule subglobular with three large esophageal teeth protruding into buccal cavity to about 1/2 its depth. Anterior rim of buccal capsule surrounded by 6 platelike structures which give appearance of the capsule being thickened anteriorly. Mouth collar well-developed with peripheral edge rounded or depressed as a ridge. Submedian papillae small, conical or slender.

Lateral papillae not prominent. ELC of numerous slender elements protrudes from buccal collar. ILC of oval plates of same number as ELC elements. Dorsal gutter extends to anterior edge of buccal capsule. Each of 3 esophageal teeth composed of 2 plates joined at an angle medially. MALE with well-developed dermal collar on genital cone. Bursa with finely denticulated margin and closed ventrally. FEMALE with vulva close or up to 3.0 mm from anus. Uteri parallel.

Type species, *T. serratus*, illustrated below. Key to species of *Triodontophorus* on pages 57–60.



Figures 42-45. Triodontophorus serratus. 42. Head, dorsal view, $\times 200$. 43. Male tail, dorsal view, $\times 45$. 44. Male tail, lateral view, $\times 50$. 45. Female tail, lateral view, $\times 40$.

B. Esophageal teeth do not extend into buccal cavity; elements of ELC few ______ Craterostomum

Craterostomum Boulenger, 1920. DIAGNOSIS: Strongylinae. Small worms, 6–10 mm long. Buccal capsule of greatest diameter in middle, wall thickened just behind anterior edge. Dorsal gutter strongly developed. Esophageal funnel shallow with 3 small triangular teeth that do not project into buccal cavity. Elements of ELC large, transparent, and less numerous than short, broad elements of ILC that ring anterior edge of buccal capsule. Mouth collar depressed; submedian papillae extend beyond mouth collar. MALE. Bursa with finely denticulated border, closed. FEMALE. Tail long, pointed. Vulva relatively far from anus, but not more than 1.0 mm from it.

The only species of this genus that occurs in North America is the type species, C. acuticaudatum. It is illustrated below. A discussion of this genus is given on pages 56–57.



Figures 46-49. Craterostomum acuticaudatum. 46. Head, dorsal view, \times 310. 47. Male tail, dorsal bursal ray, \times 60. 48. Male tail, lateral view, \times 100. 49. Female tail, lateral view, \times 50.

- 17A. Esophagus dilated posteriorly into a distinct bulb ______ 18
 - B. Esophagus without dilated bulb 20
- 18A. Parasitic in tissues; microscopic in size (less than 500 μ long).
 - B. Parasitic in digestive tract; at least 2–3 mm long _____ 19

Micronema deletrix—only parasitic species. DIAGNOSIS: Rhabditina. Microscopic, cylindrical body 250-445 μ long tapering anteriorly and rapidly posterior to anus. Cuticle with fine striations about $\frac{1}{2}$ μ apart near midbody. Cephalic region transparent, composed of 6 lips bearing 6 papillae and amphids. Stoma cephaloboid. Cheilorhabdions present, prorhabdions long, mesorhabdions shorter and thinner than prorhabdions, dorsal metarhabdion bears tooth, telorhabdions form ring at base of stoma. Esophagus panagrolaimoid

70–92 μ long, metacorpus a distinct bulb, procorpus and isthmus about equal in length, basal bulb pyriform with refractive valvular apparatus. Nerve ring at middle of isthmus. Excretory pore indistinct. Lateral cephalic papillae prominent near base of isthmus. Tail conical, 49–70 μ long, abruptly tapered to sharp point. Phasmids near middle of tail. Vulva slightly posterior to midbody, vulval lips protrude slightly. Gonad single, extends about 3 or 4 body widths anteriorly before reflexing posteriorly 1½ body widths beyond vulva where it reflexes dorsally and anteriorly. Each large ovum 9–17 by 32–46 μ develops alone sometimes to larval stage. Probably parthenogenic, oviparous. MALE unknown. See Discussion and photographs of M. deletrix in tissue on pages 61-62.



Figure 50. Micronema deletrix, female, lateral view, × 300.

19A. Transparent, small slender nematodes with relatively long narrow stoma; esophagus expanded in posterior bulb; large prominent suckerlike excretory pore; viviparous Probstmayria

> Probstmayria vivipara—only species in horses. DIAGNOSIS: Probstmayriinae. Small, slender, transparent, 2–3 mm long. Mouth with 6 small lips. Buccal capsule cylindrical, long and narrow. Esophagus

with long cylindrical part and separated flask-shaped bulb. Large suckerlike excretory pore present. Tail long and pointed in both sexes. MALE. Caudal alae absent. Caudal papillae inconspicuous. Two small, nearly equal spicules 58–67 μ long. Gubernaculum absent. FEMALE. Vulva near midbody. Viviparous; early developmental to large immature stages visible inside females.



Figures 51-54. Probstmayria vivipara. 51. Anterior region, lateral view, \times 160. 52. Esophagointestinal junction and excretory pore, lateral view, \times 120. 53. Vulva and developing larvae in female, lateral view, \times 160. 54. Male tail, lateral view, \times 160.

 B. White, large, stouter nematodes with relatively short broad stoma; esophagus expanded anteriorly and posteriorly; excretory pore not prominent; oviparous _____ Oxyuris

> Oxyuris equi—only species in horses, except O. poculum which occurs in Ceylon and has spicules 440 μ long. DIACNOSIS: Oxyurinae. Medium to large, white; males 9– 12 mm long, females up to 100 mm long. Mouth hexagonal, 2 suckerlike papillae on each lateral lip. Buccal capsule short with bristles at bottom. Esophagus expanded in anterior $\frac{1}{2}$, followed by con

stricted $\frac{1}{2}$, and a posterior bulb with a valvular apparatus. MALE. Caudal alae short supported by one large pair of preanal and one large pair of postanal papillae. Another pair of papillae flank the vent. Spicule single and needlelike about 120–200 μ long. Gubernaculum absent. FEMALE. Vulva in anterior part of body. Excretory pore quite posterior to esophagus, just anterior to vulva. Tail varies greatly in length, may be extremely long and whiplike. Eggs with operculum, 85–95 by 40–45 μ , embryonated.



Figures 55–58. Oxyuris equi. 55. Anterior region, dorsal view, \times 35. 56. Male tail, ventral view, \times 154. 57. Male tail, lateral view, \times 154. 58. Female tail, lateral view, \times 15.
- 20A. Head with 3 large lips; long, thick, opaque worms; esophagus short stout muscular, difficult to see except in dissected specimens
 - B. Head not as above; relatively slender worms; esophagus usually long with 2 distinct parts _____ 21

Parascaris equorum—only species in horses. DIAGNOSIS: Ascaridinae. Large, 15–50 cm; thick; opaque. Mouth surrounded by 3 large quadrangular lips separated by small interlabia. Each lip with a denticulated inner surface. Each lip divided by horizontal groove except on outer surface. Two large double papillae on dorsal lip and one large double papilla on each subventral lip. Each subventral lip with large additional pair of papillae in anterolateral part of lip. Buccal capsule absent. Cervical alae absent. MALE. Tail bluntly conical with small caudal alae. Spicules equal, 2-2.5 mm long. Gubernaculum absent. About 6 pairs of postanal papillae; many preanal papillae. FEMALE. Vulva near beginning of second quarter of body. Tail ends in short conical projection. Oviparous; eggs with pitted thick shell, subglobular, 90-100 μ in diameter.



Figures 59-61. Parascaris equorum. 59. Head, ventral view, showing large pair of papillae and one of lateral pair of papillae on each subventral lip, \times 40. 60. Male tail, ventral view, only distal tips of spicules are shown, \times 40. 61. Female tail, lateral view, \times 30.

21A. Sclerotized buccal capsule present; vulva near midbody; oviparous 22

B. Buccal capsule absent or rudimen-

 Thelazia lacrymalis—only species of genus in horses. DIACNOSIS: Thel-

aziinae. Males 8–12 and females 14–18 mm long. Mouth small, without lips, dorsoventrally elongated. Six small papillae surround mouth; 8 larger cephalic papillae and lateral papillae in outer circle



Figures 62-66. Thelazia lacrymalis. 62. Anterior end of female, lateral view, $\times 50$. 63. Head, lateral view, $\times 160$. 64. Male tail, lateral view, $\times 100$. 65. Female tail, lateral view, $\times 100$. 66. Female tail, ventral view of posterior end, $\times 100$.

of 10. Buccal capsule short, thickwalled, oval, without teeth. Esophagus short and thick. Cuticle transversally annulated with fine striations. MALE. Tail blunt and recurved without caudal alae. Preanal papillae numerous, paired except for one anterior to vent; 3-4 postanal papillae. Spicules unequal, left 170–190 μ long; right 130–140 μ long. Female. Tail blunt with a pair of papillae near tip. Vulva just posterior to esophagointestinal junction. Uterine branches directed posteriorly. Viviparous.

Draschia megastoma—only species in genus. DIAGNOSIS: Habronemat-

inae. Medium-sized, 7-13 mm long, white. Mouth with 2 unlobed lateral lips (pseudolabia). Interlabia present, well developed. Lips separated from body by constriction, forming knobs. Four submedian papillae each with a smaller one next to it. Lateral papillae on pseudolabia. Anterior part of buccal capsule thickened and funnelshaped, without teeth. Esophagus with anterior muscular and posterior glandular parts. Lateral alae present. MALE. Tail with spiral twist. Four pairs pedunculated preanal papillae, 2 pairs postanal, and a cluster of very small ones near the tip. Spicules markedly unequal-left longer. Gubernaculum present. FEMALE. Vulva anterior to midbody. Viviparous.



Figures 67-69. Draschia megastoma. 67. Head, lateral view, \times 220. 68. Male tail, lateral view, \times 220. 69. Female tail, lateral view, \times 380.

> Habronema Diesing, 1861. DIAG-NOSIS: Habronematinae. Mediumto large-sized, 8–35 mm long. Two lateral trilobed lips (pseudolabia) with or without teeth on inner surface. Interlabia present. Four submedian papillae, each with a smaller one next to it. Lateral papillae on lateral lips. Buccal capsule well developed, cylindrical or fusiform. Esophagus consists of short anterior muscular part and longer posterior part of glandular

and muscular tissue. Cuticular alae bilateral or unilateral. Cervical papillae anterior to nerve ring. MALE. Tail with spiral twist. Caudal alae wide, 4 pairs pedunculated papillae preanal and 1–2 pairs postanal. Additional 2–3 pairs of small papillae near tip of tail. Spicules markedly unequal left longer. Gubernaculum present. FEMALE. Vulva near midbody uteri divergent; tail coneshaped. Oviparous, eggs embryonated.

Type species, *H. muscae*, illustrated below. Key to species of *Habronema* on pages 63–64.



Figures 70–72. Habronema muscae. 70. Head, lateral view, \times 220. 71. Male tail, lateral view, \times 75. 72. Female tail, lateral view, \times 120.

- - B. Mouth without peribuccal crown; head without hornlike spines 25

Setaria equina—type of genus and only species in horses. DIAGNOSIS: Setariinae. Long, white; male 51– 66 mm long; female 110–130 mm long. Mouth surrounded by peribuccal crown that is modified into 4 projecting lips. Surrounding the 4 raised lips are 4 hornlike cephalic spines. Slightly more posteriorly are 4 pairs of papillae. Esophagus

divided into anterior muscular and posterior glandular parts. MALE. Caudal alae very small. Usually 4 pairs of preanal papillae; one preanal and one postanal unpaired papillae located medially; and 3-4 pairs of postanal papillae. Very small caudal appendages near end of tail. Spicules unequal and dissimilar, left 610-640 μ and right 280–290 μ long. Right spicule with processes at tip that serve to support left spicule that usually protrudes from vent. Left spicule with expanded loop near middle. FEMALE. Vulva in cervical region. Tail with 2 small lateral appendages near knobby tip.



Figures 73-76. Setaria equina. 73. Head, lateral view, \times 70. 74. Head, ventral view, \times 70. 75. Male tail, lateral view, \times 100. 76. Female tail, ventral view, \times 100.

- 25A. Parasitic in aorta or other arteries or veins; female with slender anterior end and sharply expanded posterior; male filiform; special annulation in cuticle beneath surface layers ______ Elaeophora*

*Elaeophora boehmi—only species in horses. DIAGNOSIS: Onchocerinae. Long, slender, white; male 45-60 mm; female 40-200 mm long; sexual dimorphism pronounced. Mouth without lips, but small papillae present. Cylindrical esophagus very long. Intestine very narrow. MALE. Tail curved ventrally; caudal alae absent; 2 pairs of preanal and 3 pairs of postanal papillae. Spicules unequal, left 270-300 $\mu,$ right 90–100 μ long. FE-MALE. Vulva in esophageal region, 460-600 μ from anterior end. Diameter of posterior part of body 5-6 times that of anterior part. Viviparous.

26A. Parasitic in subcutaneous and intramuscular connective tissue; cuticle of anterior end with elliptical or circular bosses _____ Parafilaria*

> *Parafilaria multipapillosa—only species in horses. DIAGNOSIS: Filariinae. Long, filiform, white; male

about 30 mm and female 40–60 mm long. Mouth simple, with 2 lateral lips. Cuticle of cervical region with elliptical or circular bosses in 13–15 rings. Esophagus very short, undivided. MALE. Tail short, bluntly rounded. Many preanal and postanal papillae. Spicules unequal and dissimilar—left 680–750 μ , right 130–140 μ long. FE-MALE. Vulva very near to mouth. Posterior end blunt, anus subterminal. Oviparous, embryonated.

> Onchocerca Diesing, 1841. DIAG-NOSIS: Onchocercinae. Both sexes filiform, very long. Mouth without lips or prominent papillae. Cuticle thick, transversally striated; always in female and usually in male with spiral thickenings. Esophagus short, not clearly divided into 2 parts. MALE. Tail spirally coiled, without caudal alae, with 4 circumanal papillae and one or more papillae anterior or posterior to these. Spicules unequal. FEMALE. Vulva about 500 μ from anterior end. Microfilariae unsheathed.

Type species, *O. reticulata*, not illustrated because specimens were unavailable. *O. cervicalis* illustrated below. See page 64 for a key to the 2 species.

^{*} Not known to occur in North America but reported elsewhere in domestic equids. Specimens were not available for study and no illustrations are given.

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Figures 77-80. Onchocerca cervicalis. 77. Anterior end of female, lateral view, \times 120. 78. Male tail, lateral view, \times 200. 79. Female tail, lateral view, \times 120. 80. Spiral thickenings and internal striae in cuticle, \times 150.

D. Keys to Species

The following keys to species of nematodes include only those known to occur in North America unless noted otherwise. Exotic species of each genus are listed following the key and compared with North American species. Usually only key characters are illustrated. References to complete descriptions of each species are included in the keys.

Genus Cyathostomum

For species descriptions see Popova (1958, English translation, 1965)

- 1A. Extra-chitinous supports of ELC prominent and ILC inserted in even line around buccal cavity _____ 2
- B. Extra-chitinous supports of ELC not prominent and/or ILC inserted in uneven line around buccal cavity 5
- B. Buccal cavity much broader than deep, walls relatively straight ______ 3



Figures 81, 82. Cyathostomum coronatum heads, \times 450. 81. Medial, dorsoventral view showing extrachitinous supports (arrow). 82. Dorsal view showing ILC, ELC, and two submedian papillae.

- B. Extra-chitinous supports much smaller than wall of buccal capsule, usually not in line with buccal capsule wall ... 4



Figures 83, 84. Cyathostomum tetracanthum heads, \times 430. 83. Medial, dorsoventral view showing large extra-chitinous supports (arrow), ELC, ILC, and lateral papillae. 84. Dorsal view showing submedian papillae, ELC, and ILC (arrow).

 Mouth collar notched to form 4 distinct lips; ILC elements one-half as long as ELC elements; extra-chitinous supports of ELC spindle-shaped; 

Figures 85-87. Cyathostomum labiatum heads, \times 320. 85. Medial, dorsoventral view showing ELC, ILC (arrow), extra-chitinous supports, and lateral papillae. 86. Dorsal view showing notched mouth collar (arrow), submedian papilla, ELC, ILC, and dorsal gutter. 87. Submedian view showing extra-chitinous supports (arrow).

B. Mouth collar not notched; ILC elements more than one-half as long as ELC elements; extra-chitinous supports of ELC pyriform in shape; excretory pore near middle of esophagus C. labratum



Figures 88–90. Cyathostomum labratum heads, \times 350. 88. Medial, dorsoventral view showing buccal capsule wall, ILC, extra-chitinous supports, and lateral papillae (arrow). 89. Dorsal view showing submedian papillae and ILC (arrow). 90. Medial lateral view showing buccal capsule wall, extra-chitinous supports (arrow), and a dorsal tooth in the esophageal funnel.

- 5A. Walls of buccal capsule of nearly uniform thickness posterior to insertion of ILC; ILC inserted at about one-third depth of buccal capsule *C. alveatum**

* Probably does not occur in North America; included because paratypes were available for study.



Figures 91–93. Cyathostomum alveatum heads, \times 230. 91. Medial, dorsoventral view showing buccal capsule wall, ELC, ILC, and lateral papilla. 92. Medial, lateral view showing extra-chitinous supports (arrow). 93. Lateral view showing ILC and ELC.

6A. ILC inserted in sinuous line deep in buccal cavity (best observed in lateral view) _____ C. pateratum



Figures 94–96. Cyathostomum pateratum heads, \times 220. 94. Medial, dorsoventral view showing ELC, ILC, and lateral papillae. 95. Dorsal view of submedian papillae (arrow) and ELC. 96. Lateral view showing sinuous insertion (arrow) of ILC and extra-chitinous supports (arrow, right).

B. ILC inserted more anteriorly on lateral sides of buccal capsule than on dorsal and ventral sides, but not in sinuous line _____ C. catinatum



Figures 97–99. Cyathostomum catinatum heads, \times 370. 97. Medial, dorsoventral view showing lateral papillae, ELC, ILC, and cuticular lining (arrow) of buccal capsule. 98. Dorsal view of submedian papillae and elements of ELC. 99. Medial, lateral view showing line of insertion of ILC (arrow) and extra-chitinous supports (arrow, right).

Exotic species of Cyathostomum:

- *C. alveatum*—reported in Africa, USSR, and Italy. Included in above key because paratypes were available for study.
- C. montgomeryi—occurs in East Africa in zebra and in South Africa in horses and mules (Mönnig, 1928). Although specimens were not seen, this species appears to be similar to C. labiatum and C. labratum but without well-defined lips. Walls of buccal capsule longer in dorsoventral view than in lateral view. The presence of extra-chitinous supports in this species has not been demonstrated.
- C. sagittatum—occurs in equines in Europe, Indonesia, Siberia. This species is very similar to C. coronatum except for a more shallow buccal cavity.

Discussion

McIntosh (1951) established the validity of the genus *Cyathostomum* and listed a synonymy of the type species. The present writer agrees with the conclusions of McIntosh regarding the validity of *Cyathostomum*, but combines in this genus three species included by McIntosh (1951) and others in *Cylico*- cercus Ihle, 1922. Like K'ung (1964), I believe that reliance on the shape of the female tail to separate Cylicocercus from Cyathostomum is inadequate and impractical. Species of both genera share the distinguishing generic characteristics of the deep origin of the internal leaf-crown and presence of extra-chitinous supports for the ILC. A species described by Yamaguti (1943), C. subcoronatum, was considered by Baruš (1962) to be a synonym of C. coronatum. The species were separated by Yamaguti on the basis of a greater number of ILC elements than indicated by Looss (1900) in his description of C. coronatum. After studying Looss' paratypes of C. coronatum, I agree with Baruš that C. coronatum has about 80 elements in the ILC and that C. subcoronatum, therefore, is its synonym.

Genus Cylicocyclus

For species descriptions see Popova (1958, English translation, 1965)

- 1A. Buccal capsule extremely shallow with very delicate inconspicuous walls
 - B. Buccal capsule not extremely shallow or delicate _____ 2



Figures 100, 101. Cylicocyclus brevicapsulatus heads, \times 300. 100. Medial, dorsoventral view showing delicate walls of buccal capsule with small hoop-shaped thickening (arrow). 101. Dorsal view showing submedian papillae and ELC.

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- 2A. Both lateral papillae and ELC prominent, extending beyond mouth collar; dorsal gutter present ______3
 - B. Either lateral papillae or ELC may be prominent, but not both; dorsal gutter absent ______4
- 3A. Dorsal gutter extends for one-half of depth of buccal cavity; submedian papillae long, extend beyond mouth collar; ELC consists of 20 elements; buccal capsule usually with internal shelflike cuticular projection
 - C. nassatus



Figures 102–104. Cylicocyclus nassatus heads, $\times 255$. 102. Medial, dorsoventral view of prominent lateral papillae and shelflike cuticular projection (arrow) on inside wall of buccal capsule. 103. Dorsal view showing dorsal gutter (arrow). 104. Lateral view of dorsal gutter (arrow) and hooplike thickening at base of buccal capsule.

B. Dorsal gutter short, little more than a button; submedian papillae relatively short, do not extend beyond mouth collar; ELC consists of 30 elements; buccal capsule without internal projection _____ C. triramosus*

* Although this rare species has been reported in Puerto Rico, specimens were not available.

4A. Lateral papillae extremely long, earlike or hornlike; extend much higher than mouth collar and submedian papillae;

excretory pore and cervical papillae behind esophagointestinal junction ... *C. auriculatus*



Figures 105, 106. Cylicocyclus auriculatus heads, \times 220. 105. Medial, dorsoventral view showing large hornlike lateral papillae and hooplike thickening at base of buccal capsule. 106. Lateral view of two submedian papillae, mouth collar, and lateral papilla.

- B. Lateral papillae not extremely long; excretory pore and cervical papillae at or anterior to esophagointestinal junction ______5
- 5A. Excretory pore and cervical papillae near esophagointestinal junction 6
- B. Excretory pore and cervical papillae

6A. ELC elements broad, number 10 to 12; ILC elements as long or longer than ELC elements, 12 of 46 ILC elements longer than others ______ C. ultrajectinus



Figures 107, 108. Cylicocyclus ultrajectinus heads, \times 190. 107. Subventral view showing 2 submedian papillae, buccal capsule with hoop-shaped thickening, and ILC elements (note length). 108. Ventral view of ELC and ILC elements. Note width of ELC and ILC elements and extra length of some ILC elements (arrow).



Figures 109, 110. Cylicocyclus insigne heads, \times 215. 109. Medial, dorsoventral view showing prominent lateral papillae, elements of ELC and ILC, buccal capsule, and large, lightly sclerotized esophageal funnel surrounded by thick muscle. 110. Lateral view of submedian papillae, long ELC elements, and short ILC elements (arrow).

7A. Esophageal funnel nearly as large as buccal capsule; esophagus greatly elongated with posterior half enlarged but cylindrical C. elongatus*

* This species can be separated into two distinct subspecies. See Discussion.

111

B. Esophageal funnel small; esophagus long with posterior half enlarged and pyriform ______ 8



Figures 111, 112. Cylicocyclus elongatus heads, \times 240. 111. Medial, dorsoventral view of lateral papillae, buccal capsule, and large, heavily sclerotized esophageal funnel. 112. Lateral view of buccal capsule and esophageal funnel.

> 8A. Esophagointestinal valve elongated; buccal cavity small, about 30 μ deep by 60 μ wide; elements of ELC almost as long as buccal capsule is deep _____ C. leptostomus



Figures 113–115. Cylicocyclus leptostomus. 113. Medial, dorsoventral view showing lateral papillae, buccal capsule, and elements of ELC and ILC, \times 400. 114. Subdorsal view showing submedian papillae, buccal capsule, and elements of ELC and ILC, \times 400. 115. Dorsal view of posterior half of esophagus showing pyriform-shaped swelling and elongated esophagointestinal valve, \times 180.

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Figures 116-119. Cylicocyclus radiatus heads, \times 375. 116. Medial, dorsoventral view of lateral papilla and buccal capsule. 117. Dorsal view of submedian papillae. 118. Medial dorsoventral view of deteriorating specimen in which esophagus is pushed into mouth cavity spreading cephalic structures. Note buccal capsule wall including hooped-shaped ring (arrow on right) and bent anterior edge (arrow on left) of buccal capsule. 119. Same specimen as preceding figure showing submedian papillae (one broken), ELC elements, and ILC elements (arrow).

Other species of Cylicocyclus:

- C. adersi—in horse, donkey, mule, and zebra in Russia and Africa. Similar to C. insigne but with walls of buccal capsule of more uniform thickness, dorsal gutter short but well developed, and fewer, wider elements in the ILC.
- C. largocapsulatus-described from horse in

Turkey. No subsequent reports. Similar to *C. radiatus* but has more, longer ILC elements, a small dorsal gutter, and a shorter bursa.

C. matumurai—described from horse in Japan. No subsequent reports. Similar to C. adersi but differs in having much smaller buccal capsule and body size and more elements in internal leaf-crown.

Discussion

The name Cylicocyclus, calling attention to the hooplike thickening at the base of the buccal capsule, was proposed by Ihle (1922) as a subgenus. Cram (1925) elevated the group to generic level. There has been general agreement concerning the relationship of most of the species presently included in this genus, exceptions being C. ultrajectinus, C. leptostomus, C. brevicapsulatus, and C. prionodes.

Ihle (1922), Cram (1924), and McIntosh (1951) included *C. ultrajectinus* in the genus *Cylicodontophorus* because of its rather long ILC elements. However, *C. ultrajectinus* has a distinct hooplike thickening of the buccal capsule; and, unlike the genus *Cylicodontophorus*, the ILC elements are much thinner than the broad ELC elements. I agree with Ershov (1939) and K'ung (1964) who placed *C. ultrajectinus* in the genus *Cylicocyclus*.

Two species with extremely shallow buccal capsules (C. brevicapsulatus and C. prionodes) were placed in the genus Cylicobrachytus by Cram (1924), McIntosh (1951), and others. However, Ershov (1939) included one of these (C. brevicapsulatus) in Cylicocyclus and K'ung (1964) included both in this genus. Figure 100 shows C. brevicapsulatus to have a very delicate buccal capsule wall, but with the characteristics of this genus. The second species with a short buccal capsule, C. prionodes, was shown by Skrjabin and Ershov (1933) to be a synonym of C. radiatus. As illustrated in Figures 118 and 119, C. prionodes is a form of C. radiatus in which the esophagus is pushed forward spreading and compressing the cephalic structures. The typical buccal capsule wall of C. radiatus with the anterior edge flared can be seen in Figure 116. Initially, I was inclined to retain C. prionodes because of a much shorter vagina than in C. radiatus, but I now believe this apparent difference to be due to extreme contraction of the vagina in the single specimen that was available.

The available specimens of *C. elongatus* from North America consist only of lots from

the Virgin Islands and Panama. Another lot from Canada was redetermined as C. insigne. Both of the above lots are C. elongatus kotlani (Ihle, 1920) that was described as a variety with a greatly elongated bursa (1.5 mm compared with 700 μ for C. elongatus elongatus). Georgi and Whitlock (1971) also reported C. elongatus kotlani from New York. Baruš (1962) and Braide and Georgi (1974) reported C. elongatus kotlani to have 52-57 elements in the ELC rather than 36 as found in C. elongatus elongatus by Looss (1902). This difference in number of ELC elements was also reported by Popova (1958). I was able to confirm these differences between C. e. elongatus and C. e. kotlani by studying paratypes of the former which Looss deposited in the USNM Helminthological Collection. In addition I observed the vagina of C. e. elongatus females to be significantly shorter than that of C. e. kotlani. These differences between the two subspecies are as great as those between many species and further study may provide convincing evidence that they are separate species. For the present I prefer to retain the subspecies designation.

C. leptostomus was assigned by Ershov (1943) to the genus Schulzitrichonema and by K'ung (1964) to Cylicotetrapedon, but I agree with Ihle (1922) in placing this species in Cylicocyclus. Although the hooplike thickening of the buccal capsule is not as distinct as in some species of the genus, it is similar to the type species, C. radiatus, and characteristics of the lateral papillae and leaf-crowns fit this genus.

K'ung and Yang (1964) proposed to divide the genus *Cylicocyclus* into three subgenera and included a new species, *C. pekingensis*. This species appears, however, to be closer to *Poteriostomum* than to *Cylicocyclus* except for the male bursa and must be considered a *species inquirenda*. I believe the combination of *C. ultrajectinus* and *C. pekingensis* in a single subgenus by K'ung and Yang (1964) to be untenable. There are generic differences between the two species.

Genus Cylicodontophorus

For species descriptions see Popova (1958, English translation, 1965)

1A. Dorsal gutter well developed; elements

120

- of ELC and ILC of nearly equal size C. bicoronatus B. Dorsal gutter absent; elements of ILC longer and broader than elements of ELC _____ 2
- 121



Figures 120, 121. Cylicodontophorus bicoronatus heads, imes 430. 120. Medial, dorsoventral view of lateral papillae, elements of ELC and ILC, and buccal capsule. 121. Dorsal view of dorsal gutter, prominent elements of ILC, tips of elements of ELC, and two submedian papillae.

2A. Elements of ILC more than twice as long as elements of ELC, esophageal funnel not well developed _____ C. euproctus



Figures 122, 123. Cylicodontophorus euproctus heads, \times 430. 122. Subventral view showing two submedian papillae, short elements of ELC, long elements of ILC, buccal capsule, and cuticular lining of buccal capsule (arrow). 123. Dorsal view of two submedian papillae, short narrow elements of ELC, longer broader elements of ILC, and cuticular lining (arrow) of buccal capsule.

B. Elements of ILC less than twice as long as elements of ELC; esophageal funnel well developed _____ C. mettami



Figures 124, 125. Cylicodontophorus mettami heads, \times 350. 124. Subventral view showing two submedian papillae, elements of ELC and ILC, buccal capsule, and esophageal funnel. 125. Lateral view of two submedian papillae, part of a lateral papilla, and elements of ELC and ILC.

Exotic species of Cylicodontophorus:

None.

Discussion

This natural group of species was recognized by Ihle (1922) and Theiler (1923) as a subgenus. Both workers included *C. bicoronatus*, *C. euproctus*, *C. ihlei*, and *Cylicocyclus ultrajectinus*. Cram (1924) raised Ihle's subgenus to the rank of genus and included the same four species. Ershov (1943) and Popova (1958) expanded the genus *Cylicodontophorus*, including three of the above-mentioned four species (excluding *C. ultrajectinus*) and adding *Cyathostomum sagittatum*, *Cyathostomum* ornatum, Cyathostomum pateratum, and C. mettami. These Russian workers considered C. ihlei to be a junior synonym of C. mettami. K'ung (1964) considered the genus to have been improperly expanded and included only C. bicoronatus, C. euproctus, and C. mettami. I agree with K'ung in this opinion. The genus Cylicodontophorus is restricted to species with the characteristics given in the generic diagnosis in the key to genera.

The status of *C. mongolica* Tshoijo, 1957, is uncertain because the illustrations (Tshoijo, 1959) are confusing and specimens of this exotic species were not available. Another species belonging to this genus, *C. schuermanni* (Ortlepp, 1962), is known only in zebras.

Genus Cylicostephanus

For species descriptions see Popova (1958, English translation, 1965)

- 1A. Buccal capsule much deeper than broad in lateral view _____ 2
- B. Buccal capsule nearly as broad or broader than deep in lateral view 4
- 2A. Walls of buccal capsule much thicker posteriorly than anteriorly; ELC composed of about 36 elements
 - C. poculatus
- B. Walls of buccal capsule of nearly uniform thickness anteriorly and posteriorly; ELC composed of 8–18 elements _______3



Figures 126-128. Cylicostephanus poculatus heads, \times 290. 126. Medial, dorsoventral view showing lateral papillae, elements of ELC and ILC, buccal capsule with cuticular lining that forms a shelflike projection (arrow), and esophageal funnel. 127. Dorsal view of submedian papillae, elements of ELC and ILC, part of the shelf (upper arrow) formed by the cuticular lining of the buccal capsule, and buttonlike dorsal gutter (lower arrow) in the floor of the buccal capsule. 128. Lateral view showing depressed mouth collar.

3A. Elements of ELC triangular, number 8; submedian papillae notched at point one-half distance between tips and buccal collar _____ C. minutus



Figures 129–131. Cylicostephanus minutus heads, \times 500. 129. Medial, dorsoventral view showing lateral papillae, lengths of elements of ELC and ILC, and buccal capsule. 130. Dorsal view of submedian papillae, elements of ELC, and dorsal gutter (arrow). 131. Lateral view showing depressed mouth collar and dorsal gutter (arrow) in wall of buccal capsule.

B. Elements of ELC digitiform number 12–18; submedian papillae notched near tips ______ C. calicatus



Figures 132–134. Cylicostephanus calicatus heads, \times 440. 132. Medial, dorsoventral view showing lateral papillae, lengths of elements of ELC and ILC, buccal capsule. 133. Dorsal view of submedian papillae, elements of ELC, and dorsal gutter (arrow). 134. Lateral view of depressed mouth collar and dorsal gutter (arrow) in wall of buccal capsule.

- 4A. Walls of buccal capsule markedly thicker anteriorly than posteriorly; elements of ELC about as broad as long; dorsal gutter extends almost to base of ILC _____5
 - B. Walls of buccal capsule of nearly uniform thickness; elements of ELC

more than twice as long as broad; dorsal gutter extends halfway or less toward base of ILC _____6

5A. Buccal capsule asymmetrical in lateral view; walls of capsule concave; teeth in esophageal funnel not prominent *C. asymetricus*



Figures 135–137. Cylicostephanus asymetricus heads, \times 290. 135. Medial, dorsoventral view showing lateral papillae, elements of ELC, buccal capsule (arrows) with cuticular lining, and esophageal funnel. 136. Dorsal view of submedian papillae, elements, of ELC and ILC, and dorsal gutter. 137. Lateral view of elements of ELC and ILC, depressed mouth collar, buccal capsule, dorsal gutter (upper arrow), and tooth (lower arrow) in esophageal funnel.

B. Buccal capsule symmetrical; walls of capsule straight; prominent teeth in esophageal funnel *C. bidentatus*



Figures 138–140. Cylicostephanus bidentatus heads, $\times 290$. 138. Medial, dorsoventral view showing lateral papillae, elements of ELC and ILC, and two large teeth projecting into buccal cavity. 139. Dorsal view of submedian papilla, elements of ELC and ILC, and dorsal gutter (arrow). 140. Lateral view showing elements of ELC and ILC, depressed mouth collar, and dorsal gutter (arrow).

- B. In dorsal view, walls of buccal capsule with slight compound curve slightly thicker anteriorly; dorsal gutter buttonlike 7



Figures 141-143. Cylicostephanus hybridus heads, \times 440. 141. Medial, dorsoventral view showing lateral papilla, elements of ELC and ILC, and buccal capsule. 142. Dorsal view of elements of ELC and ILC, with submedian papillae and dorsal gutter (arrow) slightly out of focus. 143. Lateral view of depressed mouth collar, and buccal capsule with dorsal gutter (arrow).

7A. Elements of ELC and ILC in 1:1 ratio; dorsal ray of male bursa extremely long; female tail straight; teeth in esophageal funnel not prominent C. longibursatus



Figures 144-146. Cylicostephanus longibursatus heads, \times 610. 144. Medial, dorsoventral view showing lateral papillae, lengths of elements of ELC and ILC, curved walls of buccal capsule, and small teeth (arrow) in esophageal funnel. 145. Dorsal view of elements of ELC and ILC, with submedian papillae, buccal capsule, and buttonlike dorsal gutter (arrow) slightly out of focus. 146. Lateral view of depressed mouth collar and buccal capsule.

B. Elements of ILC almost twice as numerous as elements of ELC; dorsal ray of male bursa not unusually long; fe

Figures 147-149. Cylicostephanus goldi heads, \times 380. 147. Medial, dorsoventral view of lateral papilla, elements of ELC and ILC, buccal capsule, and esophageal funnel with teeth (arrow). 148. Dorsal view of elements of ELC and ILC and teeth (arrows) in esophageal funnel, with submedian papilla and buccal capsule slightly out of focus. 149. Lateral view of elements of ELC and ILC, depressed mouth collar, buccal capsule, and esophageal funnel with teeth (arrows).

Exotic species of Cylicostephanus:

C. ornatum—occurs in Holland, Hungary, Africa, India, and Russia; similar to C. asymetricus, but has shorter dorsal gutter and shorter, stouter bursa. Although reported in North America, all specimens available for study were redetermined as other species when examined. C. skrjabini—occurs in Russia and Mongolia; similar to C. poculatus, but according to Ershov (1943) differs by lacking the lateral projection on the inner walls of the buccal capsule and by possessing a rim of dentiform processes at the bottom of the buccal capsule.

Discussion

The name *Cylicostephanus* was coined by Ihle (1922) as a subgenus to draw attention to the depressed mouth collar of a group of species including C. calicatus, C. longibursatus, C. minutus, C. hybridus, and C. poculatus. These species also share the characteristics of an ILC composed of short rods implanted close to the anterior edge of the buccal capsule; an ELC composed of longer and broader elements; and a buccal cavity that is slightly narrower anteriorly than posteriorly. Most subsequent workers have grouped these five species together. To this group Cram (1925) added the species C. asymetricus. Cylicostephanus bidentatus, a species considered by some workers to be a synonym of C. asymetricus, is recognized as a separate species because of its large esophageal teeth and relative lack of asymmetry of the buccal capsule.

The common species *C. goldi* fits well the characteristics of this genus, being very similar in cephalic characteristics to *C. longibursatus*, and is included in *Cylicostephanus* for the first time.

The position of *C. ornatum* in this genus is provisional and is based only on published de-

scriptions. Although there are several reports of C. ornatum in North America, all specimens that could be located were redetermined as other species. The characteristics of C. ornatum fit this genus; in fact, Skladnik (1935) pointed out that the illustrations of cephalic characters of C. ornatum given by Skrjabin and Ershov (1933) and repeated by others (e.g., Popova, 1958) are very similar to those of C. asymetricus.

Ershov (1943) included C. poculatus and C. skrjabini in a new genus, Petrovinema. Although this pair of species are easily recognized as distinctive, they do share the characteristics of the genus Cylicostephanus and are retained in it.

Trichonema tsengi, recently described in China, is considered to by a synonym of *C.* calicatus. It was separated from *C.* calicatus by a greater number and different shapes of ELC elements. As Baruš (1962) and Braide and Georgi (1974) have shown, however, *C.* calicatus has a greater range in number of ELC elements (12–18) than given in earlier reports and was confused with *C.* minutus by Looss (1902).

Genus Poteriostomum

For species descriptions see Popova (1958, English translation, 1965)



Figures 150–152. Poteriostomum imparidentatum heads, \times 180. 150. Medial, dorsoventral view of lateral papillae, elements of ELC, two of six extra long elements of ILC (arrows), and buccal capsule. 151. Dorsal view of two submedian papillae, elements of ELC (some of which are broken), elements of ILC (including two of the six extra long elements), and dorsal gutter (arrow). 152. Lateral view of lengths of elements of ELC and ILC, high mouth collar, and buccal capsule with dorsal gutter (arrow).



B. All elements of internal leaf-crown of equal lengths _____ P. ratzii

Figures 153-155. Poteriostomum ratzii heads, \times 140. 153. Medial, dorsoventral view of lateral papillae and buccal capsule. 154. Dorsal view of submedian papillae, elements of ELC and ILC, and dorsal gutter. 155. Lateral view of lengths of elements of ELC and ILC, high mouth collar, and buccal capsule with dorsal gutter (arrow).

Exotic species of Poteriostomum:

P. skrjabini—in horse and ass in Russia; distinguished by poorly defined dorsal gutter and short tail with vulva very close to the anus.

Discussion

This genus is closely related to the genus *Cylicodontophorus*, especially in characteristics of the leaf-crown, size, and degree of splitting of the dorsal ray. The two genera can be separated easily, however, by characters of the buccal capsule, especially the point of insertion of the internal leaf-crown and the character of the dorsal ray. The species *P. imparidentatum* and *P. ratzii* are very similar except for the difference in the internal leaf-crown. Kotlán (1921) considered *P. imparidentatum* to be a variety of *P. ratzii*. However, they are recognized almost universally as distinct species.

Craterostomum Boulenger, 1920; Ihle, 1920b Only one species of this genus occurs in North America— *C. acuticaudatum* (Illustrated on page 27)

Exotic species of Craterostomum:

C. tenuicauda Boulenger, 1920—reported from zebra in Africa and equines in India. See Discussion below for comparison with other species.

Discussion

As pointed out by Boulenger (1920) and Ihle (1920b, 1922) this genus is similar to *Triodontophorus* except for the absence of teeth in the buccal cavity. Ihle also indicated a relationship to the Cyathostominae by the presence of submedian papillae divided into two parts. Specimens of this genus are very rare and only a few *Craterostomum acuticaudatum* were available for study. Becklund (1963) listed two species occurring in equines in North America—*C. acuticaudatum* and *C. mucronatum*. I could find reports of only *C. mucronatum*; however, the point is moot because of the synonymy discussed below.

Kotlán (1919) described Cylicostomum acuticaudatum with 12-16 elements in the ILC. Ihle (1920a) described Cylicostomum mucronatum with 24 or 25 ILC elements. Ihle (1920b) moved both species to the genus Craterostomum described by Boulenger (1920) for C. tenuicauda. Ihle (1920b, 1922) recognized all three species and accepted the number of ILC elements in C. acuticaudatum as published by Kotlán (1919). However, Kotlán (1921), in a description of another species, mentioned that he considered C. mucronatum to be a synonym of C. acuticaudatum. Furthermore, in the B. H. Ransom Reprint Collection maintained at our Institute is a reprint of Kotlán's (1919) description of C. acuticaudatum bearing the notation, "Hommage de

l'auteur," in which a pen-and-ink change has been made (apparently by Kotlán) changing the number of ILC elements from 12–16 to 22–26. The reprint was sent to Ransom on 17 June 1920. There is no doubt in my mind that Kotlán, in 1920, considered *C. mucronatum* to be a synonym of *C. acuticaudatum* and that he found *C. acuticaudatum* had more ILC elements than originally reported. I agree with Skrjabin and Ershov (1933) and subsequent eastern European workers who consider *C. mucronatum* to be a synonym of *C. acuticaudatum*.

The original description of C. tenuicauda was of immature females. Most workers subsequently regarded this species as a synonym of C. acuticaudatum. However, Rai (1960) redescribed C. tenuicauda from mature females and males, separating it on the basis of a different number of ILC and ELC elements (18 and 9, compared with 22-26 and 6-8 in C. acuticaudatum), a proportionately shorter tail although the body length is greater, and the presence of submedian cephalic papillae that

Genus Triodontophorus

of this exotic species is uncertain and needs

further study.

For species descriptions see Popova (1955, English translation, 1964) except for species for which other references are given below in the key

- 1A. Mouth collar appears in optical section as inflated round tube in ring around mouth; female tail long, vulva separated from anus by 1.5–3 mm; spicules more than 3 mm long _ T. serratus



Figures 156–158. Triodontophorus serratus. 156. Dorsoventral view of head showing dorsal buccal tooth, buccal capsule, one lateral papilla on left, and elements of ELC and ILC (arrow), \times 240. 157. Dorsal view of head showing subventral papillae, elements of ELC and ILC, and dorsal gutter, \times 240. 158. Lateral view of female tail showing anus and vulva (arrow), \times 45.

- 2A. Cuticle strongly serrated in cervical region; dorsal lobe of bursa short; teeth finely denticulated *T. tenuicollis*



Figures 159–161. Triodontophorus tenuicollis. 159. Dorsoventral view of head showing two subventral buccal teeth and mouth collar with acute edge, \times 240. 160. Dorsal view of head showing submedian papilla, elements of ELC and ILC, dorsal buccal tooth, and dorsal gutter (arrow) slightly out of focus, \times 240. 161. Lateral view of cervical region showing serrated cuticle, \times 80.

3A. Submedian papillae short, broad, and conical; teeth usually smooth except for 3 elevations on each; female tail 

Figures 162–164. Triodontophorus brevicauda. 162. Medial, dorsoventral view of head showing 3 buccal teeth and buccal capsule, \times 135. 163. Dorsal view showing dorsal buccal tooth, dorsal gutter (arrow), and elements of ELC and ILC, \times 135. 164. Lateral view of female tail showing anus (lower arrow) and vulva (upper arrow), \times 110.

- B. Submedian papillae long, narrow, and pointed; teeth usually strongly denticulated; female tail short, vulva separated from anus by more than twice tail length; dorsal lobe of bursa long, $500-525 \ \mu$ 4
- 4A. Leaf-crowns consist of 56-69 elements; usually 3 large denticulations on each lateral part of each tooth; spicules 0.800-1.00 mm long T. nipponicus For species description see Diaz-Ungria (1965).



Figures 165–167. Triodontophorus nipponicus heads, \times 200. 165. Dorsoventral view of mouth collar and subventral buccal teeth. 166. Dorsal view of submedian papillae, elements of ELC and ILC, and dorsal gutter. 167. En face view showing elements of ELC and cephalic papillae.

 B. Leaf-crowns consist of 44–50 elements; usually many small to medium denticulations on each tooth; spicules 1.2–1.8 mm long ______ T. minor



Figures 168–170. Triodontophorus minor heads, \times 200. 168. Ventral view of subventral buccal teeth. 169. Dorsal view of 2 submedian papillae, elements of ELC and ILC, dorsal buccal tooth, and dorsal gutter. 170. En face view of elements of ELC and cephalic papillae.

Exotic species of Triodontophorus:

- T. popovi—in Equus in Russia; distinguished by smaller size but similar to T. tenuicollis.
- T. brochotribulatus—in horse in Spain; distinguished by small gubernaculum. Very similar to T. nipponicus.

Discussion

For many years it has been accepted that four species of this genus occurred in equines in North America-T. serratus, T. tenuicollis, T. brevicauda, and T. minor. The present study, however, could confirm no reports of T. minor in North America but did reveal T. nipponicus including some that had been previously identified as T. minor. Only three reports of T. minor in North America are known to me. Ward (1946, 1947) reported it in Mississippi. I have not located any of his specimens. Ransom and Hadwen (1918) are sometimes listed as reporting T. minor in Canadian horses, but although they figured it, they specifically stated that this species was not found in their survey. Baker and Fincher (1937) reported T. minor in a horse in New York State, but their specimens have not been located. In current studies at this Institute T. nipponicus has been found in a single horse.

Prior to the description of T. nipponicus, T. minor was reported all over the world. Subsequently, however, T. nipponicus rather than T. minor has usually been identified. Yamaguti (1943) described T. nipponicus from Equus caballus orientalis and Equus parvis in Japan and Korea. This species has been reported subsequently in Brazil (Jorge da Silva, 1955),

Czechoslovakia (Baruš, 1962), and in in Venezuela (Diaz-Ungria, 1963, 1965). Furthermore, Diaz-Ungria (1963) extended the known range of T. nipponicus to China by making T. hsiungi K'ung, 1958, a synonym of T. nipponicus. K'ung, et al. (1959) listed T. hsiungi as one of the most common strongyles in donkeys in Peking. In addition, T. minor has been reported in Panama by Foster (1936) and in Antigua by Goodwin (1936). However, both Foster's and Goodwin's specimens have been found to be T. nipponicus. Other specimens available for study included several lots from Los Banos, Philippine Islands, previously reported as T. minor. These have also been redetermined as T. nipponicus. In these studies I have been fortunate to have for comparison numerous paratypes of T. minor. Presumably, the geographic distribution of T. minor is more restricted than previously believed.

Genus Strongylus

For species descriptions see Popova (1955, English translation, 1964)

| 1A. | Prominent teeth present in buccal cav- |
|-----|--|
| | ity 2 |
| В. | Teeth absent from buccal cavity |
| | S. edentatus |
| | |
| 2A. | Both dorsal and ventral teeth present |

- B. Only dorsal tooth with 2 rounded lobes present in buccal cavity ______ 3

- B. Lobes of tooth low and grooved, extend

only one-third depth of buccal cavity; ILC and ELC about same length _____ ______S. asini*

* Not known in North America except in zebra. Not illustrated.



Figures 171–173. Strongylus spp. heads, lateral view. 171. Strongylus edentatus, showing globular buccal capsule without buccal teeth, dorsal gutter (arrow), high mouth collar, small cephalic papillae, and elements of ELC, \times 27. 172 Strongylus equinus, showing large globular buccal capsule with dorsal and ventral buccal teeth and dorsal gutter, \times 27. 173. Strongylus vulgaris, showing dorsal buccal tooth and dorsal gutter, \times 47.

Exotic species of Strongylus:

Only S. asini-see above key.

Discussion

In 1900, Looss described three species in the genus Strongylus—S. equinus, S. edentatus, and S. vulgaris. In 1920, Boulenger described S. asini. Railliet (1923) subdivided the genus into four subgenera—Strongylus, Alfortia, Delafondia, and Decrusia. According to Ershov (1943) and others, Skrjabin divided Strongylus into three genera in 1933 (reference could not be determined) using three of the above subgenera, excluding the last, based on the number of buccal teeth present. I prefer to retain the four exceptionally similar species from equids in the genus Strongylus, without the subgeneric names.

Genus Micronema

Micronema Korner, 1954—only one species of this genus is known to occur in equids— Micronema deletrix (illustrated on pages 28 and 62).

Other species

Several other species of the genus have been described as saprophagous in decaying humus.

Discussion

This species has been found in granulomatous tissue in the nares (Anderson and Bemrick, 1965) and maxilla (Johnson and Johnson, 1966) of a horse in Minnesota; in the brain of a pony in Georgia (Stone et al., 1970); in the brains of two horses in Egypt (Ferris et al., 1972); and in the brain of a child in Canada (unpublished, Armed Forces Institute of Pathology case record). Typical of nematodes of the order Rhabditida, at least one species of the genus *Micronema*, which are normally saprophagous, can successfully lead a parasitic life. Extremely large numbers of these nematodes were found in diseased tissues by Stone et al. (1970) and by Ferris et al. (1972). *Rhabditis gingivalis* Stefanski, 1954, was described from the gum of a horse in Poland. Because the description is incomplete, it is uncertain whether this species belongs in the genus *Micronema*. If it can be shown because of stomatal characters to belong to the genus *Micronema*, the specific characters will necessitate reducing *M. deletrix* to a junior synonym of Stefanski's species.



Figures 174–176. Micronema deletrix, (figures from Chitwood and Lichtenfels, 1972). 174. Longitudinal section in human brain showing rhabditiform esophagus with corpus (upper arrow), narrow isthmus surrounded by nerve ring, and valved bulb (lower arrow), \times 550. 175. Cross section in human brain showing intestine above and ovary below, \times 1,350. 176. Part of longitudinal section in brain of horse showing gonad with germinal end of ovary reflexing dorsad (lower arrow) and ova increasing in size toward ventral flexure (upper arrow), \times 1,350.

Genus Habronema

For brief species descriptions see Soulsby (1965) or Levine (1968)



Figures 177-179. Habronema majus. 177. Head, medial, lateral view showing dorsal and ventral buccal teeth (arrows), \times 360. 178. Head, medial, dorsoventral view of buccal capsule, and lateral lips with lateral papillae (arrows), \times 360. 179. Lateral view of female showing vulva, short vagina, and large rounded muscular ovejector, \times 200.

 B. Teeth absent from buccal capsule; left spicule 5 times length of right; vagina very long and narrow, crosses body transversally before reaching long muscular ovejector ______ H. muscae



Figures 180–182. Habronema muscae. 180. Head, lateral view (slightly lateral to medial), buccal capsule with prominent projections (arrow) but no teeth (*H. majus* has similar structures at different focal plane than teeth shown above), \times 400. 181. Head, medial, dorsoventral view showing lips, lateral papillae (arrows), and debris in buccal cavity, \times 400. 182. Lateral view of female showing vulva (upper arrow) and long muscular part of ovejector (lower arrow), \times 140.

Exotic species of Habronema:

H. tyosenense—found only once in pony in Korea; similar to *H. majus* except for a different arrangement of genital papillae and a longer vagina and ovejector.

Discussion

The two well-known species can be separated easily on the bases of vaginal and spicular length and the ovejector morphology. The teeth, high in the buccal capsule of H. majus, are seen best in a lateral view and can be used effectively to separate the species.

Genus Onchocerca

For species descriptions see Levine (1968)

1A. Parasitic in connective tissue of flexor tendons and suspensory ligament of fetlocks; left spicule $248-294 \mu$ long; cuticle of female with one internal stria between each pair of ridges; microfilariae $330-370 \mu$ long

..... O. reticulata

For illustrations of *O. cervicalis*, see the Key to Genera, Figures 77–80.

Exotic species of Onchocerca:

None.

Discussion

After considerable study by many experienced workers, the question of whether Onchocerca reticulata and O. cervicalis are two separate species is still unsettled. Furthermore, the distribution of the (?) two species is also confusing because the lumpers have reported the form in the ligamentum nuchae (O. cervicalis) as O. reticulata, the older name. Although both names have been reported in North America, I have been unable to confirm reports of the form that occurs in suspensory ligaments of fetlocks. Supperer (1953) and others have separated the two species on differences between lengths of the left spicule and the microfilariae. Recently, Beaver (1974) pointed out cuticular differences, previously described by others, as further evidence for recognizing females of both species. However, Mellor (1974) considered the cuticular differences he observed in O. cervicalis to be too variable in different regions of the nematode body to be useful in separating the two species. He also reported considerable variation in morphology and size of microfilariae of O. cervicalis. In my observations of the cuticle of O. cervicalis, the internal striae are difficult to detect in the posterior and especially the anterior portions of the female where the external ridges are also reduced in size and are closer together. Where the internal striae could be observed they were found to be narrower in regions where the external ridges were closer together, but still present in the ratio of four internal striae between each pair of ridges. I did not have specimens of O. reticulata for study. Until sufficient specimens of O. reticulata become available for study, I prefer to retain both names in order to obtain separate data for what may be two different species. It will be much easier to combine data than to attempt to separate it later.

E. Larvae and Life History of Nematoda Parasitic in Equids

This section describes immature or larval stages of nematodes that are commonly encountered in horses and are so different from the adult stage that they are not easily identifiable with them. Only the part of the life cycle that occurs in horses is described.

Fourth-stage larvae of *Strongylus oulgaris* may be found in the intestinal wall or in widely scattered sites in the arterial system, especially the cranial and other mesenteric arteries, where they may cause aneurysms. The incidence of infection is very high, approaching 100 %. In the intestinal wall the most common sites are the submucosa of the cecum and colon.

Much controversy has existed over the route larvae take to reach the sites of arterial lesions (Soulsby, 1965), but the only investigators who have studied experimental infections (Enigk, 1950, 1951; Drudge et al., 1966; Duncan and Pirie, 1972) agree that the fourthstage larvae migrate upstream in the mesenteric arteries. The chronology according to Enigk (1950, 1951) is as follows: Infective larvae enter the wall of the ventral colon and cecum and molt to the fourth stage 6 to 7 days after infection. At this stage they are about 2.5 to 2.9 mm long. From about 11 to 111 days after infection they are found in the arterial lesions. Most fourth-stage larvae remain in arterial aneurysms until 44 to 111 days after infection, attaining lengths of 14 to 18 mm. The larvae then migrate downstream by way of the arterial system to the submucosa of the cecum and colon where they become immature adults after about 90 or more days. After reaching the intestinal lumen they mature, about 200 days after infection. In some cases, however, adult nematodes may be found in arterial lesions or in other sites along the migration route to the cecum and colon. Figures 183 and 184 show fourth-stage larvae of S. vulgaris from aneurysms and Figures 185 and 186 show early fifth or adult stages of the same species from the intestinal wall or lumen.

According to Wetzel (1940), larvae of *Strongylus equinus* are found in the walls of the cecum and colon where they molt to the fourth stage. The larvae then migrate to the subserosa where they grow in nodules for about 11 days, reaching lengths of 10 to 15 mm. They develop a provisional buccal capsule before migrating by way of the body cavity to the liver where they molt to the immature adult stage. After 2 to 4 months the adults migrate to the colon and cecum by way of the pancreas.

Strongylus edentatus larvae reach the liver by way of the portal vein, according to Wetzel and Keersten (1956), where they molt to the fourth stage. After 9 weeks of burrowing and growing in the liver, the larvae migrate under the peritoneal membranes to the right flank where the fourth and early fifth stages are found in hemorrhagic nodules. After molting to fifth stage in about 90 days, *S. edentatus* migrates to the wall of the colon and cecum and forms nodules that eventually open to the lumen of the intestine where the nematode matures. The larvae migrate erratically and may be found in unusual sites such as testicles, thoracic cavity, and kidneys.

Little is known of life history and larval development of strongyles other than *Strongylus*. The infective larvae of *Triodontophorus* and those of Cyathostominae enter the walls of the intestine where they cause the formation of small nodules in the mucosa, molt to the fourth stage, and usually develop to early fifth stage before returning to the lumen. There is no evidence of a migration from the intestine. Frequently fourth-stage larvae of *Triodontophorus* and occasionally those of Cyathostominae are found in the lumen of the intestine rather than in mucosal nodules. Fourth-stage *Triodontophorus* (Figs. 187–190) can be recognized by the presence of three lancet-shaped teeth that project well into the buccal cavity.

According to Popova (1958), Tiunov observed in 1949 that infective cyathostomin larvae in the intestine are about 328 to 685 μ long. The larvae penetrate the walls of the large intestine and localize in the tunica propria and submucosa. After 9 to 10 days, the larvae are 1.2 to 4.6 mm long, apparently varying with the species. Most cyathostomin larvae molt once in the wall of the intestine before returning to the intestinal lumen, but some molt twice to the adult stage. The molt to the fourth stage occurs 6 to 12 days after infection when the larvae are 2.3 to 4.9 mm long. Most of the species enter the lumen of the intestine in fourth stage after 1 to 2 months when they are 3.6 to 7.2 mm long.

Popova (1958) reported that Tiunov observed only longer larvae (6.0 to 13.0 mm) in the submucosa. These larvae have two buccal capsules, the adult capsule surrounding the larval capsule (Fig. 192). The adult buccal capsule can be identified as that of *Cylicocyclus*. These larvae, unlike some other cyathostomin larvae, remain in the submucosa until they have molted to the adult stage.

Larvae of the stomach worms, Habronema muscae, H. majus, and Draschia megastoma, undergo development in various muscid flies before they are infective for horses. Thirdstage infective larvae leave the fly by way of its mouthparts to be deposited on the lips, nostrils, or wounds of horses. It is also likely that horses become infected by swallowing flies. When larvae are swallowed they enter the mucosa of the glandular stomach. According to Ransom (1913), Bull (1919), and Roubard and Descazeaux (1921, 1922) third-stage larvae of D. megastoma leaving the fly are 2.5 to 3.0 mm long with a cylindrical buccal capsule resembling that of the adult, a spiny knobby-tipped tail, and a truncated anterior end. Third-stage larvae of H. muscae are similar to D. megastoma in size but have a rounded anterior end. Third-stage larvae of H. majus are much shorter (~ 1.6 mm long) and, according to Bull (1919), lack the longitudinal ridges found on the cuticle of the other two According to Nishiyama (1958), species. Draschia megastoma larvae have a funnelshaped buccal capsule and constricted head somewhat like the adult, and H. majus larvae have a plumper tail than do H. muscae larvae. After entering the stomach mucosa, larvae of D. megastoma reach the adult stage in about 2 months.

When infective larvae of *Habronema* and *Draschia* are deposited in wounds, they may cause a condition known as "summer sores," in which larvae may persist but do not complete development. According to Nishiyama (1958), infective larvae can initiate such cutaneous sores in addition to contaminating existing wounds. Third-stage larvae of *Habronema* spp. and *D. megastoma* can also cause a conjunctivitis when deposited near the eyes. If larvae are found in the lesions, they can be recognized by the spiny knobs on their tails.

Habronema muscae and Draschia megastoma larvae also occur in nodules in lungs of horses in localities where the nematodes are common. Typical larvae with the characteristic spiny tail can be found in early lesions. According to Soulsby (1965) they probably derive from skin lesions.

The life cycle of Oxyuris equi (Figs. 200-204) is direct, with infection resulting from ingestion of eggs on contaminated litter or fodder. The eggs hatch in the small intestine and third-stage larvae burrow into crypts of the mucosa of the cecum and ventral colon. The molt to fourth stage occurs 3 to 10 days after infection. Two sizes of fourth-stage larvae are found: males (5 to 6 mm long) with a shorter tail that tapers abruptly behind the anus and ends in a thin tapering point (Fig. 202) and females (5 to 10.5 mm long) with a long gradually tapering tail (Fig. 203). Both male and female are widest at the anterior ends and may appear to the unaided eye to be broken posterior parts of nematodes. The short broad muscular esophagus consists of a posterior oval bulb and a larger greatly expanded corpus (Figs. 200, 201) that can open very wide to serve as a buccal capsule for attaching to the intestinal mucosa (Fig. 204).

Figures 183–186. Strongylus vulgaris. 183. Fourth-stage larva, anterior end, \times 50. 184. Fourth-stage larva, head showing buccal apparatus of fourth stage and surrounding cavity in which buccal capsule of adult forms, \times 210. 185. Head of immature adult within cuticle of fourth stage, from wall of intestine, \times 50. 186. Tail of female immature adult, from wall of intestine, \times 50.

Figures 187–190. Triodontophorus sp. fourth-stage larvae. 187. Medial, dorsoventral view of head showing three buccal teeth and lateral papillae (arrow), $\times 140$. 188. Dorsal view of head showing one dorsal tooth, two submedian papillae, and elements of external leaf-crown, $\times 140$. 189, 190. Lateral views of tails of larvae that may reflect different species, $\times 110$.

Figures 191–194. Fourth-stage larvae of (?) Cylicocyclus sp. 191. Lateral view, anterior end, \times 55. 192. Lateral view of head showing buccal capsule of fourth stage surrounded by early stages of formation of adult buccal capsule (arrows), \times 220. 193. Lateral view of head showing buccal capsule with dorsal tooth (arrow), \times 220. 194. Lateral view of tail, \times 55.

Figures 195, 196. Cyathostomin fourth-stage larva. 195. Lateral view of head showing buccal capsule with dorsal tooth, \times 220. 196. Lateral view of tail, \times 220.

Figures 197–199. Habronema muscae larvae from horse stomach, \times 350. 197. Head, showing buccal capsule similar to that of adult. 198. Cuticle, showing cross-striations and longitudinal ridges. 199. Tail, showing anus and spiny knobby tip.




Figures 200-204. Oxyuris equi fourth-stage larvae. 200, 201. Anterior ends showing slightly different appearance depending on how wide the mouth is opened, $\times 110$. 202. Male tail, lateral view, $\times 60$. 203. Female tail, lateral view, $\times 60$. 204. Longitudinal section through esophagus showing corpus engorged with intestinal tissue of the host, $\times 300$.

F. Microfilariae

Microfilariae, the motile embryos that are released into host tissues by some female filariin nematodes, are sometimes found in the blood or the skin of horses. The following key for the identification of microfilariae of horses was first published by Supperer (1953), modified slightly by Soulsby (1965) and further modified slightly here.

Key to Microfilariae of Equids

- B. Without sheath or internal body 2
- 2A. Less than 200 μ long; with rounded posterior end; on surface of skin or

in hemorrhagic nodules of horse _____ _____ Parafilaria multipapillosa*

- - B. Tail long, whiplike _____ 4
- 4A. Distance from genital cell to tip of tail more than 140 μ; in skin of horse Onchocerca reticulata
 - B. Distance from genital cell to tip of tail, less than 120 μ; in blood of horse Elaeophora boehmi*

^{*} Not known to occur in North America.

V. Cestoda Parasitic in Domestic Equids

Three cestode species, in two genera of the family Anoplocephalidae, occur as adults in domestic equids. Anoplocephala perfoliata, Anoplocephala magna, and Paranoplocephala mamillana are cosmopolitan in distribution. Until recently it was believed (Soulsby, 1965) that A. magna was the most common species in North America and A. perfoliata was the most common species in other parts of the world. After corresponding with workers who have autopsied horses over many years in North America, I believe that A. perfoliata is about as common as A. magna. Massive infections with these cestodes can be quite pathogenic, resulting in perforation of the intestine and death of the equid. Oribatid mites are the intermediate hosts.

A fourth species, *Moniezia pallida*, has been found only once in South Africa causing authorities to doubt its validity (Spasskii, 1951). Because only a few cestode species are found as adults in horses, a single key to all species is given below. *Moniezia pallida* is included but not illustrated. Species diagnoses are included in the key. Characters used in the key are those that can be determined with the unaided eye without any processing of specimens.

All other cestodes reported from domestic equids are larval forms of the family Taeniidae. Only *Echinococcus granulosus* larvae occur in a significant number of equids. The larvae are listed in the section "Unusual, Accidental, or Occasional Helminths of Domestic Equids."

A. Key to Species

- B. Neck very short, well-defined wide proglottids begin closely behind scolex that is flattened anteriorly; genital apparatus not double ______2

**Moniezia pallida*—only species of genus found in horses. DIAGNOSIS:

Monieziinae. Up to 138 cm long, 21 mm wide. Craspedote. Scolex rounded, 0.75 mm wide, with 4 rounded suckers directed obliquely anteriorly. A well-defined neck follows scolex. Developing segments 0.75 mm long, 11.0 mm wide; mature segments 15-21 mm wide. Interproglottidal glands arranged linearly. Excretory system of 4 longitudinal trunks and transverse canals with dorsal canals internal to ventrals. Genital apparatus double, pores somewhat anterior to middle of lateral edges of segment. Vagina opens ventrally to cirrus pouch on the right and dorsally on the left. Numerous testes in central field of segment. Cirrus pouch 0.23 mm long and 0.08 mm thick. Cirrus unarmed. Female reproductive organs lie laterally in central field; a fan-shaped, lobed ovary 1.06 mm wide, 0.48 mm long; vitellarium dorsal to ovary; developing uterus, a net of thin tubes, occupies entire central field of segment.

- 2A. Scolex with lappet behind each sucker Anoplocephala perfoliata
- B. Scolex without lappets _____ 3

Anoplocephala perfoliata. DIAGNOSIS: Anoplocephalinae. Up to 80 mm long, but usually 25-40 mm long; 8-14 mm wide. Markedly craspedote. Scolex rounded, but with flattened anterior surface 2-3 mm wide. Four earlike lappets 0.5-1.0 mm at posterior edge of scolex. Four powerful, spherical suckers on anterior surface of scolex. Neck very short, strobila widens rapidly. Developing segments 100 times wider than long, 0.02-0.04 mm long, 2-2.5 mm wide. Hermaphrodite segments 0.16-0.20 mm long, 8-9 mm wide. Excretory system complicated reticulum of anastomosing canals. Genital apparatus single, unilateral, situated in anterior half of

^{*} Not known to occur in North America, but reported elsewhere in domestic equids, not illustrated.

lateral marginal edge of segment. Numerous testes throughout central area. Cirrus long, may be armed, in pouch 0.8-1.2 mm long. Female

organs in middle of central field, 2.4 mm wide with many lobules. Uterus in central field consists of tubes with bulges.



Figure 205. Anoplocephala perfoliata. Entire specimen, dorsoventral view, showing two of four lappets at base of scolex, $\times 4$.

3A. Scolex 4 to 6 mm wide; strobila large, 25 mm wide, up to 800 mm long _____ Anoplocephala magna

> Anoplocephala magna. DIAGNOSIS: Anoplocephalinae. Largest cestode of horses, up to 520 mm long and 25 mm wide. Markedly craspedote. Large anteriorly flattened scolex 2.8– 3.0 mm wide with 4 powerful round suckers 1.0–1.2 mm in diameter. Neck absent. Immature segments 0.05 mm long, 3.0–4.0 mm wide; hermaphrodite segments 0.25 mm long,

7.0 mm wide; mature segments 2.5 mm long, 8.0 mm wide. Excretory system of complicated network of anastomosing canals. Genital apparatus single, unilateral, with pores on posterior half of lateral edge of segment. Numerous testes in dorsal half of central field. Cirrus covered with small spines. Developed ovarium occupies entire width of central field. Uterus is thin transversal chord across central field, later becomes tube with pouches.



Figure 206. Anoplocephala magna. Entire specimen, dorsoventral view, showing large flattened scolex, $\times 2$.

B. Scolex 0.7 to 0.8 mm wide; strobila small, 4 to 6 mm wide, 10 to 40 mm long _____ Paranoplocephala mamillana

> Paranoplocephala mamillana. DIAG-NOSIS: Anoplocephalinae. About 30 mm long and 5 mm wide. Craspedote. Scolex flattened anteriorly, 1.1 mm wide, with 4 round muscular suckers. Neck very short, 0.2 mm long. Strobila short and wide with several dozens of segments. Immature segments 0.08 mm long, 1.1 mm wide; hermaphrodite segments 1.4 mm long, 5.0 mm wide. Excre-

tory system consists of 2 pairs of longitudinal vessels within 0.5 mm of edge of strobila. Ventral vessels with transverse canals in posterior part of segments. Genital apparatus single, unilateral, with ducts dorsal to excretory vessels. About 100 rounded testes in central field aporally to female reproductive glands that lie in poral half of central field. Cirrus pouch 1.0-1.3 mm long, cigar-shaped, 0.2 mm thick. Cirrus armed. Ovary fanshaped with numerous lobules. Uterus develops into stemlike sac with numerous outpocketings.



Figure 207. Paranoplocephala mamillana. Portions of two specimens, dorsoventral view, showing small scolex, \times 5.

VI. Trematoda Parasitic in Domestic Equids

Of the trematodes reported from horses, only three species in two genera (*Gastrodiscus* and *Pseudodiscus*) are primarily parasites of horses; none are known to occur in North America. A key and generic diagnoses are given below for these two exotic genera. Other trematodes that have been reported from horses, but are primarily parasites of other hosts, are listed in a special section "Unusual, Accidental, or Occasional Helminths of Horses."

A. Key to Genera

1A. Body with cylindrical anterior portion and disc-shaped posterior portion that has numerous papillae on concave ventral surface Gastrodiscus*

> *Gastrodiscus Leuckart, 1877. DIAG-NOSIS: Gastrodiscinae. Body divided into small subcylindrical anterior portion and large posterior disc with numerous papillae on its concave ventral surface. Ventral sucker small, subterminal. Oral sucker with prominent paired diverticula. Esophagus with muscular thickening. Ceca long, simple, extend to region anterior to ventral sucker. Testes lobed or branched, diagonal, in middle third of body; seminal vesicle convoluted; pars musculosa inconspicuous; cirrus pouch absent. Genital pore with

out sucker, near anterior margin of disc. Ovary lobate, submedian, posterior to testes. Laurer's canal present. Parasitic in intestine. Type species: *G. aegyptiacus*. Other species: *G. secundus* and *G. equi*. For species descriptions see Maple-

stone (1923) and LeRoux (1938). B. Body with conical anterior end widening gradually to oval leaflike shape *Pseudodiscus**

> *Pseudodiscus Sonsino, 1895. DIAG-NOSIS: Pseudodiscinae. Body conical, conspicuously serrated along anterior lateral margins. Ventral sucker Oral sucker with paired ventral. pouchlike diverticula. Esophagus without muscular thickening. Ceca long, simple, extending to level of ventral sucker. Testes multilobed, symmetrical, preovarian, in equatorial region; pars musculosa well developed; cirrus pouch absent. Genital pore without sucker. Ovary anterior to ventral sucker. Laurer's canal opens far anterior to excretory pore. Parasitic in colon.

> Type species: *P. collinsii*. Other species: None. For species descriptions see Rai (1959) or Stiles and Goldberger (1910).

^{*} Not known to occur in North America, but reported elsewhere in domestic equids, not illustrated.

VII. Unusual, Accidental, or Occasional Helminths of Domestic Equids

Records of the Index-Catalogue of Medical and Veterinary Zoology (U.S. Department of Agriculture, 1966–74, and unpublished) were searched for reports of helminths that occur in horses but normally occur in nonequid hosts. An asterisk precedes the current name of species not known to occur in North America. Only synonyms that have also been reported from horses are included.

Nematoda

Order Strongylida Suborder Strongylina Family Oesophagostomidae

Oesophagostomum venulosum (Rudolphi, 1809)

Family Syngamidae

Syngamus sp. DeDoes, 1907 Stephanurus dentatus Diesing, 1839

Family Uncinariidae

Uncinaria stenocephala (Railliet, 1884) Bunostomum trigonocephalum (Rudolphi, 1808) =Sclerostoma hypostomum (Rudolphi, 1819)

> Suborder Trichostrongylina Family Trichostrongylidae

Cooperia oncophora (Railliet, 1898) Ransom, 1907

- Nematodirus spathiger (Railliet, 1896) Railliet and Henry, 1909
- Ostertagia ostertagi (Stiles, 1892) Ransom, 1907

Trichostrongylus colubriformis (Giles, 1892) Trichostrongylus instabilis Railliet, 1893

Family Dictyocaulidae

Dictyocaulus viviparus (Bloch, 1782) =Strongylus micrurus Mehlis, 1831

> Order Ascarida Suborder Ascaridina Family Ascarididae

Ascaris lumbricoides Linnaeus, 1758 Toxocara cati (Schrank, 1788) Suborder Oxyurina Family Oxyuridae

Passalurus ambiguus (Rudolphi, 1819)

Order Spirurida Suborder Spirurina Family Thelaziidae

Thelazia rhodesii (Desmarest, 1827) Blainville, 1828

**Thelazia floresiana* Smit and Notosoediro, 1930

Family Ascaropsidae

*Simondsia paradoxa Cobbold, 1864 Physocephalus sexalatus (Molin, 1860) =Spiroptera sexalata Molin, 1860 Physocephalus cristatus (Seurat, 1912)

Family Spirocercidae

Spirocerca lupi (Rudolphi, 1809) =Spirocerca sanguinolenta (Rudolphi, 1819)

Family Gongylonematidae

Gongylonema pulchrum Molin, 1857 =Gongylonema scutatus (Leuckart, 1873) =Spiroptera scutata Mueller, 1869 =Gongylonema confusum Sonsino, 1896

> Suborder Camallanina Family Dracunculidae

Dracunculus medinensis (Linnaeus, 1758) =Filaria medinensis (Linnaeus, 1758) =Dragonneau chanterelle of Degland, 1821

> Suborder Filariina Family Dirofilariidae

Dirofilaria immitis (Leidy, 1856) =Filaria sanguinis equi Sonsino, 1876 =Filaria cordicola Linstow, 1905

Dirofilaria repens Railliet and Henry, 1911 =Filaria conjunctivae Addario, 1885

- *=Dirofilaria conjunctivae* (Addario, 1885)
- =Filaria oculi asini Condorelli-Francaviglia, 1892

=Filaria inermis Grassi, 1887

=Filaria apapillocephala Condorelli-Francaviglia, 1892

Family Onchocercidae

Onchocerca gutturosa Neumann, 1910 =Onchocerca bovis Piettre, 1912

Family Dipetalonematidae

*Dipetalonema spirovolutum (Smit and Ihle, 1925) Sprehn, 1932

Family Setariidae

Setaria labiatopapillosa (Alessandrini, 1838) =Filaria labiatopapillosa Alessandrini, 1838 Setaria digitata Linstow, 1906

=Aritionema digitata (Linstow, 1906) Yeh, 1959

> Order Trichinellida Family Trichinellidae

Trichinella spiralis (Owen, 1835)

Order Dioctophymatida Family Dioctophymatidae

Dioctophyma renale (Goeze, 1782)

=Eustrongylus gigas (Rudolphi, 1782)

=Strongylus gigas Rudolphi, 1802 =Eustrongylus visceralis (Gmelin, 1790)

Nematoda of Uncertain Classification Ancylostoma incertum Sonsino, 1896 Sclerostoma rubrum Theobald, 1898 Dispharagus reticulatus Tokishige, 1898 Filaria pellucida Brown, 1823 Piguris reticulata Schlotthauber, 1860

ACANTHOCEPHALA

Macracanthorhynchus hirudinaceus (Pallas, 1781)

CESTODA (larvae)

Family Taeniidae

Multiceps multiceps (Leske, 1780) Hall, 1910

- =Polycephalus multiceps (Leske, 1780)
- =Polycephalus coenurus (Küchenmeister, 1853)
- =Taenia coenurus Küchenmeister, 1853
- =Coenurus cerebralis (Batsch, 1786)
- =Coenurus taeniaemulticipitis Leske, 1780 Multiceps serialis (Gervais, 1847) Stiles and Stevenson, 1905
- Taenia solium Linnaeus, 1758
- Taenia tenuicollis Rudolphi, 1819

Taenia hydatigena Pallas, 1766

=Cysticercus taeniaehydatigenae Pallas, 1776

=Taenia fistularis (Rudolphi, 1805)

- =Cysticercus fistularis Rudolphi, 1805
- Echinococcus granulosus (Batsch, 1786) Rudolphi, 1801
 - =Echinococcus polymorphus Diesing, 1850
 - =Taenia granulosa (Batsch, 1786)
 - =Taenia echinococcus Siebold, 1853

Echinococcus multilocularis Leuckart, 1863

TREMATODA

Family Paramphistomidae Subfamily Paramphistominae

Paramphistomum cervi (Schrank, 1790) Fischoeder, 1901

=Monostomum conicum Zeder, 1803

Subfamily Pseudodiscinae

*Hawkesius hawkesi (Cobbold, 1875) Stiles and Goldberger, 1910

=Pseudodiscus ornatus (Cobbold, 1882) Sonsino, 1895

> Family Dicrocoeliidae Subfamily Dicrocoeliinae

- Dicrocoelium dendriticum (Rudolphi, 1819) Dujardin, 1845
 - =Dicrocoelium lanceatum Stiles and Hassall, 1896
 - =Dicrocoelium lanceolatum (Rudolphi, 1803) Weinland, 1858a

Family Fasciolidae Subfamily Fasciolinae

Fasciola hepatica Linnaeus, 1758

=Fasciola hepatica equi Gmelin, 1790

Fasciola gigantica Cobbold, 1855

- =Cladocoelium giganteum (Diesing, 1858) Stossich, 1892
- =Fasciola humana Gmelin, 1790
- Fascioloides magnus (Bassi, 1875) Ward, 1917
 - =Distomum crassum Cobbold of Leidy, 1891
 - =Fasciola americana Hassall, 1891
 - =Fasciola carnosa Hassall, 1891
 - =Distomum texanicum Francis, 1891

Family Schistosomatidae Subfamily Schistosomatinae

- *Schistosoma japonicum Katsurado, 1904
- *Schistosoma bovis (Sonsino, 1876) Blanchard, 1895
- =Bilharzia crassa Sonsino, 1888
- *Schistosoma indicum Montgomery, 1906
- Schistosoma haematobium (Bilharz, 1852) Weinland, 1858
- =Bilharzia magna Cobbold, 1859
- *Schistosoma spindale Montgomery, 1906

*Orientobilharzia turkestanica (Skrjabin, 1913) Srivastava, 1957

> Family Brachylaimidae Subfamily Brachylaiminae

*Brachylaima suis (Balozet, 1936) Yamaguti, 1971

Family Gastrothylacidae Subfamily Gastrothylacinae **Gastrohylax* sp. Henry and Joyeux, 1920

VIII. Helminths from Zebras that Do Not Also Occur in Other Equids

NEMATODA

Order Strongylida Suborder Strongylina Family Strongylidae Subfamily Cyathostominae

- Crossocephalus viviparus (Linstow, 1899) Railliet, 1909
 - =Pterocephalus viviparus Linstow, 1899
 - =Crossocephalus zebrae Yorke and Southwell, 1920
- Cylicocyclus gyalocephaloides (Ortlepp, 1938) Popova, 1952
 - =Trichonema (Cylicocyclus) gyalocephaloides Ortlepp, 1938
- Cylicodontophorus schuermanni (Ortlepp, 1962) Round, 1968
 - =Trichonema (Cylicodontophorus) schuermanni Ortlepp, 1962
- Cylindropharynx brevicauda Leiper, 1911
- Cylindropharynx dollfusi Le Van Hoa, 1962
- Cylindropharynx intermedia Theiler, 1923
- Cylindropharynx longicauda Leiper, 1911
- Cylindropharynx ornata Cram, 1924
- Cylindropharynx rhodesiensis Yorke and Macfie, 1920

Cyathostominae Not Referable to Genus

- Trichonema (Javellia) aequatorialis Ricci, 1939
- Trichonema (Cylicocyclus) aethiopicus Ricci, 1939
- Trichonema (Borania) maestrii Ricci, 1939
- Trichonema (Skladnikia) symmetrum Ricci, 1939
- Trichonema (Zebrincola) zavattarii Ricci, 1939

Order Spirurida Suborder Spirurina Family Spiruridae Subfamily Habronematinae

Habronema longistoma Berghe, 1943 Habronema zebrae Theiler, 1923

> Suborder Filariina Family Setariidae Subfamily Setariinae

Setaria hornbyi Boulenger, 1921

Order Ascarida Suborder Ascaridina Family Ascarididae Subfamily Ascaridinae

Parascaris zebrae (Skrjabin, 1916) Yorke and Maplestone, 1926

=Ascaris zebrae Skrjabin, 1916

Suborder Oxyurina Family Oxyuridae Subfamily Oxyurinae

Oxyuris tenuicauda Linstow, 1901

Cestoda

Order Cyclophyllida Family Anoplocephalidae Subfamily Anoplocephalinae

- Anoplocephala rhodesiensis Yorke and Southwell, 1921
 - *=Taenia zebrae* Collin, 1891, not Rudolphi, 1808
 - =Anoplocephala zebrae of Fuhrmann (1909, 1910)
 - =Anoplocephala perfoliata zebrae Baer, 1923. (This cestode has occasionally been reported in donkeys in Africa.)

Trematoda

Order Echinostomatida Family Paramphistomatidae Subfamily Paramphistomatinae

- Cotylophoron cotylophorum (Fischoeder, 1901) Stiles and Goldberger, 1910
 - =Paramphistomum cotylophorum Fischoeder, 1901

Order Strigeatida Family Schistosomatidae Subfamily Schistosomatinae

- Schistosoma margrebowiei (LeRoux, 1933) Price, 1933
- *=Bilharzia margrebowiei* LeRoux, 1933
- Schistosoma leiperi LeRoux, 1955
 - =Schistosoma spindalis Montgomery, 1906, of LeRoux (1932, 1933, 1939)

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XI. Alphabetic Index of Genera, Subgenera, Species, and Subspecies Including Synonyms

This index is intended to make it possible to find all places in the manuscript where any subspecies, species, subgenus, or genus is mentioned or illustrated. For species and subspecies, the author and date of the taxon are included and are followed by the genus in which it is placed in this treatise. Subgeneric names are also followed by the genus in which they are placed. Names of genera are followed by the subfamily, family, or other higher taxa in which they belong. Locations in the text are indicated by page numbers. Figure numbers of illustrations are listed with the page number on which the illustrations appear.

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