The genera *Paranoplocephala*
Lühe, 1910
and *Anoplocephaloides* Baer, 1923
(Cestoda : Anoplocephalidae),
with particular reference to species in Rodents

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Summary.

The present study redefines the systematic arrangement and taxonomic status of some anoplocephaline cestodes previously allocated among the genera *Andrya* Railliet, 1893, *Paranoplocephala* Lühe, 1910, and *Aprostotandrya* Kirshenblat, 1938. Comparisons indicated that *Paranoplocephala omphalodes* (Hermann, 1783), type species of *Paranoplocephala*, differs morphologically from its congeners, all of which conform to the diagnosis of the genus *Anoplocephaloides* Baer, 1923, hitherto considered a synonym of *Paranoplocephala*, and that it cannot be distinguished at the generic level from *Aprostotandrya macrocephala* (Douthitt, 1915), type of the genus *Aprostotandrya*. The distinction between *Andrya* and *Aprostotandrya* based on the presence or absence of a "prostate gland" does not exist, for neither the type species of *Andrya*, *A. rhopalcephala* (Riehm, 1881), nor *A. cuniculi* (Blanchard, 1891) possesses such an organ; rather, the structure of the external seminal vesicle in these cestodes does not differ fundamentally from that in *P. omphalodes* or in species of *Aprostotandrya*. Based on these findings, *Aprostotandrya* Kirshenblat, 1938 is placed in synonymy with *Paranoplocephala* Lühe, 1910, and *Anoplocephaloides* Baer, 1923 is restored to contain all species other than *P. omphalodes* formerly allocated to the genus *Paranoplocephala*. If the pattern of development of the uterus in *A. rhopalcephala* is found to be like that in *P. omphalodes*, *Paranoplocephala* Lühe, 1910 will in turn also become a synonym of *Andrya* Railliet, 1893. Three additional species of *Anoplocephaloides* are described, and the zoogeography of *Anoplocephaloides* spp. and their mammalian hosts is briefly discussed.

Résumé.

Les genres *Paranoplocephala* Lühe, 1910 et *Anoplocephaloides* Baer, 1923 (Cestoda : Anoplocephalidae) avec référence particulière aux espèces des rongeurs.

Ce travail redéfinit la classification et la position taxonomique de quelques Cestodes Anoplocéphalins auparavant rangés parmi les genres *Andrya* Railliet, 1893, *Paranoplocephala* Lühe, 1910, et *Aprostotandrya* Kirshenblat, 1938. Les études comparatives ont indiqué que *Paranoplocephala omphalodes* (Hermann, 1783), l'espèce type de *Paranoplocephala*, diffère morphologiquement de ses congénères, qui sont tous conformes à la diagnose du genre *Anoplocephaloides* Baer, 1923, jusqu'ici considéré comme un synonyme de *Paranoplocephala*, et qu'il ne se distingue pas au niveau générique d'*Aprostotandrya macrocephala* (Douthitt, 1915), l'espèce type d'*Aprostotandrya*. La distinction entre *Andrya* et *Aprostotandrya* basée sur la présence ou l'absence d'une « glande prostatique » n'existe pas, car ni l'espèce type d'*Andrya*, *A. rhopalcephala* (Riehm, 1881), ni *A. cuniculi* (Blanchard, 1891) ne possède un tel organe ; disons plutôt, que chez ces Cestodes, la structure de la vésicule séminale externe ne diffère pas fondamentalement de celle de *P. omphalodes* ou des espèces d'*Aprostotandrya*. Sur la base de ces observations, on a placé *Aprostotandrya* Kirshenblat, 1938, en synonymie avec *Paranoplocephala* Lühe, 1910, et restauré *Anoplocephaloides* Baer, 1923 pour renfermer toutes les espèces auparavant assignées au genre *Paranoplocephala*, sauf *P. omphalodes*. Si le développement de l'utérus chez *A. rhopalcephala* se trouve être comme celui de *P. omphalodes*, *Paranoplocephala* Lühe, 1910, deviendra à son tour synonyme d'*Andrya* Railliet, 1893. Trois espèces nouvelles d'*Anoplocephaloides* sont décrites et la zoogéographie d'*Anoplocephaloides* spp. et de leurs hôtes mammifères est brièvement discutée.

Cestodes usually placed in the genus *Paranoplocephala* Lühe, 1910 (Anoplocephalidae : Anoplocephalinae) make up a large component of the helminth fauna of rodents in the Holarctic. Few are known from rodents on the southern continents, and the genus is otherwise represented only in mammals of the orders Lagomorpha and Perissodactyla. The genus *Paranoplocephala* as now conceived includes several taxa of questionable allocation. Because of the uncertain limits of some anoplocephaline genera, attempts toward taxonomic revision of these cestodes have failed to produce any consensus, and the literature remains confusing and contradictory. It is evident that certain genera were distinguished on the basis of characters that do not in fact exist, either because taxa for which genera were subsequently erected had been inadequately described, or because of errors in the original interpretation of anatomic structures. Such errors have been perpetuated in the literature through the uncritical repetition of generic diagnoses.

The discrimination of taxa in the genus *Paranoplocephala* likewise has been made difficult by inadequacies in original descriptions as well as by a lack of understanding of the limits of intraspecific morphologic variation, and for a few species, the possibility of host-induced variation must be considered. Also, reliance on descriptions of the type species, *P. omphalodes* (Hermann, 1783), that incorporate the

characters of *P. blanchardi* (Moniez, 1891), has led to erroneous records of host-occurrence and geographic distribution for this cestode, notwithstanding well documented zoogeographic evidence to the contrary.

It is the purpose of this paper to contribute towards a clarification of some of these problems through a review of the taxonomy of cestodes assigned variously to *Paranoplocephala* and related genera. Three additional species of anoplocephaline cestodes are described.

MATERIAL AND METHODS

Most of the cestodes included in the present study were collected by me over a period of about 30 years: in various regions of North America during 1943-1976; in northern Japan in 1962; and in northeastern Siberia in 1975. Additional material has been obtained through the generosity of several colleagues. The cestodes were routinely fixed in a hot solution of 10 % formalin, stained in acetic carmine or acid hematoxylin, processed by standard methods, and mounted permanently. Superficial tissues were removed from the anterior portions of representative strobilae of each species to facilitate study of the genital organs, and transverse sections were prepared as required. All measurements given below are in millimeters.

SYSTEMATIC SECTION

I. - The genus *Paranoplocephala* Lühe, 1910

Paranoplocephala omphalodes (Hermann, 1783).

[Syn. *Taenia omphalodes* Hermann, 1783; *Anoplocephala omphalodes* (Hermann, 1783)].

Material studied. — 17 (numbers of cestodes by host and locality). *Microtus oeconomus* (Pallas): Pravaia Basandra Reserve (ca. 32 km NE of Atka, Magadansk Oblast', northeastern Siberia), 1; Popovka River (Magadansk Oblast', lat 64° N, long. ca. 152° E), 3; Ugashik Lake (upper Alaska Peninsula), 1; Napaskiak (Lower Kuskokwim River, Alaska), 3; St. Lawrence Island (Bering Sea), 1. *M. abbreviatus* Miller: St. Matthew Island (Bering Sea), 6. *M. miurus* Osgood: Healy Mountain (central Alaska Range), 2. Additional specimens from voles in Alaska were also examined.

The genus *Paranoplocephala* was erected by Lühe (1910, p. 44) to contain *Anoplocephala omphalodes* (Hermann, 1783) (= *Taenia omphalodes* Hermann, 1783), a cestode found in voles, *Microtus arvalis* (Pallas) and *Arvicola terrestris* (Linnaeus), in Europe. A second species, *P. acanthocirrosa* Baer, 1924, was described from an otomyine rodent, *Otomys irroratus* Brants, in South Africa. Baer had earlier established another anoplocephaline genus, *Anoplocephaloides* Baer, 1923, with *A. infre-*

quens (Douthitt, 1915) (= *Anoplocephala infrequens* Douthitt, 1915) as type species. In his monograph of the Anoplocephalidae, he (1927) suppressed the genus *Anoplocephaloides* as a synonym of *Paranoplocephala* (p. 78), « ... car il n'en diffère que par le fait que les pores sexuels sont irrégulièrement alternants au lieu d'être unilatéraux. Nous n'estimons pas que ce caractère suffise pour établir un genre ou même un sous-genre ». As a result of this action, the number of species in the genus *Paranoplocephala* was increased to 7. Additional species have been described and some have been transferred from other genera, but as is evident from the comprehensive works of Spasskii (1951) and Yamaguti (1959), there has been disagreement concerning the systematic arrangement of species assigned variously to *Paranoplocephala* or related genera.

Much of the confusion concerning the taxonomy of cestodes now included in the genus *Paranoplocephala* is attributable to uncertainties about the diagnostic characters of the type species, *P. omphalodes*. The distinction of *P. omphalodes* and *P. blanchardi* (Moniez, 1891) was accepted by Baer (1927) in his monograph of the Anoplocephalidae. However, Baer later (1932) placed *P. blanchardi* in synonymy with *P. omphalodes*, thereby establishing the concept of the latter as a dimorphic species. According to the composite description (cf. Joyeux and Baer, 1936, p. 444), *P. omphalodes* would have either a length of 20 to 40 with unilateral genital pores, or a length of 100 to 215 with irregularly alternating genital pores. Spasskii (1951, p. 308) reproduced the composite diagnosis in his monograph, but distinguished two « forms » corresponding to the respective species as previously characterized.

A description of *P. omphalodes* from voles, *Microtus miurus*, in Alaska was published by Rausch (1952), who observed no variation in form of strobila or in the arrangement of the genital pores. The apparent distinction of *P. omphalodes* and *P. blanchardi* was later recognized by Rausch (1957), who considered that the arrangement of the genital pores in species of *Paranoplocephala* in rodents was not subject to intraspecific variation. This observation was later confirmed by the study of large series of cestodes representing several species of *Paranoplocephala* from rodents. More recently, on the basis of material from voles in France, Dollfus (1961) also concluded that the two taxa represent distinct species. This concept seems in general to have been accepted by others (cf. Wahl, 1967; Murai, 1970; Tenora and Zejda, 1974). I consider *P. omphalodes* to be holarctic in distribution, although Tenora and Zejda (1974) remarked that further investigation is needed to determine that cestodes so identified in North America (Alaska) do not represent another species of *Paranoplocephala*. The morphologic characteristics of specimens from northeastern Siberia and Alaska are compared in Table 1.

The separation of *P. blanchardi* from *P. omphalodes* apparently has been overlooked by some investigators, whose reliance on the earlier, composite descriptions of *P. omphalodes* in discriminating species of *Paranoplocephala* has led to mistaken taxonomic conclusions. The cestode reported as *P. omphalodes* by Ishimoto (1974) from field mice, *Apodemus* spp., in Hokkaido was identified from the description published by Spasskii (1951) (cf. Ishimoto, 1974, p. 3). These cestodes had short

TABLE I. — Comparison of morphologic characteristics of *Paranoplocephala omphalodes* from northeastern Siberia and Alaska (measurements in millimeters).

	N. E. Siberia N = 5 (<i>Microtus oeconomus</i>)	Alaska N = 5 (<i>Microtus oeconomus</i> , <i>M. miurus</i> , <i>M. abbreviatus</i>)
Length of strobila	78-161 (av. 115)	162-198 (av. 182)
Maximum width	3.7-4.5 (av. 4.1)	4-6 (av. 4.8)
Number of segments	313-518 (av. 390)	359-487 (av. 422)
Width of scolex	0.800-0.912 (av. 0.850)	0.800-1.02 (av. 0.914)
Genital pores	Irregularly alternating, near middle of margin in mature segments; posterior in gravid segments.	Irregularly alternating, near middle of margin in mature segments; posterior in gravid segments.
Diameter of ventral longitudinal excretory canals	0.100-0.280	0.100-0.170
Length × diameter of cirrus sac	0.244-0.300 × 0.061-0.088 (av. 0.265 × 0.076)	0.195-0.330 × 0.061-0.097 (av. 0.255 × 0.082)
Cirrus	Spinose	Spinose
Extent of cirrus sac mediad	Usually not overlapping ventral longitudinal excretory canal.	Usually not overlapping ventral longitudinal excretory canal.
Distribution of testes	Aporal margin of ovary to ventral longitudinal excretory canal; occasionally extending over canal.	Aporal margin of ovary to ventral longitudinal excretory canal; frequently extending over canal.
Width × length of ovary	0.800-1.01 × 0.160-0.240 (av. 0.936 × 0.207)	0.580-1.08 × 0.170-0.300 (av. 0.803 × 0.213)
Width × length of vitelline gland	0.350-0.457 × 0.100-0.180 (av. 0.397 × 0.146)	0.250-0.390 × 0.120-0.190 (av. 0.317 × 0.145)
Dimensions of egg	0.036-0.044 × 0.032-0.044 (av. 0.041 × 0.039)	0.036-0.044 × 0.034-0.041 (av. 0.041 × 0.039)
Greater diameter of embryo	0.008-0.012	0.008-0.012

(30 to 70), rapidly widening strobilae, with a maximum width of 3 to 5 and unilateral genital pores, and the strobila was described as «thick». The cirrus sac was relatively large (0.250 to 0.310 long), apparently not extending mediad to the margin of the ventral excretory canal (cf. Ishimoto, 1974, fig. 2). The eggs were 0.033 to 0.042 in diameter. Compared with the species of *Paranoplocephala* known from rodents on the Eurasian continent (Ishimoto noted that cestodes of this genus had not been reported previously from rodents on the Japanese Islands), this cestode most closely resembles *P. blanchardi*. The reported occurrence of *P. omphalodes* from murine rodents in Africa is the consequence of Collins' (1972) conclusion that

P. acanthocirrosa Baer, 1924 is a synonym. Her decision concerning the status of the latter was based on the range of variation observed in the size of the cirrus sac, since Spasskii (1951, p. 311) considered that the larger cirrus sac of *P. acanthocirrosa* distinguished it from *P. omphalodes*. The occurrence of *P. omphalodes* in rodents in South America (Peru) was indicated by Baer's listing (1927) of *Bertiella forcipata* (von Linstow, 1904) as a synonym. This inadequately described cestode, from *Lagidium peruanum* Meyen (Chinchillidae), was retained in the genus *Paranoplocephala* by Spasskii (1951, p. 316), who considered it to be distinct from *P. omphalodes*. Yamaguti (1959, p. 375) referred it back to the genus *Bertiella* Stiles and Hassall, 1902.

Detailed comparisons of *P. omphalodes* with its congeners and with cestodes in related genera have shown that its taxonomic status requires further consideration. Not only is *P. omphalodes* the most divergent morphologically of the species now assigned to the genus *Paranoplocephala*, but the pattern of development of its uterus is unique among cestodes of this genus. As indicated by the earlier descriptions based on specimens from voles in Europe, *P. omphalodes* is a relatively large cestode having a thin, ribbon-like strobila unlike that of any other member of the genus. In form of strobila as well as in other characteristics (scolex with large, motile suckers; ventral excretory canals of unusually large diameter; relationships of the genital organs), it closely resembles cestodes of the genus *Aprostotandrya* Kirshenblat, 1938. Ostensibly, *P. omphalodes* differs from the latter species in having a transverse, tubular uterus in the mature segment, whereas that in *Aprostotandrya* spp. is reticulate. However, the study of well stained material has shown that the uterus in *P. omphalodes* differs in fundamental structure from that in its congeners formerly included by Baer (1923) in the genus *Anoplocephaloides* Baer, 1923, or in subsequently described species that conform morphologically to the latter genus.

The first detailed description of *Taenia omphalodes* Hermann, 1783 was that of Stieda (1862), who based his identification of specimens from voles, *Hypudaeus arvalis* (= *Microtus arvalis*), on the brief description by Dujardin (1845, p. 578). With reference to the form of the uterus, Stieda (p. 204) stated: « Mit dem 150sten Gliede etwa tritt die erste Andeutung des Fruchthälters oder Uterus auf (fig. 2). Nicht allein am oberen Rande, sondern auch an den beiden seitlichen Rändern des Gliedes erscheint der Uterus als ein mit Ausstülpungen versehener Hohlraum im Körperparenchym angefüllt mit einer dem Inhalte der Dotterstöcke gleichenden Masse. » Stieda's figures 2 and 3 show successive stages of the developing uterus as seen in post-mature segments of *P. omphalodes*; he probably did not observe the organ at an early stage of development. Cestodes designated *Taenia omphalodes* in the Rudolphi Collection of the Berlin Zoological Museum were studied by von Janicki (1906), who also reviewed published morphologic data. Because of the poor state of preservation of the material, he was able to supplement Stieda's description in only a few details, but he transferred *T. omphalodes* to the genus *Anoplocephala* Blanchard, 1848, the diagnosis of which he emended. In his diagnosis, von

Janicki (1906, p. 560) characterized the uterus as "... eine quergelagerte Röhre mit taschenförmigen Anhängen."

Without discussing taxonomic relationships, Lühe (1910) erected the genus *Paranoplocephala*, with *Anoplocephala omphalodes* (Hermann, 1783) as type species. In the generic diagnosis, Lühe (p. 44) characterized the uterus as being "... sackförmig, quergestreckt, mit taschenartigen Ausbuchtungen." Lühe's figures (fig. 20, a and b) of the mature and gravid segments of *P. omphalodes* evidently were reproduced from Stieda's plate (Stieda, 1862, fig. 1 and 3), and there was no indication that Lühe had studied specimens of this cestode. After placing the genus *Anoplocephaloides* Baer, 1923 in synonymy with *Paranoplocephala*, Baer (1927) also emended the diagnosis of the latter genus. His diagnosis stated (p. 78): "Utérus en forme de tube transverse pouvant dépasser les vaisseaux excréteurs à la face ventrale et devenant sacciforme et lobé." There appears to have been no earlier published description of *P. omphalodes* in which the uterus in the mature segment was described as a transverse tube like that in species formerly assigned to the genus *Anoplocephaloides*. Baer could have reached his decision concerning the form of uterus in *P. omphalodes* on the basis of his conclusion that *P. blanchardi* is a synonym of *P. omphalodes*, since the uterus appears as a transverse tube in the mature segment of the former.

In a brief description of *P. omphalodes* from voles in Alaska, Rausch (1952, p. 423) stated: "Tubular uterus present in mature segments; uterine growth takes place through development of regular anterior and posterior sacculations. Gravid uterus nearly fills terminal segments." More recently, Murai (1970) studied in detail a specimen of *P. omphalodes* from a hamster, *Cricetus cricetus* (Linnaeus), collected in Hungary. She described (p. 47) the uterus as "... initially a diagonal tube on anterior border of segment, then, concurrently with the atrophisation of gonads, it fills the entire medullary parenchyme, passing even the line of the excretory stems. It is not sacculiform, forming numerous irregular pouches." From the available information, one has to conclude that the uterus of *P. omphalodes* has never been described in adequate detail.

The large series of *P. omphalodes* from Alaska and Siberia provided an opportunity in the present study to trace the development of the uterus and to make comparisons of that organ in cestodes of related genera. In exceptionally well stained specimens of *P. omphalodes*, the *Anlage* of the uterus could be first discerned as far anterior as the 105th segment of the strobila as a cord-like aggregation of cells extending transversely across the segment near the ventral surface, and passing bilaterally beyond the longitudinal excretory canals. With further development, the uterus appeared as a transverse band, which attained a width of about 0.030 in early mature segments. It was situated anteriorly, passing ventrally across the anterior margin of the ovary, then deviating slightly posteriad bilaterally with the ends extending laterad to just beyond the lateral margins of the ventral excretory canals. The poral end of the uterus at this stage lay anterior to the level of the genital ducts. The ends of the uterus were broader than the remainder of the organ, and sometimes had distinctly irregular margins.

In later mature segments, the lateral extremities of the uterus further increased in anteroposterior width, gradually becoming fenestrated and assuming a reticulate structure. Similar changes followed in that part of the organ lying between the excretory canals. Thereafter, the latter portion began to produce anterior and posterior sacculations, while the two ends retained their reticulate form. At this stage, the uterus consisted of a thin layer that spread posteriad ventrally, gradually covering the ovary and testes. With continuing development, the uterus increased in dorsoventral thickness, gradually occupying the parenchyma of the segment between the dorsal and ventral layers of muscle. As seen in transverse section, the portions of the organ lateral to the ventral excretory canals were thickest, and at this stage the uterus resembled that of *P. omphalodes* as portrayed by Stieda (1862, fig. 3). In early gravid segments, those areas of the uterus underlying the ventral excretory canals bilaterally were relatively thin, imparting a distinctly tripartite appearance to the organ in dorsoventral view. Later, as the uterus became distended with eggs, the canals were no longer discernible.

The pattern of development of the uterus in *P. omphalodes* thus differs fundamentally from that in congeners referable to the genus *Anoplocephaloides* Baer, 1923 [e.g., *P. mamillana* (Mehlis, 1831); *P. lemmi* Rausch, 1952]. In such species, the uterus is also first discernible as a cord-like aggregation of cells extending transversely across the early mature segment, usually near the anterior margin of the ovary and often anterior to the testes. But with further development, the uterus becomes a well defined tube of uniform diameter in which a lumen is clearly visible. The organ is situated ventrally, and may or may not extend laterad beyond the excretory canals. In species having short strobilae, with relatively few segments, the uterus develops rapidly. The diameter of the tube begins to increase in the first post-mature segment, coincident with the first appearance of ova within its lumen, and sacculations begin to appear along its anterior and posterior margins. In species having long strobilae with numerous segments (i.e., those in sciurids), development of the uterus is more gradual, but the pattern is the same. Although the uterus is initially ventral to the plane of the testes in all of the species studied, it increases rapidly in diameter and soon displaces the testes posteriad. The testes may persist along the posterior segmental margin in post-mature segments, after which they gradually degenerate and disappear. As the eggs develop, the uterus enlarges and fills the entire segment. In some species, sacculations may extend more or less laterad from the ends of the uterine tube, but there is no tendency toward formation of a reticulum.

In pattern of development, the uterus of *P. omphalodes* does not differ from that of cestodes in the genus *Aprostatan-drya* Kirshenblat, 1938 and perhaps not from that in *Andrya* Railliet, 1893. Two subgenera of *Andrya*, *Andrya* and *Aprostatan-drya*, distinguished respectively by the presence or absence of a pedunculated prostate gland, were established by Kirshenblat (1938). The subgenus *Aprostatan-drya* was elevated to generic rank by Spasskii (1951). In the genus *Aprostatan-drya*, Spasskii also erected the subgenus *Sudarikovina* Spasskii, 1951 for species characte-

rized in part by the distribution of the testes posterior to the ovary and vitelline gland. *Sudavikovina* was in turn elevated to generic rank by Hunkeler (1972; 1974). The genera *Andrya* and *Aprostatanrya* were placed by Spasskii in a new subfamily, Monieziinae Spasskii, 1951, along with various other genera whose characters include a reticulate uterus. However, this subfamily has not been generally accepted (cf. Yamaguti, 1959; Stunkard, 1961; Joyeux and Baer, 1961).

The distinction between the genera *Andrya* and *Aprostatanrya* as conceived by Spasskii has become somewhat obscured in the recent literature. In Yamaguti's (1959) allocation of species, *Andrya bialowiezensis* Sołtys, 1949 [now considered to be a synonym of *Aprostatanrya macrocephala* (Douthitt, 1915); cf. Żarnowski (1955)] and *Andrya arctica* Rausch, 1952 were retained in the genus *Andrya*, although they lack a "prostate gland." A third species, *Andrya bairdi* Schäd, 1954, from the heather vole, *Phenacomys intermedius* Merriam [erroneously reported by Schäd (1954) as *Microtus chrotorrhinus* (Miller); cf. Peterson, 1962] was transferred by Yamaguti (1959, p. 385) to the genus *Paranoplocephala*. *A. bairdi*, characterized in part by a reticulate uterus and lacking a prostate gland, is clearly referable to the genus *Aprostatanrya* as hitherto conceived.

At the time Lühe (1910) erected the genus *Paranoplocephala*, the genus *Andrya* contained but two species, *A. rhopalocephala* (Riehm, 1881) (type species) and *A. cuniculi* (Blanchard, 1891) (= *Taenia rhopalocephala* Riehm, 1881), both occurring in leporids in Europe. Both were described by Riehm (1881, pp. 9 and 20; Taf. VI, fig. 1 and 3) as having a pedunculated prostate gland. The presence of this structure in *Andrya* would seem to have provided sufficient grounds for distinguishing *Paranoplocephala* at the generic level.

Whether cestodes included in the genus *Andrya* sensu Spasskii (1951) do in fact have a "pedunculated prostate gland" has remained controversial. However, in addition to the above-mentioned two species, two more, *A. primordialis* Douthitt, 1915 (syn. *A. communis* Douthitt, 1915) and *A. montana* Kirshenblat, 1941, have been described as possessing such an organ. Rausch (1952, p. 425) was unable to confirm the presence of a prostate gland in Douthitt's original material (all sectioned), nor was the structure observed in any cestodes from voles that seemed otherwise to correspond to the description of *A. primordialis*. Schäd (1954) also could not discern a prostate gland in such cestodes, and he suggested that Douthitt's interpretation might have been erroneous.

In the present study, detailed examination of *Andrya rhopalocephala* from *Lepus europaeus* Pallas (Hungary) and *A. cuniculi* from *Oryctolagus cuniculus* (Linnaeus) (France) revealed that neither possesses a pedunculated prostate gland as described by Riehm (1881). Rather, in both, the external seminal vesicle does not differ in fundamental structure from that in cestodes assigned to the genus *Aprostatanrya* or that in *Paranoplocephala omphalodes* (see fig. 1 - 3). In the two species from leporids, the external seminal vesicle at an early stage of development appears in dorsal view as a thick-walled, sac-like structure extending mediad or anteromediad from the aporal end of the cirrus sac. The unusual relationships of the "prostate

gland" in *A. rhopalocephala* as portrayed by Riehm (1881, Taf. VI, fig. 1) and by Stiles (1896, plate VII, fig. 5) perhaps can be attributed to extreme extension of the strobilae. Stiles studied some of Riehm's specimens, but stated (p. 155) that "None of the specimens are in very good condition, on which account I am unable to enter into a detailed study of the organs." Since the afferent duct is difficult to trace, particularly in specimens mounted entire, it does not seem remarkable that the organ

FIG. 1. — *Andrya rhopalocephala* (Riehm, 1881) from *Lepus europaeus*, Hungary. Transverse section: details of the genital ducts.

FIG. 2. — *Andrya cuniculi* (Blanchard, 1891) from *Oryctolagus cuniculus*, France. Transverse section: details of the genital ducts.

FIG. 3. — *Paranoplocephala omphalodes* (Hermann, 1783) from *Microtus abbreviatus*, St. Matthew Island. Dorsal view: details of the genital ducts. Designations are: dc, dorsal longitudinal excretory canal; vc, ventral longitudinal excretory canal; v, vagina; sr, seminal receptacle; isv, internal seminal vesicle; esv, external seminal vesicle; vd, vas deferens; rm, retractor muscle.

has been hitherto conceived as a blind sac. The same misinterpretation of the structure of the external seminal vesicle was made by Darrah (1930), in his diagnosis of the closely related anoplocephaline genus *Diandrya* Darrah, 1930. The status of the single species in the latter genus will be considered elsewhere.

Thus, it would appear that any significant differences between *Andrya* and the genera *Paranoplocephala* and *Aprostatanandrya*, if indeed any exist, could only be in the characteristics of the uterus. The possibility that the uterus in *A. rhopalocephala* first appears as a transverse, tube-like structure was considered by Stiles (1896), who stated (p. 157): "Whether this uterus is primarily an actual network, or whether it is originally a simple tube with numerous proximal and distal branches which secondarily anastomose and then gradually disappear to form a common simple sac, can not be stated at present with certainty, but with the data now at hand, I incline decidedly to the latter view." Douthitt (1915) did not observe the early-stage uterus in the species of *Andrya* s. l. studied by him, since he stated (p. 401): "In the earliest stages in which indications of the uterus were observed it occupies the entire region later occupied by the fully developed reticulum." He disagreed with Stiles' concept, stating further (p. 402) that "... there is no evidence that there intervenes a transverse tubular stage which is comparable in any sense to the uterus of *Anoplocephala*." In the specimens of *A. rhopalocephala* that I studied, the uterus had already become reticulate in the earliest discernible stage of development, but it was still band-like and situated anteriorly, suggesting that it first appears as a narrow, transverse rod or tube. The study of additional, well stained specimens will be required to trace the complete development of the uterus in *A. rhopalocephala*.

In cestodes hitherto assigned to the genus *Aprostatanandrya*, the uterus likewise becomes reticulate and spreads posteriad ventrally. Since the early-stage uterus in these cestodes rarely stains intensely enough to be clearly discernible, I could observe it only in a few specimens. In *A. macrocephala*, the development of the uterus is like that described above for *Paranoplocephala omphalodes*. These species differ morphologically in proportions of the segments (short and relatively much wider in *P. omphalodes*) and in the correspondingly different relationships of organs. In North America, cestodes identified as *P. omphalodes* were reported from the cotton rat, *Sigmodon hispidus* Say and Ord, in North Carolina by Harkema (1946). The species was later determined to be *Andrya microti* Hansen, 1947 (= *Aprostatanandrya macrocephala*) (cf. Rausch, 1952 a). The form of the early-stage uterus accounted for the generic allocation of *Paranoplocephala kirbyi* Voge, 1948, described from *Microtus californicus* (Peale), and subsequently placed in synonymy with *Andrya macrocephala* (= *Aprostatanandrya macrocephala*) by Rausch (1952 a). Voge (1948, fig. 2) thus appears to have been the first to portray the early-stage uterus of this cestode. More recently, Hunkeler (1972) described the uterus of *Andrya dasymidis* Hunkeler, 1972 [= *Aprostatanandrya dasymidis* (Hunkeler, 1972) (cf. Hunkeler, 1974)] as follows (p. 122): "Utérus d'abord sous la forme d'un tube transversal puis devenant extrêmement lobé-réticulé et dépassant largement les vaisseaux excréteurs." *P. omphalodes*

has been frequently confused with *A. macrocephala* (or *macrocephala*-like species) also in Europe (cf. Tenora and Zejda, 1974, p. 17). The possibility cannot be excluded that some of the early descriptions of *P. omphalodes* in Europe were based at least in part on specimens of *A. macrocephala* or a morphologically similar species. For example, in the description of *Taenia omphalodes* published by Dujardin (1845, p. 578), the width of the strobila was stated to be only 2 to 2.5, which is about half that usually attained by the strobila of this cestode (cf. Table I). A mounted cestode in my possession, from the Institut de Zoologie, Université de Neuchâtel, is labeled "*Paranoplocephala omphalodes*," but clearly represents a species of *Aprostataandrya* as hitherto conceived.

A comparison of *P. omphalodes* with *A. macrocephala* from rodents in North America has revealed no morphologic differences that I consider to have taxonomic significance at the generic level. Consequently, since *A. macrocephala* is the type species of the genus *Aprostataandrya* Kirshenblat, 1938, the latter genus is here suppressed as a synonym of *Paranoplocephala* Lühe, 1910. An emended diagnosis of the genus *Paranoplocephala* is presented below. Further, the genus *Anoplocephaloides* Baer, 1923 is here restored to include species other than *P. omphalodes* that were formerly assigned to the genus *Paranoplocephala*.

The status of the genus *Andrya* Railliet, 1893 remains uncertain until the characteristics of the uterus of the type species, *A. rhopalocephala* (Riehm, 1881), can be more precisely defined. If the pattern of the development of the uterus in the latter species does not differ from that in *P. omphalodes* and *A. macrocephala*, the genera *Paranoplocephala* Lühe, 1910 and *Aprostataandrya* Kirshenblat, 1938 would become synonyms of *Andrya* Railliet, 1893.

***Paranoplocephala* Lühe, 1910, emend.**

[Syn. *Aprostataandrya* Kirshenblat, 1938.]

Diagnosis: Anoplocephalinae Blanchard, 1891. Cestodes of medium size, with ribbon-like strobilae. Segments usually wider than long, with relative length increasing posteriad. Scolex with prominent, motile suckers. Excretory system simple, with dorsal and ventral canals bilaterally. Genital pores unilateral or irregularly alternating. Genital ducts passing dorsal to excretory canals. Vagina opening posterior to orifice of male duct. External seminal vesicle present. Testes numerous, distributed aporally or aporally and anterior to ovary. Ovary lobed, poral or median in segment. Uterus at first rod-like, transverse, becoming reticulate and developing anterior and posterior sacculations. Egg with pyriform apparatus. Parasites of rodents.

Type species: *Paranoplocephala omphalodes* (Hermann, 1783).

II. - The genus *Anoplocephaloides* Baer, 1923.

The genus *Anoplocephaloides* was erected by Baer in 1923 to include cestodes formerly assigned to the genus *Anoplocephala* Blanchard, 1848, but which lacked anastomosing excretory ducts, and differed in distribution of testes and form of ovary. The genus was diagnosed by Baer (1923, p. 10) as follows:

« Anoplocéphaliens à segments toujours plus larges que longs ; pores génitaux unilatéraux ; conduits sexuels dorsaux, par rapport au nerf et aux vaisseaux longitudinaux ; vésicule séminale externe présente ; système excréteur non réticulé ; testicules du côté antiporal pouvant, dans certain cas, dépasser latéralement le nerf longitudinal ; ovaire poral en forme d'éventail ; vagin situé ventralement à la poche du cirre ; utérus en forme de tube transversal, devenant sacciforme et lobé par évaginations successives de ses parois ; œufs munis d'un appareil pyriforme bien développé. Adultes chez *Rodentia* et dans un cas chez *Perissodactyla*. Type : *Anoplocephaloides infrequens* (Douthitt). »

With reference to the selection of *A. infrequens* (Douthitt, 1915) as type species, Baer (1923, p. 10) stated: « Nous avons choisi comme espèce type celle qui est la mieux étudiée et dont le matériel est le plus abondant, plutôt que de prendre l'espèce la plus ancienne dont fort peu d'exemplaires sont connus. » Baer allocated 7 species to the genus *Anoplocephaloides*, retaining others as species *sedis incertae*. With reference to *Anoplocephala omphalodes*, he noted only (p. 14) that it had been taken as type of the genus *Paranoplocephala* Lühe, 1910.

The cestodes allocated to the genus *Anoplocephaloides* as conceived in the present study exhibit substantial uniformity in their morphologic characteristics, although they no doubt represent diverse phyletic lines. Differences in form of strobila and in other, less striking characteristics do not now seem to justify subdivision of the genus.

The species assigned to the genus *Anoplocephaloides* as well as those described in the present study can be segregated into three morphologic groups on the basis of form of strobila:

1. Strobila long, comprised of numerous segments; genital pores unilateral or irregularly alternating. In rodents of the family Sciuridae.
2. Strobila small to very small, usually wedge-shaped and consisting of few segments; genital pores unilateral. In lagomorphs and rodents.
3. Strobila of intermediate size, somewhat attenuated anteriorly in most species; genital pores unilateral except in species from rodents in Africa. In rodents and perissodactyls.

In order to accommodate the observed range of morphologic characters, the diagnosis of the genus as given by Baer (1923) requires emendation:

Anoplocephaloides Baer, 1923, emend.

Diagnosis: Anoplocephalinae Blanchard, 1891. Strobila usually small to medium; sometimes long, with numerous segments. All segments wider than long, with relative length increasing posteriad. Scolex usually wider than neck. Excretory system simple, with dorsal and ventral canals bilaterally. Genital pores usually unilateral; rarely irregularly alternating. Genital ducts passing dorsal to longitudinal excretory canals. Vagina opening ventral to orifice of male duct. External seminal vesicle typically present. Testes numerous, with majority aporal to ovary. Ovary lobed, usually in poral half of segment. Uterus a transverse tube, developing anterior and posterior sacculations, and filling gravid segments. Egg with pyriform apparatus. Parasites of rodents, lagomorphs, and perissodactyls.

Type species: *Anoplocephaloides infrequens* (Douthitt, 1915).

For convenience, previously known species assigned here to the genus *Anoplocephaloides* are considered according to type of strobila.

Species having long strobilae.

This group includes three species, all occurring in ground squirrels of the genera *Marmota* and *Citellus* (Sciuridae: tribe Marmotini).

Anoplocephaloides transversaria (Krabbe, 1879).

[Syn. *Taenia transversaria* Krabbe, 1879; *Anoplocephala transversaria* (Krabbe, 1879); *Paranoplocephala transversaria* (Krabbe, 1879)].

Material studied. — 2. *Marmota caudata* (Jacquemont): southern Tian'-Shan', Kirgizia, 1. *M. baibacina* (Brandt): central Tian'-Shan', Kirgizia, 1.

A. transversaria is a host-specific parasite of marmots, *Marmota* spp., in Eurasia, where it is known to occur from the Alps in the west to middle Asia (Kirgizia and Kazakhstan) (Hörning and Tenora, 1971). This cestode also has been reported from marmots in the Uzbek SSR (Chatkal'sk Range) by Sultanov *et al.* (1971). The known hosts were listed by Hörning (1969).

This cestode has been described in detail by Zschokke (1888, p. 47). Morphologically, *A. transversaria* is most similar to *A. ryjikovi* (Spasskii, 1950), with which it is compared below.

Anoplocephaloides ryjikovi (Spasskii, 1950).

[Syn. *Paranoplocephala ryjikovi* Spasskii, 1950].

Material studied. — 1. *Marmota baibacina* (Brandt): central Tian'-Shan', Kirgizia.

A. ryjikovi has been reported only from *Marmota baibacina* and *Marmota* sp. in middle Asia (Hörning, 1969; Ianushevich *et al.*, 1972, p. 127). Spasskii (1950) provided a detailed description of this cestode, but made no comparisons with other species of the genus. Hörning and Tenora (1971) considered *A. ryjikovi* to be morphologically very similar to *A. transversaria*.

Both have strobilae of similar size, but they are distinguished by different arrangements of the genital pores (irregularly alternating in *A. ryjikovi*; unilateral in *A. transversaria*). In the small amount of material that I had for comparison, the cirrus sac was of similar size in the mature segments of the two species (0.600 to 0.700 long). According to the original description, *A. ryjikovi* has 150 or more testes, as compared with 60 to 80 in *A. transversaria* (Zschokke, 1888; Baer, 1927). The two species exhibit well defined differences in the arrangement of the female genital organs. In *A. ryjikovi*, the ovary and vitelline gland are situated farther porally, so that the cirrus sac in mature segments extends mediad to the level of the poral margin of the ovary (see also Spasskii, 1950, *fig. 3*). The seminal receptacle is short and more or less globular, and when distended displaces the cirrus sac anteriorly. In *A. transversaria*, a considerable space exists between the aporal end of the cirrus sac and the ovary, and the seminal receptacle is elongate and tubular (cf. Zschokke, 1888, *pl. I, fig. 19*). Differences exist also in the relationships of the uterus, which in *A. ryjikovi* is situated near the middle of the segment, with the poral end extending laterad only slightly beyond the poral margin of the ovary. In *A. transversaria*, the uterus lies near the anterior margin of the segment, with the poral end extending laterad well beyond the ovary. Differences exist also in size of the egg and in other anatomical details.

Anoplocephaloides wigginsi (Rausch, 1954).

[Syn. *Paranoplocephala wigginsi* Rausch, 1954].

Material studied. — 4. *Citellus parryi* (Richardson): Atkasuk (Meade River, arctic slope of Alaska; lat. 70° 28' N, long. 157° 24' W), 1 paratype: 3 topotypes (leg. D. Preston).

In the original description of this cestode, the host was incorrectly designated *C. undulatus* (Pallas), a species now known to be restricted in distribution to the Palearctic (cf. Liapunova, 1969).

In arctic and subarctic regions, at least, sciurids that hibernate lose their intestinal helminths sometime after entering the den in autumn, and become reinfected after emergence in the following spring. The description of *A. wigginsi* was based

on specimens obtained from ground squirrels collected early in summer, before the cestodes had attained full development, and it was deficient in some details. Until recently, this cestode was known in North America only from the type material. In 1974, a ground squirrel trapped at the type locality during the period 26-29 June was kept at the Institute of Arctic Biology, University of Alaska, until it died on 14 October the same year. The small intestine of this animal contained 12 fully developed specimens of *A. wigginsi*. The following details, obtained from three strobilae mounted entire, supplement the original description:

Strobila 264 to 281 long, with 463 to 546 segments; maximum width, in gravid segments, 7 to 8.6. Length/width ratio of mature segments about 1:10; of gravid segments, 1:5. Scolex globular, 0.868 to 1 in transverse diameter, distinctly wider than neck. Cirrus sac thick-walled, of nearly uniform diameter, 0.573 to 0.620 long by 0.170 to 0.217 (av. 0.604 by 0.189) in mature segments, extending directly mediad, and occupying most of segmental length. Ovary in poral half of segment, with aporal margin near midline; disappearing in post-mature segments coincident with enlargement of uterus. Uterus tubular, situated transversely near anterior margin of segment, with poral end extending laterad anterior to seminal vesicle and cirrus sac. Cirrus sac displaced posteriad by enlarging uterus in post-mature segments; cirrus sac and seminal receptacle persisting at posterior margin of terminal gravid segments. Gravid uterus filling segments between longitudinal excretory canals. Eggs spherical, 0.052 to 0.072 in diameter (av. 0.064). Embryo 0.020 to 0.022 in transverse diameter. Embryonic hooks 0.009 to 0.010 long. Pyri-form apparatus well developed. Other details as in original description (Rausch, 1954).

A. wigginsi exceeds both *A. transversaria* and *A. ryjikovi* in length of strobila, and it is thus the largest cestode in the genus. Compared with *A. ryjikovi*, which also has irregularly alternating genital pores, *A. wigginsi* is distinguished by the arrangement of the female genital organs. Like *A. transversaria*, *A. wigginsi* has the ovary more widely separated from the aporal end of the cirrus sac. The tubular uterus is straight, situated anteriorly in the mature segment with the poral end extending anterior to the cirrus sac, whereas the uterus lies near the middle of the segment in *A. ryjikovi*, with the short poral end deviating posteriad and extending posterior to the cirrus sac. The two species are distinguished further by differences in dimensions and relationships of other organs.

"*P. wigginsi* has been reported in Eurasia, from *C. parryi* in northeastern Siberia (Chukotsk Peninsula) by Ovsukova (1967), who found a single specimen in 16 ground squirrels examined. This cestode was not present in 5 specimens of *C. parryi* that I examined farther to the south (Pravaia Basandra Reserve).

Species having wedge-shaped strobilae.

Five species, from lagomorphs and rodents, are included in this group. These cestodes have short strobilae, with numbers of segments ranging from about 30 to

90, and unilateral genital pores. The width of the strobila increases posteriad, with the maximum attained in gravid segments. Terminal gravid segments are often narrower. The reproductive organs develop rapidly, and the greater part of the strobilae consists of post-mature segments. Beyond the last mature segment (i.e., after which the uterus begins to enlarge), the ovary soon disappears, but the seminal vesicles and the seminal receptacle continue to increase in size. The cirrus sac does not attain full development in mature segments, so that comparisons of dimensions of this organ in mature segments may be misleading. The four species occurring in rodents occupy the terminal portion of the ileum, just above the ileo-cecal valve. The cestodes may pass into the cecum after the death of the host.

The taxonomic status of some of these cestodes has been controversial, and it was only by direct comparison of specimens that some of the uncertainties could be resolved here. The morphologic characteristics of species from rodents included in this group are compared in Table II.

Anoplocephaloides infrequens (Douthitt, 1915).

[Syn. *Anoplocephala infrequens* Douthitt, 1915; *Paranoplocephala infrequens* (Douthitt, 1915)].

Material studied. — 2. *Geomys bursarius* (Shaw): USNM Helminthol. Coll. No. 49 515 ("cotype"), 1; USNM Helminthol. Coll. No. 49520, Brainerd, Minnesota (? cotype), 1.

Anoplocephala infrequens was selected as type species of the genus *Anoplocephaloides* by Baer (1923) on the grounds that it had been described in detail, and the original material was extant. Nonetheless, uncertainties have existed concerning the diagnostic characters of *A. infrequens* and have made difficult the discrimination of other taxa in nearctic rodents.

Ten specimens of *A. infrequens* were obtained by Douthitt (1915) from pocket gophers, *G. bursarius* (Geomyidae), in northern Minnesota and at the southern border of Manitoba (Emerson). Of these, three specimens were immature, one was in poor condition, three, including the type, were sectioned for study, and observations were made also on three others preserved in alcohol (Douthitt, 1915, p. 374). Another cestode, from *Evotomys* sp. [= *Clethrionomys* sp.; evidently *C. gapperi* (Vigors)] collected in North Dakota, also sectioned, was considered by Douthitt to be morphologically identical with *A. infrequens*. For comparison with species of *Paranoplocephala* from arvicoline rodents, Douthitt's sectioned material was studied by Rausch and Schiller (1949), who concluded that *P. infrequens* was a composite, apparently consisting of small specimens of *P. variabilis* (Douthitt, 1915) and *P. troeschi* Rausch, 1946, described from voles, *Microtus pennsylvanicus* (Ord). *P. troeschi* was placed in synonymy with *P. infrequens* by Rausch and Schiller (1949).

Since it seemed questionable that *P. infrequens* would occur regularly in rodents representing different families, Geomyidae and Cricetidae, further investigation of

TABLE II. — Morphologic characteristics of some species of *Anoplocephaloides* in rodents (measurements in millimeters)

	<i>A. infrequens</i> (Douthitt, 1915)	<i>A. troeschi</i> (Rausch, 1946)	<i>A. dentata</i> (Galli-Valerio, 1905)	<i>A. baeri</i> sp. nov.	<i>A. lemni</i> (Rausch, 1952)	<i>A. kontrinavi- chusi</i> sp. nov.
Length of strobila	10.5 and 18	6.5-11 (av. 8.4)	5.5-8 (av. 6.2)	11-22 (av. 13.4)	16-20 (av. 17.5)	9.5-11.5 (av. 10.4)
Maximum width	3 and 3.5	1.5-3.5 (av. 2.6)	2.0-2.5 (av. 2.4)	1.9-2.7 (av. 2.2)	5-6.5 (av. 5.8)	3.5-5 (av. 4.2)
Number of segments . .	60 and 73	31-47 (av. 38)	27-35 (av. 32)	41-74 (av. 49)	71-94 (av. 82)	40-48 (av. 44)
Width scolex	0.580 and 0.672	0.500-0.976 (av. 0.711)	0.650-1.2 (av. 1.0)	0.806-0.975 (av. 0.885)	1.2-1.5 (av. 1.4)	0.992-1.4 (av. 1.2)
Last mature segment . .	17 and 20	8-16 (av. 12)	9-12 (av. 11)	16-19 (av. 18)	31-43 (av. 35)	13-18 (av. 15)
Maximum length cirrus sac (post-mature seg- ments)	0.360					
Number of testes	50-60	0.230 35-50	0.350 ca. 50	0.323 80-90	0.900 56-73	0.470 ca. 90
Distribution of testes . .	Middle of vitel- line gland to ex- cretory canals	Aporal margin of vitelline gland to excretory canals.	Aporal margin of ovary to excretory canals.	Poral margin of ovary to excretory canals.	Middle of vi- telline gland to or slightly beyond excretory canals.	Aporal margin of vitelline gland to beyond excretory canals.
Width ovary (last mature segment)	--- and 0.768	0.350-0.690 (av. 0.498)	0.410-0.650 (av. 0.510)	0.370-0.425 (av. 0.401)	0.650-0.940 (av. 0.765)	0.640-0.860 (av. 0.740)
Width vitelline gland (last mature segment)	---	0.174-0.220 (av. 0.192)	0.200-0.260 (av. 0.233)	0.130-0.160 (av. 0.143)	0.210-0.390 (av. 0.300)	0.300-0.350 (av. 0.330)
Uterus	Anterior in seg- ment, overlapping long. ex. canals bilaterally.	Anterior in seg- ment, overlapping long. ex. canals bilaterally.	Anterior in seg- ment, overlapping long. ex. canals bilaterally.	Anterior in seg- ment, not over- lapping long. ex. canals in mature segment.	Middle of seg- ment, may or may not overlap long. ex. canals.	Near middle of segment, over- lapping long. ex. canals bilaterally.
Egg	0.039-0.044 × 0.034-0.041 (av. 0.041 × 0.036)	0.034-0.058 × 0.032-0.049 (av. 0.041 × 0.038)	0.039-0.051 × 0.032-0.049 (av. 0.042 × 0.038)	0.045-0.057 (av. 0.050)	0.051-0.067 × 0.041-0.056 (av. 0.058 × 0.051)	0.034-0.041 × 0.032-0.039 (av. 0.038 × 0.035)

the status of this cestode has been necessary. However, certain identification of the species seemed possible only if intact specimens of Douthitt's cestodes could be obtained. On the assumption that the preserved material mentioned by Douthitt (1915, p. 374) might have been deposited in the H. B. Ward Collection, which was later incorporated in the Helminthological Collection of the U.S. National Museum, a search was made and the two above-mentioned cestodes were located by Dr. J. Ralph Lichtenfels, who kindly permitted me to stain and mount them. The cestodes were discolored, probably from having been stored in a cork-stoppered vial, but they stained well enough for comparison with Douthitt's original description of *Anoplocephala infrequens*. A brief redescription of the cestodes from *Geomys* is presented here:

Strobila 10.5 and 18 long, with 60 and 73 segments; maximum width, attained in early gravid segments, 3 and 3.5. Strobilar margins non-serrate. All segments wider than long; anterior segments very short. Length/width ratio of last mature segment about 1:14; of late gravid segments, about 1:9. Terminal segments narrower, with ratio of about 1:4. Velum well developed, 1/3 to 1/2 as long as gravid segments. Neck 0.112 and 0.160 long. Scolex 0.580 and 0.672 wide, distinctly wider than neck. Suckers about 0.430 in greater diameter. *Anlagen* of genital organs visible in first segment. Genital pores unilateral, sinistral, opening somewhat anterior to middle of segmental margin. Genital ducts passing dorsally across longitudinal excretory canals. Cirrus sac attaining maximum size of 0.310 to 0.360 long by 0.090 to 0.160 in post-mature segments, with average of 0.249 by 0.097. Cirrus sac extending 1/3 to 1/2 of its length mediad to poral ventral excretory canal. After attaining maximum size in early gravid segments, cirrus sac becoming smaller; not discernible in late gravid segments. Internal seminal vesicle beginning to fill in last mature segments, increasing in size and attaining maximum length of about 0.210 in early gravid segments. Elongate external seminal vesicle extending directly mediad, dorsal to seminal receptacle; attaining maximum size, about 0.400 long by 0.090 to 0.100 in diameter, in early post-mature segments. Testes subspherical, about 50 in number, distributed dorsally from near middle of vitelline gland laterad to aporal ventral excretory canal. Thick-walled vagina, 0.200 to 0.210 long, opening in genital atrium ventral to orifice of male duct, and passing mediad ventral to cirrus sac. Vagina enlarging at level of ventral excretory canal, forming thin-walled seminal receptacle. Seminal receptacle beginning to fill in late mature segments, attaining maximum size in 5th or 6th post-mature segments. Seminal receptacle up to 0.790 long by 0.170 to 0.190 in diameter, extending mediad beyond poral margin of vitelline gland. Lobed ovary, 0.560 to 0.768 wide about 0.100 long in last mature segments; situated in poral half of segment with aporal margin near midline. Ovary disappearing in early post-mature segments. Vitelline gland about 0.160 wide in last mature segments, situated dorsally near middle of ovary, at posterior margin of segment. Uterus tubular, transverse, situated anteriorly in segment with ends passing laterad beyond excretory canals bilaterally. Testes and anterior margin of ovary slightly overlapping uterus in late mature segments. Uterus filling rapidly in post-

mature segments, enlarging in diameter and producing anterior and posterior sacculations. Uterus filling terminal gravid segments. Eggs subspherical to spherical, 0.039 to 0.044 by 0.034 to 0.041. Pyriform apparatus well developed.

Douthitt's type specimen, having been sectioned, is of little value for comparative purposes. I propose that the cotype, USNM Helminthol. Coll. No. 49515, be designated lectotype of *Anoplocephaloides infrequens* (Douthitt, 1915). This specimen was obtained from a pocket gopher, *G. bursarius*, collected by H. Douthitt in 1911. The locality was northern Minnesota or Emerson, Manitoba (cf. Douthitt, 1915, p. 374.) Details of the mature segment of this cestode were shown by Douthitt (1915, pl. III, fig. 25).

The cestode described as *Paranoplocephala troeschi* Rausch, 1946, from *Microtus* spp. in North America, is morphologically similar to *A. infrequens*. However, contrary to the opinion of Rausch and Schiller (1949), the differences are sufficient to indicate that they are distinct. *A. troeschi* is further considered below.

A. infrequens has been reported from the plains pocket gopher, *G. bursarius*, in Kansas (Ubelaker and Downhower, 1965), and from the northern pocket gopher, *Thomomys talpoides* (Richardson), in Utah (Frandsen and Grundmann, 1961) and Wyoming (Todd *et al.*, 1971). I did not find this cestode in six northern pocket gophers collected at Emerson, Manitoba, in October 1975. At this locality, *G. bursarius* has been displaced by *T. talpoides* since the time of Douthitt's work (cf. Wrigley and Dubois, 1973).

***Anoplocephaloides wimerosa* (Moniez, 1880).**

[Syn. *Anoplocephala wimerosa* Moniez, 1880; *Paranoplocephala wimerosa* (Moniez, 1880)].

Material studied. — 6. *Lepus timidus* Linnaeus: Flanthey, Valais, Switzerland (leg. B. Hörning).

The strobila of *A. wimerosa* ranges up to 14.5 length, with as many as 37 segments. Among species of *Anoplocephaloides* included in the present group, *A. wimerosa* is distinguished by its relatively large cirrus sac, which attains a length of 0.730 in early gravid segments, and extends mediad across nearly 1/3 of the width of the segment. Detailed descriptions were provided by Stiles (1896) and Douthitt (1915).

A. wimerosa, a host-specific parasite of leporids of the genera *Lepus* and *Oryctolagus*, is known only from western Eurasia. According to Gvozdev *et al.* (1970), it has not been recorded so far east as the western border of the Soviet Union.

Anoplocephaloides dentata (Galli-Valerio, 1905).

[Syn. *Anoplocephala dentata* Galli-Valerio, 1905; *Paranoplocephala dentata* (Galli-Valerio, 1905); *Paranoplocephala brevis* Kirshenblat, 1938].

Material studied. — 17. *Microtus oeconomus* (Pallas): Pravaia Basandra Reserve (Magadansk Oblast'), 1; Popovka River (Magadansk Oblast'), 7; Staryi Chaun (Chaunsk Gulf, East Siberian Sea), 6 (leg. L. Smirnova). *M. arvalis* (Pallas): Orchimont, Belgium, 3 (leg. J. Bernard).

The taxonomic status of this cestode, described from the snow vole, *Microtus nivalis* (Martins) in the Veltlin Alps (northern Italy), has long been controversial. Having been unsuccessful in his efforts to obtain the original material for study, Baer (1923) designated *Anoplocephala dentata* Galli-Valerio, 1905 as a *nomen nudum*. Later, in his monograph of the Anoplocephalidae, Baer (1927) listed it as a synonym of *Paranoplocephala blanchardi* (Moniez, 1891). Spasskii (1951) recognized *P. dentata* as a distinct species, noting that both *P. brevis* Kirshenblat, 1938 and *P. troeschii* Rausch, 1946 were morphologically very similar.

In their review of the species of *Paranoplocephala* in voles in North America, Rausch and Schiller (1949) considered that *P. brevis* might be conspecific with *P. infrequens* (Douthitt, 1915). They did not consider *P. dentata*. Spasskii (1956) listed both *P. infrequens* and *P. brevis* as synonyms of *P. dentata*. Until recently, in agreement with Spasskii, the name *P. dentata* has been applied to the small, wedge-shaped cestodes occurring in voles in Eurasia (Tokobaev, 1960; Tenora, 1963; Dorosz, 1968). The validity of *P. dentata* was evidently accepted also by Dollfus (1961, p. 400), who, in a footnote, briefly described the morphologic characteristics of "... quelques spécimens de *Par. dentata* (Galli-Valerio) = *brevis* Kirschenblatt," from *Microtus arvalis* in France (Lorraine), although earlier in the same paper he questioned their conspecificity. Specimens from the same host in Switzerland (val de l'Allondon) were designated *P. brevis* by Wahl (1967) on the grounds that *P. dentata* had been so inadequately described as to be unrecognizable, and therefore a *nomen nudum*. Contrary to the earlier systematic concept of Tenora (1963, 1967), Wahl's conclusion concerning the validity of the name *P. brevis* was accepted by Tenora *et al.* (1971), and this designation was applied subsequently by Tenora (1972) and Tenora and Zejda (1974).

In the original description of *Anoplocephala dentata*, Galli-Valerio (1905) established that the single cestode found in a snow vole had a strobila 8 mm long and 5 mm wide at the posterior end, with 42 segments. The genital pores were unilatéral, opening near the middle of the segmental margin, but the cirrus sac was described only as being club-shaped ("keulenförmig"). The eggs had a diameter of 0.032. The described arrangement of the genital organs (p. 521) ("Uterus quer gelagert, etwas dem Vorderrande genähert. Hoden und Keimstock im Mittelfeld.") is compatible with the allocation of this cestode to the genus *Anoplocephala* as then conceived.

Although discrepant in the width of the strobila, the description of *A. dentata* by Galli-Valerio is in substantial agreement with the description of *P. brevis* by several others (Kirshenblat, 1938; Akhumin, 1956; Wahl, 1967), and with that of *P. dentata* by Dollfus (1961). That *P. brevis* is conspecific with *P. dentata* is strongly supported by the fact that only a single species of cestode having a small, wedge-shaped strobila and referable to the genus *Anoplocephaloides* as here conceived is known to occur in arvicoline rodents in Eurasia (excepting northeastern Siberia; see below). The distinctive form of the strobila of *A. dentata* was recognized by Galli-Valerio, who remarked (1905, p. 521) that "Es ist dies die kleinste der bis heutigen Tags in Angehörigen der Gattung *Arvicola* [i.e., *Microtus*] beobachteten *Anoplocephala*, denn *A. omphalodes* Hermann ist 135 mm lang; *Anoplocephala* sp. von Janicki ist 90 mm lang; *A. Blanchardi* Moniez ist 32 mm lang." Small cestodes designated variously as *P. dentata* or *P. brevis* have been found in snow voles wherever the parasites of these animals have been investigated (cf. Tenora *et al.*, 1971). In the Tirolean Alps, for example, Tenora *et al.* reported that 22 % of 63 snow voles were infected. The evidence seems to justify the conclusion that *P. dentata* (Galli-Valerio, 1905) [= *Anoplocephaloides dentata* (Galli-Valerio, 1905)] is the senior synonym of *P. brevis* Kirshenblat, 1938.

Anoplocephaloides dentata has an extensive geographic range in Eurasia, where it has been recorded from western Europe to northeastern Siberia. A morphologically similar cestode was found in *Apodemus* and *Microtus* in Korea by Byong *et al.* (1968). *A. dentata* is a common parasite of arvicoline rodents, especially of voles of the genus *Microtus*. In Iakutia, where Gubanov and Fedorov (1970) examined 3784 arvicoline rodents representing four genera, cestodes designated *Paranoplocephala dentata* were found in all of the 7 species included. Rates of infection ranged from 0.3 % in *Clethrionomys rutilus* (Pallas), to 19.5 % in *Microtus gregalis* (Pallas). Numbers of cestodes in infected animals ranged from 1 to 12, with the highest average number of 3.4 in *Arvicola terrestris* (Linnaeus). In eastern Siberia (Popovka River), I found 2 of 18 *M. oeconomus koreni* Allen to be infected. Several investigators in Europe have reported this cestode from murine rodents of the genus *Apodemus*, although rates of infection were quite low (cf. Tenora, 1967). None was infected of 702 field mice representing three species of *Apodemus* examined in Hungary by Murai (1972).

Spasskii (1951, p. 314) found that the Siberian form of *A. dentata* differs from that in Europe in having a longer cirrus sac, more numerous testes, and apparently larger eggs. The two morphologic types possibly represent distinct species. The characteristics of *A. dentata* from voles in northeastern Siberia are summarized in Table II. A slide containing three specimens from *Microtus oeconomus* collected at Staryi Chaun has been deposited in the Helminthological Collection of the U.S. National Museum, No. 74078.

***Anoplocephaloides troeschi* (Rausch, 1946).**

[Syn. *Paranoplocephala troeschi* Rausch, 1946].

Material studied. — 27. *Microtus pennsylvanicus* (Ord): East Lansing, Michigan (paratypes), 5; Cheboygan County, Michigan, 4 (leg. J. D. Tiner); Horicon

Marsh, Wisconsin, 2; Union County, Ohio, 2; La Grange, Illinois, 1; Missoula, Montana, 3 (leg. J. M. Kinsella); Saskatoon, Saskatchewan, 4; McPhee Lake (central Saskatchewan), 3. *M. montanus* (Peale): Fremont County, Wyoming, 3. Numerous additional specimens from *Microtus* spp. in North America also were examined.

Of the species of *Anoplocephaloides* occurring in rodents, *A. troeschi* most closely resembles *A. dentata* (Galli-Valerio, 1905) and *A. infrequens* (Douthitt, 1915). Compared with the former, *A. troeschi* has a longer strobila with more numerous segments and a smaller cirrus sac. Differences also exist in the proportions and relationships of other organs. The strobila of *A. troeschi* is shorter than that of *A. infrequens*, and consists of fewer, relatively longer segments. The cirrus sac is smaller, attaining a maximum length of about 0.230 in post-mature segments, whereas that of *A. infrequens* attains a length of 0.360. Other morphological characteristics of these cestodes are compared in Table II.

A. troeschi has an extensive geographic distribution in North America, where it is a characteristic parasite of voles of the genus *Microtus* (cf. Rausch, 1952).

***Anoplocephaloides lemmi* (Rausch, 1952).**

[Syn. *Paranoplocephala lemmi* Rausch, 1952].

Material studied. — 18. *Lemmus sibiricus* (Kerr): (Alaska) Point Barrow, 2 (paratypes); Beaufort Lagoon (eastern arctic coast), 3; Lake Schrader (eastern Brooks Range), 4; Chandler Lake (central Brooks Range), 2; Paimiut (near Cape Romanzof, western Alaska), 1; Becharof Lake (Alaska Peninsula), 1; Ugashik Lake (Alaska Peninsula), 2; (Canada) Melville Peninsula, 3.

A. lemmi is a host-specific parasite of the brown lemming, occurring in this mammal throughout its range in North America. It has been reported from *L. sibiricus* in Siberia by Gubanov and Fedorov (1970), who found 58 lemmings infected of 430 examined in northern Yakutia; numbers of cestodes ranged from 1 to 17 in infected animals.

Species having strobilae of intermediate form.

Six species of *Anoplocephaloides* have relatively short strobilae that can be considered neither wedge-shaped nor ribbon-like. In some, the scolex is small and weakly developed. The species in rodents in the Holarctic and *A. mamillana* (Mehlis, 1831) in horses have unilateral genital pores; those in rodents in Africa have irregularly alternating genital pores. These cestodes are considered as a group, although they are morphologically heterogeneous.

***Anoplocephaloides mamillana* (Mehlis, 1831).**

[Syn. *Taenia mamillana* Mehlis, 1831; *Anoplocephala mamillana* (Mehlis, 1831); *Paranoplocephala mamillana* (Mehlis, 1831)].

Material studied. — 3. *Equus caballus* Linnaeus: Brasil (USNM Helminthol. Coll. No. 17272).

The strobila of *A. mamillana* attains a length of about 30, with as many as about 50 segments. A maximum width of 4 to 6 is attained in gravid segments, but the strobilar margins are essentially parallel. In the present material, the last mature segment was the 11th to 15th. The ovary, situated in the poral half of the segment, increased in size in the first 5 post-mature segments, after which it disappeared abruptly. The vitelline gland persisted in a few more segments. The uterus in mature segments had the form of a slender, transverse tube situated near the middle of the segment and not extending lateral to the ventral excretory canals. The testes were distributed from the level of the middle of the ovary laterad to near the aporal excretory canals. The cirrus sac, when straight (this organ is frequently arched) attained a length of 0.975 to 1.12 in post-mature segments.

The cirrus sac of *A. mamillana* is provided with a well developed retractor muscle which extends anteromediad from the proximal end of the organ to the anterior margin of the segment at the midline (fig. 4). This muscle attains a degree of development that I have not observed in other species of *Anoplocephaloides*.

Detailed descriptions of *A. mamillana* have been given by Zschokke (1888, p. 18), Stiles (1896), and Spasskii (1951, p. 319). As a result of introductions by means of infected horses, this cestode appears to have a cosmopolitan distribution. It has been recorded also by Round (1968, p. 25) in a zebra, *Equus burchelli* (Gray), in Kenya.

FIG. 4. — *Anoplocephaloides mamillana* (Mehlis, 1831) from *Equus caballus*, Brasil. Ventral view: relationships of the genital ducts. Designations are: v, vagina; sr, seminal receptacle; isv, internal seminal vesicle; esv, external seminal vesicle; vd, vas deferens; rm, retractor muscle.

Anoplocephaloides blanchardi (Moniez, 1891).

[Syn. *Taenia blanchardi* Moniez, 1891; *Anoplocephala blanchardi* (Moniez, 1891); *A. campestris* Kholodkovskii, 1912; *Paranoplocephala blanchardi* (Moniez, 1891)].

Material studied. — None.

A. blanchardi appears to be an uncommon parasite of arvicoline rodents in Europe. Its geographic distribution in other regions of Eurasia is uncertain.

In his monograph of the Anoplocephalidae, Baer (1927) recognized *P. blanchardi* as a distinct species, which he characterized as follows (p. 80): «Ce parasite du Campagnol a 20 à 40 millimètres de long et 2,5 à 4 millimètres de large. Le scolex a 0,7 millimètre de diamètre. Les pores sexuels sont unilatéraux et débouchent au milieu du bord latéral du segment. Il y a environ 50 testicules situés dans la moitié antiporale du segment. La poche du cirre a 0,5 millimètre de long et contient une vésicule séminale. Il y a aussi une vésicule séminale externe. Les glandes sexuelles femelles sont situées dans la moitié porale du segment. L'utérus mûr remplit tout le segment. Les œufs ont 40 à 50 μ de diamètre et l'embryon est muni d'un appareil piriforme.» A few years later (1932, p. 6), Baer placed *P. blanchardi* in synonymy with *P. omphalodes* on the grounds that the differences in size of strobila and arrangement of the genital pores were not constant. This synonymy was retained by Joyeux and Baer (1936, p. 444), although they distinguished two forms of *P. omphalodes*, corresponding with the two species as formerly characterized. Baer (1949) listed *P. blanchardi* as one of three species of *Paranoplocephala* in which an external seminal vesicle is lacking, contrary to the description given in his monograph. At the same time, he reiterated his view that the alleged differences between *P. omphalodes* and *P. blanchardi* had been based on the study of material in a poor state of preservation, stating (p. 43) that the genital pores were never completely unilateral in these cestodes.

Spasskii (1951, p. 308) considered the published information concerning the morphologic characteristics of *P. omphalodes* and *P. blanchardi* to be contradictory. Although he reproduced the composite description of *P. omphalodes*, he separately described cestodes from common voles ["obyknovennaia polevka" = *Microtus arvalis*] in the Novosibirsk region, which he considered to correspond morphologically with earlier descriptions of *P. blanchardi*. More recently, Dollfus (1961) studied cestodes identified by him as *P. blanchardi* from *M. agrestis* (Linnaeus) and *Clethrionomys glareolus* (Schreber), in France. His conclusion concerning the taxonomic status of these was as follows (p. 400): «Nos spécimens de Richelieu à pores unilatéraux et vésicule séminale externe ont de trop grandes dimensions pour être rapportés à *dentata* ou à *brevis*; nous estimons qu'ils correspondent à *blanchardi* et à *campestris*, qui sont pour nous synonymes. Comme *blanchardi* est plus ancien, nous adoptons *blanchardi*, que nous éliminons de la synonymie d'*omphalodes*.» Thus, only two species of *Anoplocephaloides*, *A. blanchardi* (Moniez, 1891) and *A. dentata* (Galli-Valerio, 1905) are distinguishable in arvicoline rodents in Europe.

The identity of the cestodes described by Spasskii (1951) is still uncertain, since the range of morphologic variation in *A. blanchardi* has not been defined. *Blanchardi*-like cestodes apparently have not been reported from eastern Siberia. The cestodes identified as *P. omphalodes* by Ishimoto (1974) from *Apodemus* spp. in Hokkaido appear to be distinct from *A. blanchardi*, and may represent an undescribed species that is host-specific for these murine rodents. I obtained a single specimen from a field mouse, *Apodemus argenteus* (Temminck), collected on Mt. Moiwayama, near Sapporo, Hokkaido, in 1962, and a second was found in *A. argenteus* trapped on Hakkoda Mountain, near Sukayu Hot Springs in northern Honshu. These cestodes are clearly referable to the genus *Anoplocephaloides*, as is evident also from Ishimoto's (1974) description. To establish the possible range of hosts of this cestode, it would be useful to investigate the parasites of the indigenous vole, *Microtus montebelli* (Milne-Edwards), on the Island of Honshu.

***Anoplocephaloides variabilis* (Douthitt, 1915).**

[Syn. *Anoplocephala variabilis* Douthitt, 1915; *Paranoplocephala variabilis* (Douthitt, 1915)].

Material studied. — 9. *Geomys bursarius* (Shaw): USNM Helminthol. Coll. No. 7410 ("type material"), 2. *Thomomys talpoides* (Richardson): Emerson, Manitoba, 2; 10 km north of Prince Albert, Saskatchewan, 2; 5 km south of Saskatoon, Sask., 3.

The description of *Anoplocephala variabilis* was based on cestodes from pocket gophers, *G. bursarius*, collected in "central Illinois" (Douthitt, 1915, p. 370). Like that of *A. infrequens*, the taxonomic status of this cestode has been uncertain.

Anoplocephala variabilis was one of the species removed to the genus *Anoplocephaloides* by Baer (1923). Later, in his monograph of the Anoplocephalidae, Baer (1927) listed *Anoplocephaloides variabilis* as a synonym of *P. infrequens*. Hansen (1947) found that these cestodes represented distinct species, based on differences in the development of the velum. Rausch and Schiller (1949) also considered *P. variabilis* to be distinct, and provided a redescription based on specimens from *Microtus*. Spasskii (1951, p. 330) recognized the validity of *P. variabilis* in his monograph of the Anoplocephalata, but later (1956), in his review of the genus *Paranoplocephala*, listed it as a synonym of *P. omphalodes*. Yamaguti (1959, p. 385) followed Baer in listing *P. variabilis* as a synonym of *P. infrequens*.

Three specimens of *Anoplocephala variabilis*, labeled "type material," in the Helminthological Collection of the U.S. National Museum, No. 7410, were sent by Dr. J. Ralph Lichtenfels to me for study. Two were stained and mounted, permitting detailed comparisons with Douthitt's (1915) description and with cestodes from pocket gophers, *T. talpoides*, and arvicoline rodents. I conclude that *Anoplocephala variabilis* is a morphologically distinctive species referable to the genus *Anoplocephaloides* as here conceived.

The cotypes were in good agreement morphologically with Douthitt's (1915, p. 370) description of *Anoplocephala variabilis*. The cestodes had been excessively relaxed, so that the anterior portions of the strobilae were more attenuated than is the case in well fixed material. The larger specimen was 64 long, with 196 segments, and 2 in maximum width. The scolices were relatively small, not wider than the neck. The last mature segments in the strobilae were the 80th and 70th, respectively. The ovary in mature segments was relatively large compared with that in other species of *Anoplocephaloides*, extending from the poral ventral excretory canal, to which its margin was closely apposed, medially well beyond the midline of the segment. It measured 0.480 to 0.720 wide in mature segments (av. 0.622), and extended through the length of the segment. The relatively large vitelline gland was situated dorsally over the poral half of the ovary, from near the posterior margin of the segment. In one specimen, the seminal receptacle had begun to fill in the 59th segment, after which it gradually increased in size, attaining maximum dimensions of about 0.700 long by 0.250 in diameter in the 90th segment. The testes, situated dorsally, were distributed from the level of the aporal third of the ovary laterad beyond the aporal longitudinal excretory canals. The cirrus sac was about 0.160 long by 0.075 in diameter in the last mature segment; thereafter, it increased in size, attaining maximum dimensions of about 0.300 long by 0.130 in diameter in the 102nd segment [Douthitt (1915, p. 371) gave the dimensions of the cirrus sac as "200 μ long by 75 μ wide"]. The internal and external seminal vesicles also increased in size posteriorly, attaining maximum dimensions in early gravid segments. The uterus in mature segments appeared as a transverse tube situated anteriorly with the lateral portions curving posteriorly and extending across the longitudinal excretory canals bilaterally. The poral end of the uterus lay just anterior to the cirrus sac; the aporal end was slightly more posterior. The development of the uterus was typical, with formation of anterior and posterior sacculations; the uterus filled the gravid segments. The subspherical eggs ranged from 0.030 to 0.034 in greater diameter by 0.027 to 0.034 (av. 0.032 by 0.030) (Douthitt gave the dimensions of the egg as 30 to 35 μ). Mature segments of *A. variabilis* were portrayed by Douthitt (1915, pl. III, fig. 22 and 23).

Douthitt (1915, p. 374) reported that *A. variabilis* in *Geomys* exhibited a gradual decrease in size of strobila northward from central Illinois, with a corresponding reduction in numbers of segments and numbers of testes. He recognized a "northern form," which he designated a subspecies, *A. variabilis borealis* Douthitt, 1915. However, his samples were too small to establish that a clinal reduction in size does in fact occur. One of my specimens, from *T. talpoides*, collected at Emerson, Manitoba, had 192 segments -- only 4 less than the mean obtained by Douthitt for cestodes in central Illinois.

Anoplocephaloides variabilis was found in 5 of 16 *T. talpoides* collected by me in central Saskatchewan, and in 1 of 6 trapped at Emerson, Manitoba. These cestodes corresponded with those from *Geomys* in all morphologic characters considered to have taxonomic significance. The study of well preserved material disclosed that

the cirrus of *A. variabilis* is spinose, contrary to the statement of Douthitt (1915, p. 371) that it is aspinose. This cestode has been reported from *T. talpoides* in Utah (Frandsen and Grundmann, 1961), Wyoming (Todd *et al.*, 1971), and Alberta (Lubinsky, 1957). I also obtained it in two of 11 of these rodents at Moran, Wyoming, in 1948. A specimen of *A. variabilis* from *T. talpoides* collected 5 km south of Saskatoon, Saskatchewan, has been deposited in the Helminthological Collection of the U.S. National Museum, No. 74084.

Compared with the type material and with specimens from *T. talpoides*, cestodes tentatively identified as *A. variabilis* from arvicoline rodents had much smaller strobilae, but otherwise did not seem to differ significantly in relationships and relative proportions of organs. A brief description, based on cestodes from arvicoline rodents, is presented here.

Anoplocephaloides cf. variabilis (Douthitt, 1915).

Material studied. — 27. *Microtus pennsylvanicus* (Ord): Anchorage, Alaska, 9; Swanson, Saskatchewan, 1; Fond du Lac County, Wisconsin, 1. *M. miurus* Osgood: Tulugak Lake (central Brooks Range, Alaska), 6; Hatcher Pass (Talkeetna Mountains, Alaska), 4. *M. oeconomus* (Pallas): St. Lawrence Island, 2. *M. ochrogaster* (Wagner): Havana, Illinois, 1. *M. montanus* (Peale): Fremont County, Wyoming, 2. *Lemmus sibiricus* (Kerr): Point Barrow, Alaska, 1.

Description. Strobila 18 to 29 long, with 103 to 133 segments; maximum width, attained in early gravid segments, 2 to 3. All segments wider than long, with relative length increasing posteriad. Length/width ratio of last mature segment 1:8 to 1:7; of terminal gravid segments, about 1:5. Scolex small, 0.330 to 0.430 wide and 0.300 to 0.380 long. Neck 0.250 to 0.464 long. Genital pores unilateral, usually sinistral, opening near middle of segmental margin. Genital ducts passing dorsally across longitudinal excretory canals. Cirrus sac elongate, with maximum diameter near proximal end; extending mediad beyond ventral excretory canal. Cirrus sac 0.170 to 0.233 long by about 0.070 in diameter in last mature segment; in post-mature segments, attaining length of 0.190 to 0.360 by 0.060 to 0.100 (av. 0.255 by 0.083). Cirrus spinose; about 0.150 long when extruded, and 0.020 in diameter at base. Internal seminal vesicle beginning to fill in last 4-7 mature segments; in post-mature segments attaining length of 0.100 to 0.161 by 0.070 to 0.095. Cirrus sac displaced anteriorly by poral end of seminal receptacle in early post-mature segments; extending directly mediad in early gravid segments. External seminal vesicle extending anteromediad from proximal end of cirrus sac, attaining maximum size of about 0.154 by 0.050. Testes subspherical, about 60 in number, distributed dorsally from level of aporal margin of vitelline gland laterad beyond aporal excretory canals. Vagina opening in genital atrium ventral to orifice of male duct; extending mediad posteroventral to cirrus sac. Seminal receptacle beginning to fill in last 3-4 mature segments, increasing in size thereafter. Fully developed seminal receptacle ellipsoidal, 0.330 to 0.400 long by 0.120 to 0.168 in maximum diameter, situated ventrally

near posterior margin of segment, and extending from poral ventral excretory canal mediad to poral margin of vitelline gland. Lobed ovary extending from poral ventral excretory canal mediad beyond midline of segment; 0.592 to 0.750 wide by 0.190 to 0.240 long (av. 0.709 by 0.198) in mature segments. Ovary disappearing in early post-mature segments. Vitelline gland bilobed, with larger lobe aporal; situated dorsally near posterior margin of segment, over poral half of ovary. Vitelline gland 0.230 to 0.290 wide by 0.110 to 0.150 long (av. 0.261 by 0.136) in mature segments. Uterus in mature segments appearing as transverse tube situated anteriorly, extending beyond longitudinal excretory canals bilaterally; lateral portions of uterus curving posteriad, with poral end lying just anterior to cirrus sac. Uterus beginning to enlarge in 52nd to 60th segment, thereafter producing anterior and posterior sacculations; fully developed uterus filling gravid segments. Eggs subspherical to spherical, 0.034 to 0.041 by 0.032 to 0.039 (av. 0.038 by 0.035). Embryo 0.012 in greater diameter. Pyriform apparatus well developed.

A representative specimen, from *Microtus miurus* Osgood, collected at Tulugak Lake, central Brooks Range, arctic Alaska, has been deposited in the Helminthological Collection of the U.S. National Museum, No. 74083.

Anoplocephaloides cf. *variabilis* has an extensive geographic range in arvicoline rodents in North America. It inhabits the duodenum, as does *A. variabilis* in pocket gophers. Numbers in infected voles ranged from 1 to 6. In contrast, Douthitt (1915, p. 370) found as many as 50 specimens of *A. variabilis* in a single pocket gopher.

***Anoplocephaloides neofibrinus* (Rausch, 1952).**

[Syn. *Paranoplocephala neofibrinus* Rausch, 1952].

Material studied. — 6. *Neofiber alleni* True: Putnam County, Florida (paratypes).

A. neofibrinus is a nearctic species that appears to be a host-specific parasite of the round-tailed muskrat, *N. alleni*, an arvicoline rodent occurring locally in southeastern North America (southern Georgia and Florida). This cestode is known only from the type material.

***Anoplocephaloides isomydis* (Setti, 1892).**

[Syn. *Taenia isomydis* Setti, 1892; *Paranoplocephala isomydis* (Setti, 1892); other probable synonyms have been listed by Baer (1949)].

Material studied. — 2. *Otomys tropicalis* Thomas: Mt. Kenya (elev. ca. 4 500 m), Kenya.

Taenia isomydis was described from a murine rodent, *Isomys abyssinicus* Rüppell [= *Arvicanthis abyssinicus* (Rüppell)] from Cundi, Eritrea. This cestode was placed in the genus *Paranoplocephala* by Baer (1949), who provided a redescription

from the original material in the Institute of Zoology, University of Naples. Mahon (1954) obtained three specimens from another murine rodent, *Oenomys hypoxanthus* (Pucheran), in the Belgian Congo. Mahon also examined the original material, and attributed discrepancies in her findings as compared with the description by Baer to differences in methods of fixation and in condition of the material.

Single specimens of this cestode were obtained from each of two *O. tropicalis* that died at the Institute of Arctic Biology, University of Alaska, soon after their arrival from Kenya. I am indebted to Mr. D. W. Hartbauer for the opportunity to examine the animals.

Morphologically, the cestodes from *O. tropicalis* were in good agreement with the descriptions of *P. isomydis* by Baer (1949) and Mahon (1954). Of the nominal species of *Anoplocephaloides* reported from rodents in Africa, *A. isomydis* is the only one possessing an external seminal vesicle (cf. Baer, 1949, p. 43; Mahon, 1954, fig. 36). So far as can be determined from the descriptions, it appears also to be the only one in which the uterus does not extend laterad to the longitudinal excretory canals.

***Anoplocephaloides acanthocirrosa* (Baer, 1924).**

[Syn. *Paranoplocephala acanthocirrosa* Baer, 1924].

Material studied. — None.

In a preliminary report, Baer (1924) described *Paranoplocephala acanthocirrosa* from an otomyine rodent, *Otomys bisulcatus* Cuvier (= *O. irroratus* Brants) in South Africa. Later, Baer (1926, p. 77) provided a more detailed description of this cestode, and compared it with *P. omphalodes*, the only other species in the genus at the time. *P. acanthocirrosa* differed in having a shorter, more robust strobila, fewer segments, and a much larger cirrus sac, the dimensions of which were given as 0.800 long by 0.200 in maximum diameter. *P. acanthocirrosa* was next recorded from the same host in Rhodesia by Baer (1933), who remarked that the specimens agreed morphologically with the type material. Spasskii (1951, p. 311) recognized *P. acanthocirrosa* as distinct from *P. omphalodes*, although he considered the two to be morphologically very similar except for the differences in size of the cirrus sac. Spasskii presumably relied on the composite description of *P. omphalodes*, as published in his monograph, in comparing these cestodes.

Cestodes obtained from *Otomys kempfi* Dollman (= *O. denti* Thomas) at Rutshuru, in the Belgian Congo, were described by Baer (1959) as a subspecies of *P. acanthocirrosa*, designated *P. a. kivuensis* Baer, 1959. In his discussion, without explanation of the discrepancy, Baer stated (p. 57) that the cirrus sac in the nominate form measured only 0.366 to 0.686 long by 0.137 to 0.178 in diameter, compared

with 0.800 by 0.200 as given in his earlier descriptions of *P. acanthocirrosa* (cf. Baer, 1924, 1926). According to Baer (1959), the subspecies *P. a. kivuensis* differed from the nominate form in having a smaller cirrus sac (0.215 to 0.367 long), more numerous testes (60 to 65 as compared with 40 to 60), and an aspinose cirrus (p. 57) « ... armé d'une cuticule réfringente, » whereas that of the nominate form (Baer, 1926, p. 77) was "... thickly beset with small spines." The figure of the mature segment of *P. a. kivuensis* (cf. Baer, 1959, fig. 33) indicates that differences exist in the relationships of some of the organs: the cirrus sac does not extend medially to the ventral excretory canal, whereas it extends well beyond the canal in the nominate form; the ovary has a more poral location, and the testes appear to have a more extensive distribution. The relationships of the uterus in the mature segment were not shown for either taxon in the published figures.

The taxonomic status of *P. acanthocirrosa* was further considered by Collins (1972), who studied four cestodes, including a paratype of *P. acanthocirrosa*, and some additional fragments, all from *Otomys* spp. in South Africa. She found that the length of the cirrus sac ranged from 0.378 to 0.483 in the paratype and from 0.400 to 0.700 in the other specimens. With reference to Spasskii's (1951) opinion concerning the importance of the size of the cirrus sac in discriminating the two species, Collins considered the ostensible overlap in the dimensions of this organ to be sufficient grounds for placing *P. acanthocirrosa* in synonymy with *P. omphalodes*. Collins relied on Spasskii's (1951) composite description of the latter species, in which the cirrus sac was stated to range from 0.200 to 0.500 in length. The possible significance of other taxonomic characters was not considered.

Another species of *Paranoplocephala*, *P. otomyos* Collins, 1972, was described on the basis of a single complete cestode and fragments of another from *Otomys irroratus* in South Africa. Collins (p. 30) considered that the structure of the cirrus sac characteristically separated this cestode from all other species in the genus. *P. otomyos* was distinguished from *P. omphalodes* sensu Collins (= *P. acanthocirrosa*) by its smaller cirrus sac (0.144 to 0.280 long by 0.120 to 0.160 in diameter) and aspinose cirrus.

These three taxa, *P. a. acanthocirrosa*, *P. a. kivuensis*, and *P. otomyos*, are here assigned to the genus *Anoplocephaloides*, with which they seem to conform in most morphologic characteristics. These cestodes have been described as lacking an external seminal vesicle. Although the published descriptions and figures indicate that these cestodes are morphologically very similar, they are too deficient in detail to permit evaluation of the described differences. The characteristics of *A. a. kivuensis* suggest that it may differ specifically from the nominate form. The absence of spines on the cirrus may not be significant, since these structures are frequently lost from poorly fixed material. The study of a large series of well preserved cestodes from *Otomys* spp. in various regions of Africa will be necessary to define the range of morphologic variation in *A. acanthocirrosa*, and to establish the status of the other

two taxa. Until contrary evidence is obtained, I consider *A. a. kivuensis* (Baer, 1959) and *A. otomyos* (Collins, 1972) to be species *sedis incertae*.

The taxonomic status of Paranoplocephala indicata Sawada and Tongchai, 1966.

Cestodes from an Asiatic tapir, *Tapirus indicus* Desmarest (Perissodactyla), in Thailand were assigned to the genus *Paranoplocephala* by Sawada and Tongchai (1966) and described as *P. indicata* Sawada and Tongchai, 1966. This cestode is referable to the genus *Flabellokrjabinia* Spasskii, 1951, rather than to the genus *Paranoplocephala* (= *Anoplocephaloides* as here conceived).

The genus *Flabellokrjabinia* was erected by Spasskii (1951, p. 275) to contain *Anoplocephala tapirus* Chin, 1938 from *Tapirus* sp. (evidently also *T. indicus*), geographic origin uncertain. At the same time, Spasskii conditionally transferred *Anoplocephala globiceps* (Diesing, 1856) to this genus. *Taenia globiceps* Diesing, 1856, described from a tapir [evidently *T. terrestris* (Linnaeus)] in Brasil, was transferred to the genus *Anoplocephala* by Lühe (1895), and later placed in synonymy with *Paranoplocephala mamillana* (Mehlis, 1831) [= *Anoplocephaloides mamillana* (Mehlis, 1831)] by Baer (1927, p. 81). The genus *Flabellokrjabinia* was recognized by Yamaguti (1959, p. 377), but Joyeux and Baer (1961, p. 550) listed it as a synonym of *Paranoplocephala*.

Flabellokrjabinia is distinguished from *Paranoplocephala* (= *Anoplocephaloides*) on the basis of the different distribution of the testes. In *F. tapirus*, the type species, the very numerous testes are situated across the entire mature segment, extending porad beyond the ovary nearly to the excretory canals, both anterior and posterior to the genital ducts (cf. Spasskii, 1951, fig. 130). In *F. tapirus* also, the uterine sacculations remain discrete in the gravid uterus, which does not fill the segment.

The cestode described as *Paranoplocephala indicata* has a longer, broader strobila, with a greater number of segments, than does *F. tapirus*. According to the original description, *P. indicata* has 350 to 358 testes that are distributed (Sawada and Tongchai, 1966, p. 127) from "... about aporal edge of ovary to aporal longitudinal excretory canals." However, so far as can be determined from the photograph of the mature segment (Sawada and Tongchai, fig. 3), the testes in *P. indicata* appear to extend porad at least to the poral margin of the ovary. According to the photograph of "senile proglottides" (Sawada and Tongchai, fig. 6), the uterus is somewhat smaller and more anteriorly situated than that in *F. tapirus*, and the testes persist in gravid segments. The morphologic similarities between *F. tapirus* and *P. indicata* are sufficient to indicate that they are congeneric, and differences in distribution of the testes and in other morphologic characteristics seem sufficient to distinguish these cestodes at the specific level. The study of additional material from *Tapirus indicus* would permit a more complete characterization of these cestodes. Further consideration of the status of *F. globiceps* (Diesing, 1856) should be undertaken only after the study of additional material from tapirs in South America.

III. - Descriptions of new species

Three species of cestodes referable to the genus *Anoplocephaloides* are described here as new. They occur respectively in field mice in Japan (Hokkaido), rabbits in Costa Rica, and bog lemmings in northwestern North America.

1) Rodents examined for helminths in Japan in 1962 were collected as follows [nomenclature of field mice of the genus *Apodemus* is that of Kobayashi and Hayata (1971)]: Rebun Island (in the Sea of Japan, northwest of Hokkaido) — *Clethrionomys rufocanus* cf. *bedfordiae* (Thomas), 17; *Clethrionomys* sp. (referred to *C. rex* Imaizumi, 1971; described subsequently from nearby Rishiri Island), 2. Hokkaido. — *C. rufocanus bedfordiae*, 36; *C. rutilus mikado* (Thomas), 10; *Apodemus argenteus* (Temminck), 51; *A. speciosus ainu* (Thomas), 19. Northern Honshu (Aomori Prefecture) — *Clethrionomys* sp., 1; *A. argenteus*, 33; *A. speciosus*, 1.

The following description is based on cestodes found in two specimens of *Apodemus argenteus*, collected on 25 July 1962 near Sapporo, Hokkaido. Infections consisted of 2 and 5 cestodes. All had gravid segments, and apolysis had occurred in 5.

Anoplocephaloides baeri (fig. 5-7).

Description: Strobila 11 to 22 long, with 41 to 74 segments. Maximum width, attained in gravid segments, 1.9 to 2.7. Strobila widening rapidly anteriorly, with strobilar margins nearly parallel; segmental margins serrate. All segments wider than long. Length/width ratio of mature segments about 1:7, with relative length increasing posteriad; ratio of early gravid segments about 1:5; of terminal 2-3 segments, as little as 1:2. Scolex 0.806 to 0.975 wide by 0.496 to 0.666 long, slightly wider than beginning strobila; suckers round, 0.288 to 0.340 in greater diameter. Neck not discernible. *Anlagen* of genital organs visible immediately posterior to scolex, before external segmentation becomes evident. Genital pores unilateral, usually sinistral (dextral in one specimen), opening near middle of segmental margin. Genital atrium 0.070 to 0.088 deep. Genital ducts passing dorsally across longitudinal excretory canals. Ventral canals 0.012 to 0.040 in diameter, connected across posterior margin of segment by transverse duct 0.004 to 0.016 in diameter; dorsal canals 0.016 to 0.036 in diameter, situated lateral to ventral canals in approximately same plane. Cirrus sac 0.192 to 0.248 long by 0.045 to 0.084 in maximum diameter (av. 0.220 by 0.070) in mature segments, with 1/2 to 3/5 of its length mediad to ventral longitudinal excretory canals. In post-mature segments, cirrus sac attaining maximum dimensions of 0.323 by 0.104. Cirrus about 0.140 long by 0.028 in diameter when extruded; densely covered by minute spines. Internal

seminal vesicle beginning to fill in first post-mature segments, increasing in size posteriad; 0.120 to 0.260 long by 0.076 to 0.120 in maximum diameter (av. 0.177 by 0.093). External seminal vesicle forming several loops; in mature segments, extending anteromediad from aporal end of cirrus sac, dorsal and partly anterior to seminal receptacle. In post-mature segments, external seminal vesicle becoming distended with spermatozoa, 0.200 to 0.460 long by 0.060 to 0.180 in maximum diameter, usually extending mediad, but sometimes forming loop anterior to proximal end of cirrus sac. Testes spherical, 0.028 to 0.052 in diameter (av. 0.041), 80 to 90 in number, distributed dorsally from level of poral margin of ovary laterad to aporal ventral excretory canal; arranged 2-3 deep, and extending through most of length of segment. Testes persisting in early, post-mature segments, initially overlapping enlarging uterus dorsally, then becoming displaced posteriad. Vagina consisting of thick-walled tube 0.120 to 0.130 long by 0.020 to 0.036 in diameter, opening in genital atrium ventral to orifice of male duct and passing mediad ventral to cirrus sac; vagina dilating medial to ventral excretory canal, forming elongate seminal receptacle. Seminal receptacle, beginning to fill in last mature segments, 0.220 to 0.388 long by 0.068 to 0.108 in maximum diameter near aporal end (av. 0.311 by 0.088), extending mediad ventrally near posterior margin of segment, reaching level of poral margin of vitelline gland. Seminal receptacle often empty in post-mature segments, appearing as thick-walled, tubular structure, but greatly distended in other segments. Seminal duct short, about 0.009 in diameter. Lobed ovary situated ventrally in poral half of segment, with aporal margin near midline, 0.360 to 0.698 wide by 0.120 to 0.165 long (av. 0.448 by 0.153), extending through most of length of segment. Ovary disappearing in early post-mature segments. Vitelline gland lobed, 0.130 to 0.216 wide by 0.060 to 0.100 long (av. 0.161 by 0.081), dorsal to ovary near posterior margin of segment. Small, discrete masses of vitelline tissue sometimes present, usually medial to vitelline gland at same level. Vitelline gland persisting longer than ovary in post-mature segments. Uterine duct passing antero-ventrad from origin; uterus first visible as transverse tube 0.012 to 0.016 in diameter, situated ventrally near anterior margin of segment, not extending across longitudinal excretory canals bilaterally in mature segments; overlapping canals in post-mature and gravid segments. Uterus first enlarging in 17th to 20th segment of strobila, forming anterior and posterior sacculations, and filling entire gravid segment. Genital ducts, including collapsed seminal receptacle, displaced to posterior margin of gravid segments and persisting. Eggs thin-walled, spherical, 0.045 to 0.057 in diameter (av. 0.050). Embryo 0.017 to 0.020 in greater diameter. Pyriform apparatus well developed.

Type host: Field mouse, *Apodemus argenteus* (Temminck).

Type locality: Mt. Moiwayama, near Sapporo, Hokkaido.

Habitat: Duodenum of host.

Type: Holotype No. 74079 and paratype No. 74080, both from the same host, have been deposited in the Helminthological Collection of the U.S. National Museum.

This cestode is named in honor of the late Professor Jean G. Baer, an authority on the systematics of the Anoplocephalidae, and one of the first to consider the origins of helminth-host assemblages.

Remarks: Compared with the species of *Anoplocephaloides* known from the Eurasian continent, *A. baeri* sp. nov. is distinguished by its small strobila from all but *A. dentata* (Galli-Valerio, 1905). The strobila of *A. baeri* is longer with nearly parallel margins, and consists of 41 to 74 segments; that of *A. dentata* is markedly cuneate, with only 27 to 37 segments. The margins of *A. baeri* are serrate, and the velum is little developed. The length/width ratio of the segments is also greater than that in *A. dentata*. As a consequence of more gradual development of the reproductive organs, the uterus in *A. baeri* begins to enlarge in the 17th to 20th segment, as compared with the 10th to 13th in *A. dentata*. The ovary in *A. baeri* is smaller and more strongly lobed. The cirrus sac is both relatively and absolutely smaller than that in *A. dentata*, and it extends farther medially across the ventral excretory canal. In *A. dentata*, the cirrus sac attains a maximum length of 0.350 in early gravid segments. *A. baeri* has a greater number of testes, with a more extensive distribution (80 to 90 testes, as compared with 24 to 33 in the European form of *A. dentata*, and about 50 in the Siberian form). Differences exist also in the dimensions and relationships of other organs.

2) The second species is described on the basis of published information. From comparisons with published descriptions, Flores-Barroeta *et al.* (1961) considered that cestodes obtained from the bile ducts of rabbits, *Sylvilagus brasiliensis* (Linnaeus), in Costa Rica closely resembled *Paranoplocephala lemni* Rausch, 1952 and *P. infrequens* (Douthitt, 1915). They concluded that the cestodes were conspecific with the latter, the identity of the host and the unusual site of localization notwithstanding. Although the original material could not be obtained for study, these cestodes clearly represent a hitherto unrecognized species, referred here to the genus *Anoplocephaloides*. The following description is based on the original data and figures published by Flores-Barroeta *et al.* (1961).

Anoplocephaloides floresbarroetae sp. nov.

Description: Strobila up to 21 long, with maximum width of 7 attained in post-mature segments. All segments wider than long, with length/width ratio increasing posteriad. Mature segments 0.343 to 0.358 long and 1.7 to about 1.8 wide (length/width ratio ca. 1:5). Tegument of strobila spinose throughout. Scolex large and distinct from strobila, 1.2 long by 1.6 to 2.2 wide. Suckers large and muscular, 0.253 to 0.373 long by 0.358 to 0.402 wide. Neck very short. *Anlagen* of genital organs visible immediately behind neck. Genital pores unilateral, dextral, situated posterior to middle of segmental margin. Genital ducts passing dorsally across longitudinal excretory canals. Cirrus sac elongate, 0.358 to 0.447 long by 0.134 to 0.149

FIG. 5. — *Anoplocephaloides baeri* sp. nov., complete specimen. FIG. 6. — *A. baeri*, mature segment (ventral view). FIG. 7. — *A. baeri*, details of female genital ducts (dorsal view). FIG. 8. — *Anoplocephaloides kontrimavichusi* sp. nov., complete specimen. FIG. 9. — *A. kontrimavichusi*, mature segment (ventral view). FIG. 10. — *A. kontrimavichusi*, details of female genital ducts (dorsal view).

in maximum diameter, not extending mediad across ventral excretory canal. Cirrus short and stout, provided with large spines; spines of extruded cirrus continuous with those of strobilar tegument. Internal seminal vesicle ovoid, occupying 1/4 to 1/3 of length of cirrus sac. External seminal vesicle consisting of thick, somewhat convoluted duct extending mediad from proximal end of cirrus sac anterior to seminal receptacle. Testes spherical, 0.049 to 0.083 in diameter, 23 to 37 per segment, distributed dorsally from medial margin of ovary laterad to aporal ventral excretory canal. Vagina consisting of thick-walled tube, opening in genital atrium posterior to orifice of male duct and passing mediad posterior to cirrus sac. Vagina dilating medial to ventral excretory canal, forming thin-walled, pyriform seminal receptacle 0.224 to 0.253 long by 0.149 to 0.209 in maximum diameter; situated poral to ovary and vitelline gland in mature segments. Seminal receptacle increasing in size in early gravid segments. Lobed ovary situated ventrally in poral half of segment, with medial margin near midline; extending through greater part of segmental length, with similar transverse dimensions. Vitelline gland oval to reniform, situated near posterior margin of segment dorsal to ovary. Uterus first visible as transverse tube extending across segment anterior to testes, apparently not overlapping longitudinal excretory canals. Uterus producing anterior and posterior sacculations, filling entire gravid segment between longitudinal excretory canals. Cirrus sac and seminal receptacle persisting in gravid segments. Eggs spherical, with well developed pyriform apparatus.

Type host: Rabbit, *Sylvilagus brasiliensis* (Linnaeus).

Type locality: Aserri, Province of San Jose, Costa Rica.

Habitat: Bile ducts of host.

Type: Not designated; original material in the personal collection of the late D^r. Luis Flores-Barroeta, No. 181-21. Anatomical details are shown in Flores-Barroeta *et al.* (1961, fig. 1 and 6-9). I propose that these figures be designated the lectotype, according to Article 74, International Code of Zoological Nomenclature (Stoll *et al.*, 1961, p. 79).

This cestode is named in honor of the late D^r Luis Flores-Barroeta, formerly of the Departamento de Microbiología y Parasitología, Escuela Superior de Medicina Rural, México, D.F.

Remarks: Although this cestode exhibits some unusual morphologic features, including the spinose tegument and the opening of the vagina posterior, rather than ventral, to the male duct, it is compatible in fundamental organization with assignment to the genus *Anoplocephaloides*. When more adequate comparisons are possible, based on additional specimens, it may be found that the erection of a new genus for this cestode is justified.

A. floresbarroetae sp. nov. exhibits a combination of characters that distinguishes it from all other species in the genus. From *A. wimerosa* (Moniez, 1880), the only other species of *Anoplocephaloides* known from leporids, it is immediately separable

by its relatively small cirrus sac, which only slightly overlaps the poral ventral excretory canals. In addition to differences in dimensions and in relationships of organs, *A. floresbarroetae* is unique among its congeners in possessing a spinose tegument, and in its site of localization in the host.

The acquisition of a spinose tegument by this cestode probably represents an adaptation to its habitat. As described by Flores-Barroeta *et al.* (1961), the presence of this cestode evokes a severe response by the host-tissue, with hyperplasia of the biliary epithelium, formation of crypts, proliferation of biliary capillaries, and marked fibrosis. Leukocytic infiltration was observed in sections, but the cells were not identified. The described lesions resemble those caused by spinose trematodes in the bile ducts of certain mammals.

3) During the period 1961-1973, I occasionally obtained cestodes representing a species of *Anoplocephaloides* from bog lemmings, *Synaptomys borealis* (Richardson), in northwestern North America. This cestode, of which 18 specimens were obtained, represents an undescribed species.

***Anoplocephaloides kontrimavichusi* sp. nov. (fig. 8-10).**

Description: Strobila 9.5 to 11.5 long, with 40 to 48 segments. Maximum width, attained in early gravid segments, 3.5 to 5 (av. 4.2). Strobila widening posteriad, then narrowing in last few gravid segments; strobilar margins serrate. Velum long, equaling ca. 1/3 of length of gravid segments. All segments wider than long, with relative length increasing posteriad. Length/width ratio of mature segments about 1:20; of terminal gravid segments, 1:6 to 1:5. Scolex sessile, its posterior margin usually overlapping first segments, 0.992 to 1.4 wide by 0.800 to 0.944 long. Suckers large and well developed, 0.450 to 0.560 by 0.370 to 0.460. Neck not discernible. *Anlagen* of genital organs visible in first segment. Genital pores unilateral, dextral or sinistral, opening at middle of segmental margin. Genital ducts passing dorsally across longitudinal excretory canals. Ventral canals 0.024 to 0.031 in diameter, connected across posterior margin of segment by transverse canal of similar diameter; dorsal canal about 0.010-0.020 in diameter. Cirrus sac not fully developed in last mature segment (13th to 18th in strobila); in post-mature segments, size of cirrus sac increasing with filling of internal seminal vesicle. In early gravid segments, cirrus sac attaining maximum dimensions, 0.360 to 0.470 long by 0.110 to 0.160 in maximum diameter near proximal end. Cirrus sac sometimes slightly overlapping ventral excretory canal. Cirrus spinose, about 0.090 long when extruded. Internal seminal vesicle beginning to fill in early post-mature segments, attaining dimensions of 0.260 to 0.330 by 0.120 to 0.140 in early gravid segments. External seminal vesicle initially somewhat coiled, extending mediad from proximal end of cirrus sac in mature segments; attaining length of about 0.200 by 0.120 in early gravid segments. Testes subspherical, about 90 in number, arranged 2-3 deep, and distributed dorsally across segment from level of vitelline gland laterad beyond aporal ventral excretory canal.

Testes 0.029 to 0.044 (av. 0.034) in greater diameter in last mature segment, increasing in size posteriad coincident with filling of seminal vesicles. Testes 0.036 to 0.075 (av. 0.063) in greater diameter in third post-mature segment, thereafter attaining maximum diameter of 0.087 to 0.110 (av. 0.098). Testes displaced posteriad by enlarging uterus in post-mature segments, disappearing as uterus fills early gravid segments. Vagina a straight, thick-walled tube 0.220 to 0.250 long by about 0.030 in diameter in post-mature segments; opening in genital atrium ventral to orifice of male duct, and passing mediad posteroventral to cirrus sac. Vagina dilating near poral margin of ventral excretory canal, forming initially somewhat convoluted seminal receptacle. Seminal receptacle beginning to fill in last 3-5 mature segments, attaining maximum length of 0.850 to 0.880 by 0.200 to 0.220 in post-mature segments. With maximum development, seminal receptacle extending from poral ventral excretory canal mediad to middle of vitelline gland, filling all of segment between successive transverse excretory ducts. Ovary transversely elongate, with slightly developed lobes, situated in poral half of segment initially, and with maturity extending mediad beyond midline. Ovary 0.640 to 0.860 wide by 0.096 to 0.130 long in last mature segment; attaining maximum size of 0.770 to 0.910 wide by 0.140 to 0.150 long in first post-mature segment, thereafter disappearing in early post-mature segments. Vitelline gland somewhat bilobed, situated dorsally over poral half of ovary with larger lobe aporal; 0.300 to 0.350 wide by 0.090 to 0.130 long in last mature segments; usually slightly longer in first post-mature segment. Vitelline gland disappearing soon after ovary in post-mature segments. Uterus first visible as transverse tube situated ventrally in segment, slightly anterior to ovary and testes, and extending beyond longitudinal excretory canals bilaterally. Uterus 0.014 to 0.024 in diameter in last mature segment; first enlarging in 14th to 19th segment of strobila, forming anterior and posterior sacculations, and filling gravid segments. Enlarging uterus displacing cirrus sac posteriad, but latter retains position dorsal to uterus. Genital ducts not discernible in terminal gravid segments. Eggs thin-walled, subspherical, 0.034 to 0.041 by 0.032 to 0.039 (av. 0.038 by 0.035). Embryo 0.012 to 0.015 in greater diameter. Pyriform apparatus well developed.

Type host: Bog lemming, *Synaptomys borealis* (Richardson).

Type locality: Jan Lake, east central Alaska (lat. 63° 34' N; long. 143° 55' W).

Habitat: Terminal portion of ileum, just above ileo-cecal junction.

Type: Holotype, U.S. National Museum Helminthological Collection No. 74081, from a bog lemming collected at Jan Lake, August 1965; paratype, USNM Helminthol. Coll. No. 74082, from bog lemming collected on the Seward Highway (Kenai Peninsula), 116 km south of Anchorage, Alaska, in August 1961.

This cestode is named in honor of Dr. V. L. Kontrimavichus, Institute of Biological Problems of the North, Far East Scientific Center, Magadan.

Remarks: Of its congeners, *A. kontrimavichusi* sp. nov. most closely resembles *A. dentata* (Galli-Valerio, 1905), *A. troeschi* (Rausch, 1946), and *A. lemni* (Rausch, 1952). It is distinguished from the former two species by its longer, much broader

strobila, more numerous segments, and much larger cirrus sac, as well as by differences in the dimensions and relationships of other organs. Compared with *A. lemmi*, *A. kontrimavichusi* has a shorter strobila of different form and fewer segments. Its relatively short cirrus sac only slightly overlaps the ventral longitudinal excretory canal, if at all, whereas the much longer (up to 0.900), relatively slender cirrus sac of *A. lemmi* overlaps the ventral canal by about half its length. Differences exist also in the extent of the uterus laterad, in number and distribution of the testes, and in dimensions and relationships of other organs. The morphologic characteristics of these cestodes are compared in Table II.

This cestode appears to be a host-specific parasite of the bog lemming. It was recorded from these rodents from the southern end of the Kenai Peninsula north to east-central Alaska, including the Wrangell Mountains (Nabesna region), and east to central Yukon Territory (lower Dempster Highway, east of Dawson). Numbers of cestodes in infected animals ranged from 1 to 3.

DISCUSSION

The lack of consensus concerning the systematic arrangement of anoplocephaline cestodes assigned variously to the genera *Andrya* Railliet, 1893, *Paranoplocephala* Lühe, 1910, and *Aprostotandrya* Kirshenblat, 1938 has been attributable in large part to the inadequate characterization of taxa, following which taxonomic concepts based on such incomplete morphologic data or on misinterpretation of ill described anatomic structures have been accepted without much question and perpetuated. In addition, the uncritical acceptance of superficial morphologic similarities in discriminating taxa has led to concepts of geographic distribution and host-occurrence that are zoogeographically unsound. Apparently, all who have worked with these groups have been influenced by these long standing deficiencies.

As here conceived, the genus *Paranoplocephala* includes *P. omphalodes* (Hermann, 1783) and an undetermined number of species formerly placed in the genera *Andrya* and *Aprostotandrya*. Cestodes of the genus *Paranoplocephala* are common parasites of arvicoline rodents in the Holarctic. Only two species are known from the southern continents, described respectively from murid and octodontid rodents: *P. dasymidis* (Hunkeler, 1972) in Africa, and *P. octodonensis* (Babero and Cattán, 1975) in South America.

P. omphalodes is distributed from western Europe to northwestern North America. Its geographic range on the latter continent does not apparently exceed that of a holarctic species of vole, *Microtus oeconomus*, which is considered to have spread into eastern Beringia during the last (Würm) glacial period, and thence eastward during post-glacial time (cf. Rausch, 1976). The earlier presence of this cestode in voles in Beringia is suggested by its occurrence in *Microtus abbreviatus* on the St. Matthew Islands in the Bering Sea, for although these islands were connected with the continent once during the last 100,000 years, between 20,000 and 16,000 years ago, the extent to which *M. abbreviatus* has diverged from its precursor, *M. miu-*

rus, on the continent suggests a longer period of isolation (Rausch and Rausch, 1968; Hopkins, 1973). *P. omphalodes* has not been recorded from *M. pennsylvanicus*, which has spread into northwestern North America during post-glacial time. The occurrence of this cestode in Africa would seem possible only in Libya, where a relict species of vole, *Microtus mustersi* Hinton, inhabits the Cyrenaican Plateau and adjacent regions (Ranck, 1968, p. 47).

Reports indicate that a second species, *P. macrocephala* (Douthitt, 1915), is widely distributed over the continents of Eurasia and North America. However, determinations of this species in Eurasia have been based on published descriptions of *P. macrocephala*, without the possibility of adequate comparison with material from North America. Rausch and Schiller (1949 a) found that cestodes identified as *P. macrocephala* in North America exhibited a wide range of variation in number and distribution of testes and in other characters. As a result, the species has been characterized within limits so broad as to prevent discrimination between variants and *macrocephala*-like species. Compared with other species of the genus, including *P. omphalodes*, *P. macrocephala* is the least host-specific and the most variable morphologically, which suggests that it represents a complex of species. It alone among anoplocephaline cestodes in rodents has an extensive geographic distribution on both continents, for which there is no apparent zoogeographic basis. The infection of experimental animals would seem to provide the best means to establish the limits of morphologic variation and host-specificity in these cestodes.

Further investigation is required as well to determine the status of the genus *Andrya*. If it is determined that the pattern of development of the uterus in the type species, *A. rhopalcephala* (Riehm, 1881), does not differ from that in *P. omphalodes*, the genus *Paranoplocephala* must be suppressed as a synonym of *Andrya*.

The restored genus *Anoplocephaloides* Baer, 1923, as here conceived, includes at least 17 species, of which all but three occur in rodents. The fundamental similarity of these cestodes must be in part attributable to morphologic convergence, since some seem certainly to represent diverse phyletic lines. The generic concept applied here thus violates Mayr's (1969, p. 92) definition of the genus as "... a taxonomic category containing a single species, or a monophyletic group of species, which is separated from other taxa of the same rank ... by a decided gap." Such an application can be accepted only temporarily and only because knowledge of the phylogeny of these cestodes is too incomplete to justify the erection of new genera on the basis of morphologic characters of uncertain taxonomic significance.

Three species of *Anoplocephaloides*, characterized in part by long, ribbon-like strobilae and occurring in squirrels of the tribe Marmotini, appear to represent a distinct phyletic line not found in rodents of other families. *A. transversaria* (Krabbe, 1879) and *A. ryjkovi* (Spasskii, 1950) are host-specific parasites of marmots, *Marmota* spp., while *A. wigginsi* (Rausch, 1954) has been recorded from a single species of ground squirrel, *Citellus parryi*. The chronology of intercontinental dispersals of marmots is understood sufficiently to permit some inferences about the origins of anoplocephaline cestodes in these mammals.

Arising in North America, the genus *Marmota* appeared in Eurasia during the early Pleistocene (Villafranchian), more than a million years ago, thereafter spreading westward to central Europe by the penultimate (Riss) glacial period (Gromov *et al.*, 1965; Repenning, 1967; Kurtén, 1968). Excepting *M. camtschatica* (Pallas), in northeastern Siberia, which is of more recent nearctic derivation, the Eurasian marmots are distinguished from North American species by well defined chromosomal characteristics (Rausch and Rausch, 1971). The two groups of marmots harbor anoplocephaline cestodes representing different genera (*Anoplocephaloides* and *Ctenotaenia* Railliet, 1893 in Eurasia; *Diandrya* Darrah, 1930 in North America), indicating that their host-specific cestodes were acquired independently after early Pleistocene time.

In North America, *Diandrya composita* Darrah, 1930 occurs in the four species of marmots of the *caligata*-group and in *M. broweri* Hall and Gilmore, a species found only in the Brooks Range of arctic Alaska and possibly northwestern Yukon Territory, but it has not been reported from *M. monax* (Linnaeus). Both *M. camtschatica* and *M. broweri* appear to be derived from a nearctic precursor that invaded Beringia later during the Pleistocene (? pre-Riss), as indicated by cytogenetic evidence and other characteristics (Liapunova and Vorontsov, 1969; Rausch and Rausch, 1971). Marmots of both species are infested by a palaearctic flea, *Oropsylla silantiewi* Wagner, but they have no cestodes in common. Cestodes have not been found in *M. camtschatica*, although numerous animals have been examined for the presence of helminths (cf. Kapitonov, 1963). The data indicate that the nearctic cestodes of marmots did not occur in the precursor of *M. camtschatica* and *M. broweri*, and that there has been no transfer of palaearctic cestodes to the former. The presence of *Diandrya composita* (and *Catenotaenia reggiae* Rausch, 1951) in *M. broweri* could be explained by transfer through secondary contact with *M. caligata* (Eschscholtz), which has spread into northwestern North America during post-glacial time.

The third cestode of this group, *A. wigginsi*, has a holarctic distribution in *Citellus parryi*, which inhabited Beringia during the late Pleistocene, and which now occurs on both sides of Bering Strait (cf. Rausch, 1976). Post-glacial dispersal from Beringia accounts for the rather extensive range of this ground squirrel in northern North America. *A. wigginsi* is known from only two localities in the Arctic (Chukotsk Peninsula and northern Alaska). It has been recorded twice at the type locality in Alaska, but it has not been found in more than 300 ground squirrels examined from other localities, including Kodiak and St. Lawrence Islands.

Of the second group of species in *Anoplocephaloides*, characterized in part by their short, wedge-shaped strobilae, four occur typically in arvicoline rodents: *A. dentata* (Galli-Valerio, 1905); *A. troeschi* (Rausch, 1946); *A. lemmi* (Rausch, 1952); and *A. kontrimavichusi* sp. nov. *A. dentata* appears to be the least host-specific, occurring in arvicoline rodents of various genera and occasionally in murine rodents (*Apodemus* spp.). *A. troeschi* is a characteristic and common parasite of voles of the genus *Microtus*, while *A. lemmi* and *A. kontrimavichusi* appear to be host-specific in *Lemmus sibiricus* and *Synaptomys borealis*, respectively.

Of these four species, the palaearctic *A. dentata* and the nearctic *A. troeschi* are the most similar morphologically. That *A. dentata* may occur in northwestern North America is a possibility not to be excluded from consideration, since it, like *Paranoplocephala omphalodes*, might have been present in voles that spread eastward into Beringia during the late Pleistocene. Cestodes from *Microtus oeconomus* on St. Lawrence Island have been tentatively identified as *A. dentata*. The range of morphologic variation in *troeschi*-like cestodes in Alaska is sufficiently great to suggest that more than one species is present, but their certain discrimination will depend on the study of additional material. The relationship of *A. troeschi* and the morphologically similar *A. infrequens* (Douthitt, 1915) is considered below.

A. lemmi is known only from the brown lemming, *Lemmus sibiricus*, which apparently has inhabited Beringia since pre-Mindel time, perhaps 1.0 ± 0.5 million years (Guthrie and Matthews, 1971; Hopkins, 1972). The continuous distribution of the brown lemming in the arctic lowlands from the Lena Delta eastward into Beringia during periods of glaciation would account for the holarctic distribution of this cestode (Rausch and Rausch, 1975). Its occurrence in brown lemmings on the Melville Peninsula, in eastern arctic Canada, suggests that it is a parasite of this rodent throughout its range on the North American continent.

A. kontrimavichusi is not known from arvicoline rodents of other species with which the northern bog lemming, *Synaptomys borealis*, often shares habitat in Alaska [i.e., *Clethrionomys rutilus* (Pallas); *Lemmus sibiricus*; *Microtus* spp.; *Ondatra zibethicus* (Linnaeus)]. The genus *Synaptomys* is known in the Palaearctic only from late Pliocene deposits in Mongolia (Sher, 1973, p. 58). It has been present in North America since the early Pleistocene (Blancan fauna) (Hibbard *et al.*, 1965; Repenning, 1967). As pointed out by Guthrie (1968), the pattern of distribution of the two species of *Synaptomys* in North America is such as to suggest that *S. borealis* differentiated in a northern refugium. This hypothesis would seem to be supported if *A. kontrimavichusi* is found not to occur in the southern bog lemming, *S. cooperi* Baird.

The two remaining species in this group, *A. wimerosa* (Moniez, 1880) and *A. baeri* sp. nov., occur respectively in leporids (*Lepus* and *Oryctolagus*) and in murid rodents (*Apodemus*). *A. wimerosa*, known only from western Eurasia, has a curiously restricted geographic distribution relative to that of the mountain hare, *Lepus timidus*. Its other known host, *Oryctolagus cuniculus*, disappeared from middle Europe during post-glacial time and was reintroduced as a domestic animal during the Middle Ages, after which it again became established as a feral species (Thenius, 1972, p. 201). The geographic origin and affinities of *A. wimerosa* are thus uncertain.

A. baeri is known only from *Apodemus argenteus* on the Island of Hokkaido, although it may be found in the future to occur also in field mice on the islands to the south. The Japanese Islands, with Sakhalin, were a part of the Eurasian continent during the glacial maximum of Würm time, more than 18,000 years ago.

(Kotani, 1969). The mammalian fauna of Hokkaido includes a large Siberian component as a consequence of immigrations during the late Pleistocene. These mammals have differentiated only subspecifically from those on the continent. The mammalian fauna of the other islands appears to have been of earlier, southern Asiatic origin (Kotani, 1969). An earlier immigration might also be postulated for *Apodemus*, as indicated by speciation and its extensive distribution (south to the Island of Kyushu). *A. baeri* may be an endemic species in *Apodemus*, but further investigation is required to determine that it is not also present in field mice in eastern Asia.

Of the remaining seven species assigned here to the genus *Anoplocephaloides*, *A. mamillana* (Mehlis, 1831), *A. blanchardi* (Moniez, 1891), and *A. neofibrinus* (Rausch, 1952) are not considered further. Two taxa in this group, *A. variabilis* (Douthitt, 1915) in *Geomys* and *Thomomys* and *Anoplocephaloides* cf. *variabilis* in *Microtus*, are so similar morphologically that they may be only variants of a single species. The relationship of two other taxa, *A. infrequens* (Douthitt, 1915) and *A. troeschi* (Rausch, 1946), in the same hosts appears to be analogous.

The nearctic family Geomyidae has been traced to the upper Oligocene, and the genera *Geomys* and *Thomomys* appeared in the late Pliocene (Russell, 1968). *Microtus* was first recorded in North America from the middle Pleistocene Irvingtonian fauna (Repenning, 1967). Records of *Geomys*, *Thomomys*, and *Microtus* from local faunas in the Great Plains region indicate that these rodents might have been sympatric since at least Kansan time (Hibbard, 1970), thus providing a long period during which adaptive transfer of their respective helminths might have occurred. However, compatible with the concept of phylogenetic parallelism between host-specific cestodes and their hosts, pocket gophers have a distinctive fauna of helminths, including at least three species of anoplocephaline cestodes in addition to *A. variabilis* and *A. infrequens*: *Monoecocestus anoplocephaloides* (Douthitt, 1915); *Cittotaenia prae-coquis* (Stiles, 1895); and *C. megasacca* Smith, 1951. A fourth species known only from pocket gophers, *Hymenandrya thomomyis* Smith, 1954, was also placed in the family Anoplocephalidae, but this allocation is questionable. One additional species, *Paranoplocephala macrocephala*, was described from *Geomys* and has been identified also from *Microtus*.

With the possible exception of *A. variabilis* and *A. infrequens*, the respective species of *Anoplocephaloides* are restricted almost exclusively to mammals of a single genus or of closely related genera (e.g., *A. wimerosa* in *Lepus* and *Oryctolagus*). The regular occurrence of the aforementioned two species in rodents of different families would seem to imply an unusual lack of phylogenetic specificity, permitting the inference that infection of the final host depends primarily on ecologic factors, since a single species of cestode could hardly be host-specific in mammals representing disparate phyletic lines. If the two taxa in voles are not specifically distinct from those in pocket gophers, it would seem that rodents of arvicoline genera other than *Microtus* would be at least as susceptible to infection as the geomyids. However, all evidence indicates that the respective species of *Anoplocephaloides* in arvicoline rodents exhibit strongly defined segregation by host when rodents representing the

various genera share the same habitat. Morphologically, the two taxa in voles are distinguished from those in pocket gophers mainly by differences in size, indicating that they might exemplify discontinuous ecotypic variation, but the data seem more strongly to support the hypothesis that the four taxa represent two pairs of sibling species. Attempts to establish reciprocal infections in voles and pocket gophers in the laboratory would seem to provide the best means by which the status of these cestodes could be determined.

Members of the genus *Anoplocephaloides* are predominantly parasites of mammals in the Holarctic, and only three species recognized here are apparently restricted geographically to the southern continents. *A. isomydis* (Setti, 1892) and *A. acanthocirrosa* (Baer, 1924) differ from all other species in the genus, excepting the two species in sciurids, in having irregularly alternating genital pores. *A. acanthocirrosa* appears to be a host-specific parasite of rodents of the genus *Otomys*, which perhaps arose in South Africa (Thenius, 1970, p. 184). The two species in African rodents may thus represent a different phyletic line from that of *Anoplocephaloides* spp. in rodents in the Palaearctic.

The last member of this group, *A. floresbarroetae* sp. nov., is tentatively included in the genus *Anoplocephaloides* pending the availability of the original material or new collections for further study. This cestode is known only from rabbits, *Sylvilagus brasiliensis*, in Costa Rica. *Sylvilagus* is a nearctic genus that entered South America by way of the Isthmus of Panama during the late Pleistocene (Patterson and Pascual, 1968). Since the helminth fauna of *Sylvilagus* in North America includes no *Anoplocephaloides*-like cestodes, *A. floresbarroetae* must represent a relatively recent parasite-host adaptation. Perhaps the addition to the fauna of South America of mammals of a family not previously represented would have provided an unoccupied biotope that favored rapid speciation by the precursor of this cestode.

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