Capsulata edenensis gen. et sp. nov. a New Cestode with an Unusual Type of Growth, from *Limosa lapponica* (L.); with Systematic Notes on the Genera *Southwellia* Moghe, 1925 and *Malika* Woodland, 1929

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CAPSULATA EDENENSIS gen. et sp. nov.

*Host* : *Limosa lapponica* (Linn. 1758)

Locality : The estuary of the River Eden, Fife, Scotland.

Description : The specimens were collected from three Bar-tailed Godwits shot in the winters of 1956 and 1957. The description below applies mainly to the first infestation found. There are certain differences between the infestations which are noted later. There were up to 150 individuals in each infestation, varying from immature worms consisting of a scolex and a few proglottides to mature strobilas containing some 300 segments and reaching a length of 75 mm. The maximum breadth of the strobila is 1·8 mm. The onset of maturity is accompanied by a marked increase in the breadth of the strobila and the mature proglottides are broader than long.

The scolex (Fig. 4) has a diameter of 200–280μ and a length, including neck and rostellum, of 580–730μ. The rostellum, of length up to 300μ and diameter of 30–50μ at the base, bears 16 hooks (Fig. 5) of length 37–45μ in two slightly separated rows. The hooks are the same size in the two crowns. The suckers face forward slightly and have a diameter of 90–120μ. The neck is very short, of length 175μ and breadth 160μ. The genital apertures are unilateral and situated in the middle of the length of the proglottis. The genital ducts pass between the longitudinal excretory vessels. The vagina opens in the genital atrium ventrally, and occasionally slightly postero-ventrally, to the cirrus-sac. It runs, parallel to the

cirrus-sac but in a ventral position, towards the centre of the pro-
glottis. There are 30–45 testes completely surrounding the female
glands, the greater bulk of them lying anterior and lateral to the
female glands. The testes reach a size of 50–60µ in the more mature
proglottides. The cirrus-sac, which is 100–185µ long by 52–75µ,
extends beyond the longitudinal excretory canals. It contains a
much coiled ductus ejaculatorius. The cirrus is short, of length
about 40µ and diameter 10µ, and is covered with many tiny spines.
The distal portion of the cirrus-sac has an internal lining of cells
which are probably myoblasts. The vas deferens runs from the
cirrus-sac towards the centre of the proglottis, where it is coiled in
an area slightly poral to the female glands. There is no external or
internal seminal vesicle but the vas deferens and the ductus ejacula-
torius become expanded with sperms in the mature proglottides
and probably function as such. The female glands are in the posterior
half of the proglottis. The ovary consists of from 4 to 9 separated
round lobes situated in a semicircle round the vitelline gland. The
vitelline gland is situated behind the ovary, it is compact and may
be slightly lobed. In mature segments a dorsal loop of the vagina
is expanded to form a very large receptaculum seminis. It reaches
a size of 350 by 270µ and dominates the centre of the gravid
proglottis. The vagina is ventral to the cirrus-sac and is a wide
tube, of diameter 24–38µ; its wall is composed partly of what
appear to be glandular cells. The uterus is first formed as a reticulum
(Fig. 3) extending forward from the female glands, and occupying,
in a ventral position, an area anterior and lateral to the ovary and
vitelline gland. Later the uterus becomes filled with eggs and occupies
the whole ventral part of the medulla. Some portions of the network
seem to be more expanded with eggs and it is these regions that prob-
ably develop into capsules. The gravid proglottides contain from
4 to 15 egg capsules each containing 40–120 eggs. The egg capsules
vary in size from 115×160µ to 270×400µ, the largest being found
in those segments with fewer capsules. The egg capsules are liberated
by laceration of the gravid proglottides and many were found free
in the intestinal contents of the hosts of two of the infestations.
The wall of the capsule, in the early stages, is a syncytium derived
from the single layer of cells of which the uterine wall is composed.
Later, the inner and outer surfaces of the syncytial layer become
thickened, and the wall of the capsule has the appearance of being
composed of a single non-living layer except where the two surfaces
are separated by the remains of a nucleus. In the liberated condition
the capsule wall is thin, about 1µ thick, and appears to be a single
layer of non-living material. The eggs are round, or, due to the
natural pressures from the neighbouring eggs, polygonal. They have

a diameter of $36-45\mu$. The onchospheres have a diameter of $30-42\mu$. The lateral onchosphere hooks are of two different sizes, 17μ and 19μ and the medial hooks have a length of about 22μ.
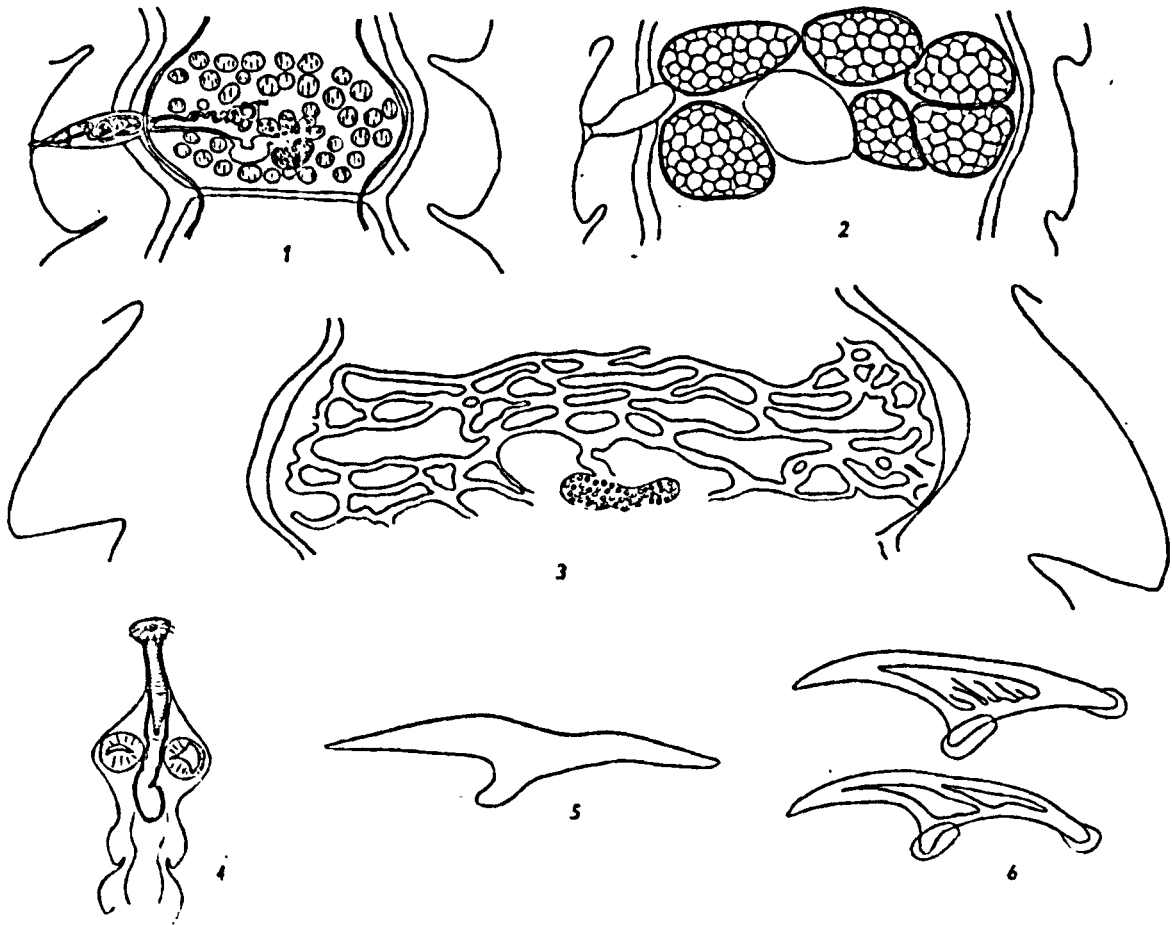
Capsulata edenensis n.gen., n.sp.

Fig. 1.—Mature proglottis. Fig. 2.—Gravid proglottis. Fig. 3.—Mature proglottis, showing the reticulate uterus soon after its formation. Fig. 4.—Scolex. Fig. 5.—Rostellar hook.

Malika odhneri (Fuhrmann, 1909)

Fig. 6.—Rostellar hooks.

There are two layers of longitudinal muscle fibres, the inner is composed of 50-60 bundles each with 10-20 fibres and the outer layer consists of small bundles or of single fibres. Transverse fibres are absent except for a single bundle of fibres at the anterior margin

of the proglottis. The fibres of which this transverse bundle is composed arise from the lateral longitudinal fibres and from the subcortical layer at the anterior lateral border of the segment. These transverse fibres are internal in relation to the longitudinal fibres.

Anatomical differences were noted between specimens from different infestations. In the first infestation the gravid segments contain 4–8 egg capsules, in the other two infestations there were 7–15 egg capsules per segment. In the first infestation the ovary has 4–7 lobes, while in the other infestations the ovary has 5–9 lobes. There was also a slight variation in hook size, 41–44µ in the first infestation and 37–39·6µ in the other infestations.

Systematics and notes on the new species and on the related genera *Southwellia* Moghe, 1925 and *Malika* Woodland, 1929

The described species approaches most nearly to three genera ; *Southwellia* Moghe, 1925, *Malika* Woodland, 1929 and *Similuncinus* Johnston, 1909 all of which have unilateral genital apertures and "egg capsules" containing several eggs.

Southwellia Moghe, 1925

This genus has contained two species: *Southwellia ransomi* Chapin, 1926 which is a synonym of *Dilepis undula* (Schrank, 1788), vide Fuhrmann, 1932, and *Southwellia gallinarum* (Southwell, 1929). I have examined the types of this last species and am in full accordance with the findings of Baer (1957). Egg capsules are not formed, the uterus is persistent as a reticulum which extends laterally to fill completely the medulla of the proglottis. In the oldest segments when the uterus is swollen with eggs, small lobes may be forced out between the longitudinal muscle fibres ; these lobes have the appearance of egg capsules. The tubular uterus, when doubled back on itself may also have been mistaken for egg capsules. The cirrus-sac of *Southwellia gallinarum* is long (about 650µ) and reaches almost to the centre of the proglottis. In view of the structure of its uterus, this species should be transferred to the genus *Dilepis* Weinland, 1858, it becomes *Dilepis gallinarum* (Southwell, 1921) and the genus *Southwellia* Moghe, 1925 lapses into synonymity with *Dilepis* Weinland, 1858.

Malika Woodland, 1929

The genus *Malika* Woodland, 1929 has one inconsistency which should be mentioned. The definition of the genus takes the form, following Fuhrmann (1932) for example, "Dipylidiinés avec rostre armé d'une couronne de crochets". However Woodland in his original paper did not stipulate the number of rows of hooks. Examination of the types of *Malika oedicnemus* in the British Museum left me with no doubt that there are actually two rows of hooks. Thus any definition of the genus which stipulates the number of rows of hooks as one is not acceptable.

Malika Woodland, 1929 at the present time contains 6 species : *Malika oedicnemus* Woodland, 1929 ; *Malika pittae* Inamdar, 1933 ; *Malika kalawewaensis* Burt, 1940 ; *Malika himantopodis* Burt, 1940 ; *Malika zeylanica* Burt, 1940 and *Malika skrjabini* Krotov, 1953. I have had the opportunity of examining Burt's Ceylon material, and my findings for the hook characteristics of these specimens are recorded in the Table I below with those of *Malika oedicnemus* Woodland, 1929 and *Dilepis odhneri* Fuhrmann, 1909. The figures given in brackets are those of the original author, other figures are personal observations.

TABLE I

	Hook No.		Hook Size	
Dilepis odhneri Fuhrmann, 1909	30	(32)	76–84·5µ	(70–80µ)
Malika oedicnemus Woodland, 1929	—	(30)	—	(73µ)
Malika kalawewaensis Burt, 1940	30	(26–28)	76–80µ	(58µ)
Malika himantopodis Burt, 1940	32	(30)	76–80·5µ	(73–75µ)
Malika zeylanica Burt, 1940	30	(32)	75–79·5µ	(76–83µ)

Scolices of this material were mounted and crushed in Berlese fluid. This procedure enables the hooks to be seen clearly so that accurate drawings and measurements can more easily be made. The results recorded above emphasize the importance of mounting hooks so that they can be seen clearly. The original determination of the hook characteristics of these species was from whole mounts in balsam, and in the case of *Malika kalawewaensis*, from a single scolex with its rostellum invaginated. The hooks of these three species are identical in shape (Fig. 6) and their dimensions are well within the range to be expected from different infestations of the same species. Formerly, these three species could be separated by differences in the number and size of the hooks (Burt, 1940), but as these three species can no longer be distinguished by their hook characteristics, the slight differences in anatomical detail are not in themselves sufficient to separate them as species.

I did not have the opportunity of examining a scolex of *Malika oedicnemus* in Berlese but the original figures of the hooks of this species and those for example of *M. zeylanica* from balsam mounts are similar. Burt separated his species from *M. oedicnemus* mainly on the grounds that the latter species has only one row of hooks. As *Malika oedicnemus* has in fact two rows of hooks these four species should be considered as synonymous. The deviation in anatomicas detail of the form described as *M. himantopodis* may be due to itl occurrence in another, possibly accidental, host (*M. himantopodis* was described from a Stilt, the others from Stone Curlews).

Dilepis odhneri Fuhrmann, 1909 has been recorded from the White Nile (Fuhrmann, 1909) and from Omo-Sagan (Fuhrmann and Baer, 1943). The material is in a highly contracted condition and does not contain gravid segments, but it is possible to see that the anatomy as well as the hook characteristics correspond with the Indian and Ceylon material discussed earlier. Thus we come to the conclusion that these five species are synonymous. The first description was under the name *Dilepis odhneri* Fuhrmann, 1909, accordingly, as the genus *Malika* is retained, the type species should be designated *Malika odhneri* (Fuhrmann, 1909) with the following synonyms : *Dilepis odhneri* Fuhrmann, 1909 ; *Malika oedicnemus* Woodland, 1929 ; *Malika kalawewaensis* Burt, 1940 ; *Malika himantopodis* Burt, 1940 and *Malika zeylanica* Burt, 1940.

Also attributed to the genus *Malika* Woodland, 1929 are the species *M. pittae* Inamdar, 1933 and *M. skrjabini* Krotov, 1953. Little is known of the parasites from the group of hosts (Pittidae) in which the former species was found, and although *M. pittae* seems to bear little relationship to the type of the genus, it should remain in that genus until re-examined or more material is investigated. *M. skrjabini* on the other hand, from *Limosa limosa melanuroides* Gould bears a very close resemblance to *Dilepis limosa* Fuhrmann, 1907 recorded from a different sub-species of the same host and also from the U.S.S.R. (Kholodkovsky, 1912 and Dubinina, 1953). The two forms have the same wide strobila which is characteristic for *Dilepis limosa* and almost unique for dilepid tapeworms from Charadriiformes. The hooks have the same shape and are within the same range for number and size (*M. skrjabini* 16–22 hooks, 81–124μ and *D. limosa* 20 hooks, 99–110μ). In *D. limosa* the hooks are distributed in two crowns while in *M. skrjabini* the number of rows of hooks is not stipulated. A character of the genus *Malika* is that the genital canals pass between the longitudinal excretory

vessels. *Malika skrjabini* is described as having the genital canals passing ventrally to the excretory vessels (although the dorsal canal is given as the wider of the two) and in this respect approaches nearer to the genus *Dilepis* which has the genital canals passing to one side of the excretory vessels. The anatomy is identical for the two species *M. skrjabini* and *D. limosa* except as regards the structure of the cirrus-sac and uterus. The type specimens of *D. limosa* have a very long cirrus-sac (790–870μ), examples of this species from the U.S.S.R. are described as having a cirrus-sac which extends beyond the excretory canals (Dubinina, 1953), and *M. skrjabini* is described as having a cirrus-sac (138μ by 179μ) which does not normally reach the excretory vessels. The cirrus-sac of the type specimens of *D. limosa* is long and narrow, and in contracted material it is difficult to see where it ends and where the vas deferens begins, as they are of similar diameters and are obscured by the overhang of the posterior end of the preceding segment. The uterus of *M. skrjabini* is described as being reticulate, later becoming constricted off into egg capsules, while the uterus of *D. limosa* is reticulate but does not form egg capsules. In the type specimens of *D. limosa* however, the gravid uterus has the appearance of being strongly lobed or at times having the appearance of egg capsules. It is important to note that the uterus of *Dilepis undula* (Schrank, 1788), the type species of the genus *Dilepis*, is reticulate "though in whole mounts it appears to be broken up into capsules, each containing several eggs, accurate examination of serial sections reveals that each lobe is in communication with the rest of the uterus", (Davies, 1935). *Dilepis gallinarum* (Southwell, 1929) was erronously described as having a short cirrus-sac and egg capsules and one cannot preclude the possibility that the same mistake could have been made in this instance with *M. skrjabini*. Apart from these two discrepancies, the description of *Malika skrjabini* Krotov, 1953 makes it clear that this species is in fact a synonym of *Dilepis limosa* Fuhrmann, 1907.

The species that I have described has dilepid hooks and egg capsules and therefore belongs to the sub-family Dipylidiinae (Stiles, 1896). It bears some relationship to the genus *Similuncinus* Johnston, 1909 but is distinguished from this genus by the difference in the relative positions of the genital canals and the excretory vessels.* It approaches nearest to the genus *Malika* Woodland,

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*There is some confusion in the description of the type species of the genus, *Similuncinus dacelonis* Johnston, 1909. The genital ducts are described as passing ventrally to the excretory canals while at the same time the dorsal vessels are the larger and possess the transverse connection. The general anatomy and the form of the uterus [reticulate, with the eggs later lying in groups in the parenchyma (Johnston, 1909)] make it possible that *Similuncinus* is another synonym of *Dilepis*.

1929 which has egg capsules containing several eggs and genital ducts passing between the longitudinal excretory canals. The new species differs from the genus *Malika* in two fundamental ways. The new species has female glands posterior in the segment and testes mainly anterior, whereas in *Malika* the female glands are anterior and the testes posterior in position. The uterus is at first reticulate, as in the genus *Dilepis*, but egg capsules are formed and actually released into the intestine of the host. In *Malika* on the other hand, the uterus is at first sac-like, it later becomes lobed and constricted off into egg capsules.

The described form, while being placed in the sub-family Dipylidiinae (Stiles, 1896) has an anatomy which bears a similarity to that of certain Davainiids, but its hook characteristics of course preclude the possibility of its being included in that group. The release of egg capsules, an outstanding feature of this species, has been described from a *Hymenolepis* by Joyeux and Baer (1955). These capsules are somewhat similar in this instance but they have a different mode of formation and are from a relatively distant group of tapeworms so do not have much bearing on the species described. The anatomy of members of the genus *Dipylidium* Leuckart, 1863 has many characters in common with that of the present form. In both the testes are numerous and are situated anterior and posterior to the female glands, the vagina in *Dipylidium* sometimes opens ventrally to the cirrus-sac, and the uterus is reticulate and later breaks down into egg capsules containing several eggs. The double genitalia and the hook characteristics are however very different from the species that I have described, but it would appear that the new species is a truer monopylidium than many of the other species that have been given this title at one time or another. As the new species differs from the other existing members of the sub-family Dipylidiinae (Stiles, 1896) in certain fundamentals which have been outlined above, and as it also has an unusual type of growth which is described in the second half of this paper, a new genus is made which is designated *Capsulata* n.gen. The definition of the new genus is as follows :—

Capsulata n.gen.

Dipylidiinae with dilepid hooks. Genitalia single. Female glands posterior in the segment. Testes surrounding the female glands, but mainly anterior. Genital pores unilateral. Genital ducts passing between the longitudinal excretory vessels. Vagina ventral to the cirrus-sac. Large receptaculum seminis. Uterus

reticulate, later forming egg capsules. Egg capsules few in number and each containing many eggs—Parasites of birds.

The new species that has been described above is given the name *Capsulata edenensis* n.gen., n.sp. and is designated the type species of the genus *Capsulata* n.gen.

Type host of *Capsulata edenensis* n.gen., n.sp. is *Limosa lapponica* (Linn.) and the type locality the estuary of the River Eden, Fife, Scotland.

The type material will eventually be deposited in the British Museum (Nat. Hist.).

A note on the growth of *Capsulata edenensis* n.gen., n.sp.

The following description refers mainly to the first infestation found. The infestation consisted of over a hundred individuals of this species situated in the duodenum, as well as an estimated 6,000 specimens of *Ophryocotyle proteus* Friis, 1869, the specimens of the latter species as well as being of much smaller size, were confined to the posterior part of the intestine. The specimens of *Capsulata edenensis* n.gen., n.sp. vary in length from 1 mm. to 70 mm. The smallest specimen (Fig. 8) consists of a scolex, a short neck, a single segment and a thicker posterior region. This posterior region has indentations which become closer together and less distinct as one proceeds towards the posterior end, the indentations disappear about half way along. Larger specimens (Figs. 9 and 10) have a greater number of distinct segments behind the scolex but the segments become more compressed together and less distinct as one proceeds towards the hind end, and signs of segmentation have disappeared completely in the last portion. In specimens 20–30 mm. long external segmentation disappears completely in the last 5–10 mm., but internal segmentation can be discerned in this region (Fig. 11). The genital anlage is also visible in the hindermost segments of this region. In still larger worms external segmentation becomes distinct along the whole length of the strobila, although not quite so pronounced towards the posterior end.

Further examination was made of 20 larger specimens, and measurements were made of the total number of segments, the distance from the scolex at which the genital anlage is discerned, the distance from the scolex at which maturity is apparent, the distance

from the scolex at which eggs are first seen in the uterus, and the maximum breadth and the length of the strobila. With respect to the position of anlage, the onset of maturity and the appearance of eggs in the uterus the distance is expressed as the number of segments from the scolex. The segments are deemed to be mature when their genital ducts become cuticularised, this takes place over one or two segments. The results are recorded in Table II.

In the discussion following certain assumptions have been made : firstly, that "length $\times$ maximum breadth" of the strobila is a reasonable representation of the size of the specimen ; secondly, that the size is a function of the age of the specimen, as long as the worm is complete and has not shed any segments. In these specimens this last state can be seen from the character of the last segment ; it is either rounded if complete, or lacerated if segments have been lost. All the specimens represented in the table are deemed to be complete. The word "age" I have here used to refer to the stage of development reached, rather than in any absolute sense. In the figures the units of "length $\times$ maximum breadth" are actually sq. mm., but this is of little importance as only the relative sizes of the worms are being compared.

1.   The total number of segments.

The points on Fig. 12 lie in a more or less horizontal band. This indicates that the total number of segments is nearly constant within this size range of specimens.

2.   The genital anlage (Fig. 12).

The genital anlage is confined to the relatively close limits of the 37th to the 51st segment behind the scolex regardless of the size of the strobila.

3.   The position of the onset of maturity. (Fig. 13).

The results indicate that the distance from the scolex at which mature segments are found decreases with increase in size of the worm. Put in another way, the onset of maturity moves towards the scolex as the strobila ages, or alternatively, the number of mature segments is proportional to the age of the worm.

4.   The appearance of eggs in the uterus (Fig. 13).

The same type of result as in the last case is found here. The commencement of the production of eggs in the strobila moves

towards the scolex as the worm ages, or alternatively, the number of gravid segments is proportional to the age of the strobila. It can be seen from this figure that the separation between the onset of maturity and the commencement of egg production becomes considerably less as the worm ages and that these approach very close to the genital anlage.
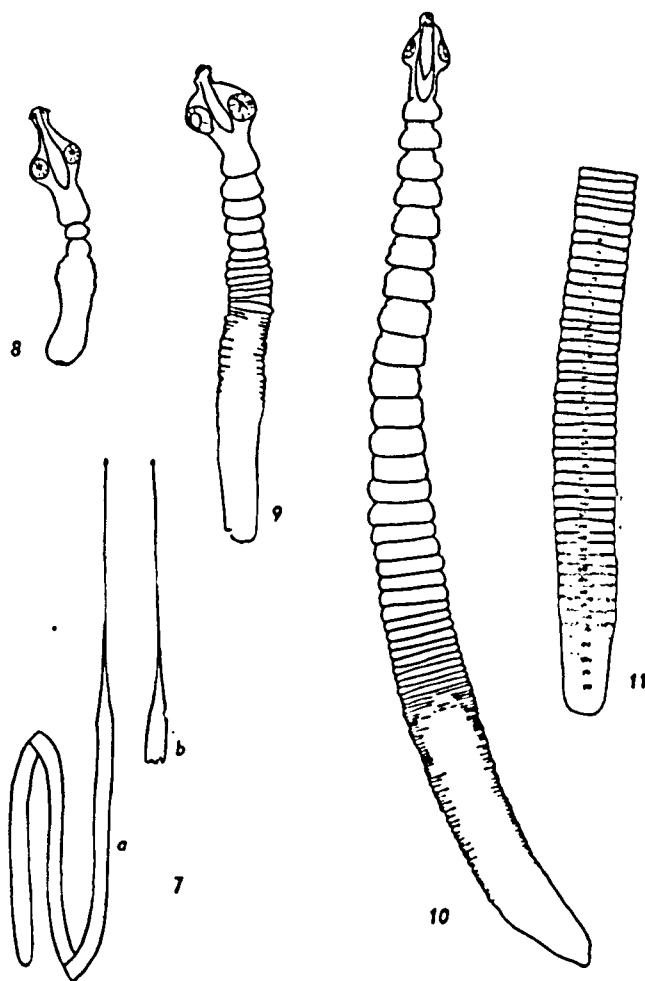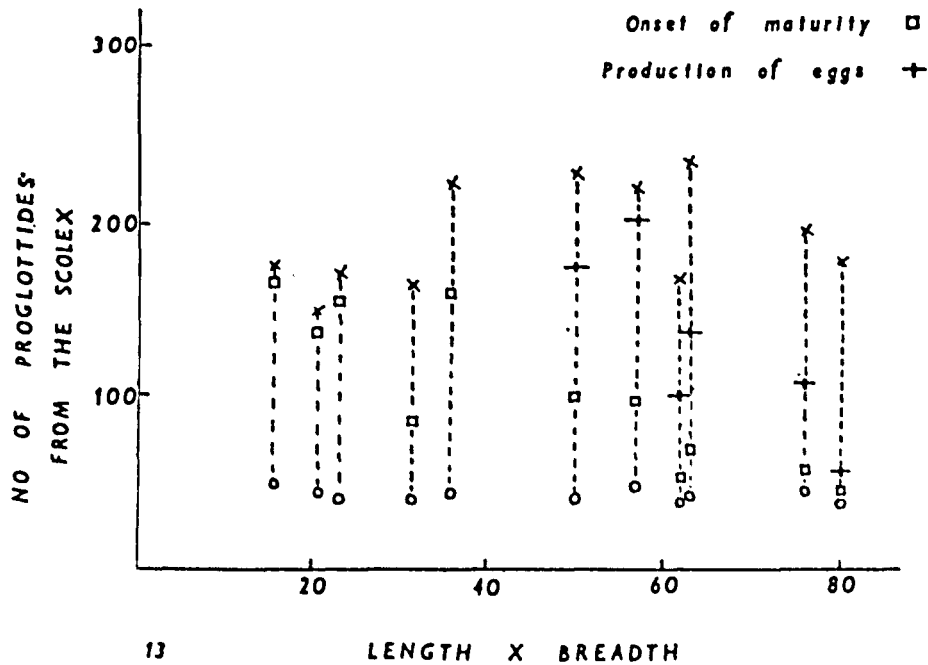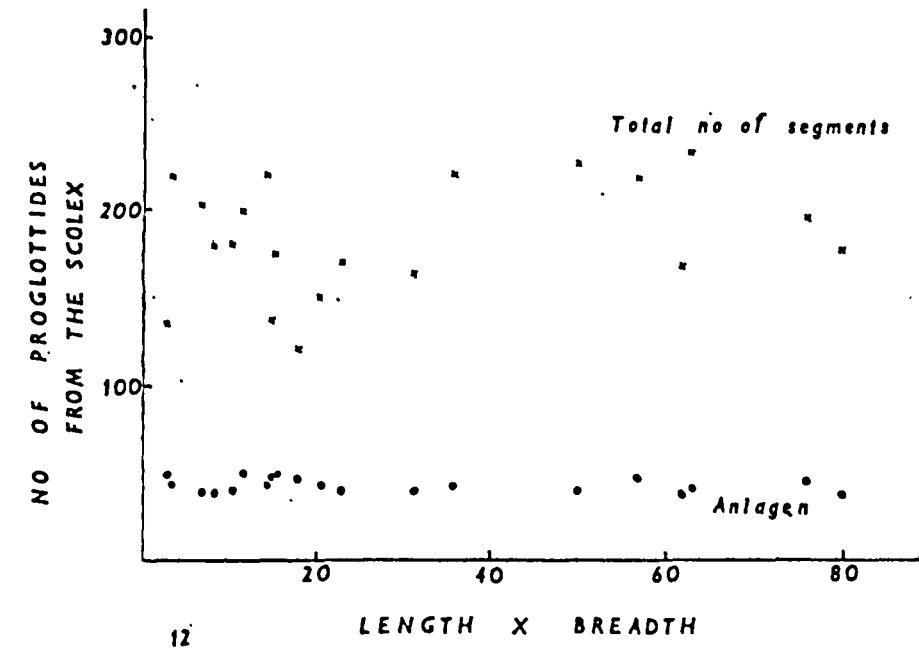

Capsulata edenensis n.gen., n.sp.

Fig. 7a.—Strobila before the gravid segments have been shed. Fig. 7b.—Strobila after the gravid segments have been shed. Fig. 8.—Young specimen, length 1 mm. Fig. 9.—Young specimen, length 1·8 mm. Fig. 10.—Young specimen, length 3·5 mm. Fig. 11.—Posterior end of a young specimen, length 21 mm.

From these results and the appearance of the younger specimens described earlier certain conclusions can be drawn as to the probable type of growth that this species undergoes. It can only be a probable sequence of events as the examples examined are a static cross-section of a growing population.

TABLE II

Number of specimen	Total No. of proglottides	Production of eggs	Onset of Maturity	Anlage	Length mm.	Max. breadth mm.	Length × Breadth
Sl/C. 1	197	105	57	44	60	1·22	76
2	233	136	68	41	61	1·04	63
3	178	56	44	37	65	1·22	80
4	169	—	154	41	49	0·47	23
5	219	—	—	44	42	0·35	14·4
7	173	—	165	50	39	0·4	15·6
8	199	—	—	51	33	0·36	11·8
11	135	—	—	50	15	0·19	2·9
16	138	—	—	48	35	0·5	17·5
17	150	—	136	43	38	0·54	20·5
19	219	—	—	43	18	0·19	3·4
21	203	—	—	39	26	0·26	6·7
22	221	—	159	42	62	0·58	36
24	163	—	84	39	51	0·62	31·5
26	179	—	—	40	35	0·3	10·5
28	178	—	•	38	33	0·25	8·25
29	120	—	—	47	28	0·64	18
31	169	99	52	37	47	1·3	62
32	228	173	98	41	68	0·73	50
33	219	201	96	47	67	0·85	57

Capsulata edenensis n.gen., n.sp.

Fig. 12.—Distribution of the total number of segments and of the position of anlage for strobilas of different sizes. Fig. 13.—Distribution of the position of the onset of maturity and of the first production of eggs for strobilas of different sizes. The position of anlage and the total number of segments are also shown.

The figure showing the total number of segments indicates that this is more or less constant whatever the size of the strobila. When the actual difference in size of the strobila is considered this fact becomes more interesting. Thus a strobila 18 mm. long and with a maximum breadth of 190μ has about the same number of segments as a worm 65 mm. long and 1·2 mm. wide. The latter worm probably has a weight a hundred times that of the former, and the difference in size is similar to that between a piece of thread 2 cm. long and a 6·5 cm. length of shoelace. This constancy in the number of segments and the series of young specimens (Figs. 8–11) indicate that segmentation takes place when the worm is very small. There are three possible explanations that would account for the absence of segmentation of the posterior end of young strobila. Firstly, the young worms could be considered abnormal. Abnormality might be due to infestation of an unfavourable host; this is unlikely as this species was found in every specimen of the Bar-tailed Godwit that was examined and in no other Charadriiformes examined from the same locality. Abnormality could also be due to effects from overcrowding. This again seems unlikely as one of the hosts had a relatively small infestation yet still contained immature individuals as well as mature ones. It is also possible that abnormality could be due to an effect caused by successive infestations of the same host. The high rate of infestation and the size of infestation found indicate that this parasite of the Bar-tailed Godwit is fairly common in this locality and that multiple infestation is probably frequent. There is no argument against the possibility of abnormality being caused by multiple infestation, which no doubt occurs and which accounts partly for the many different stages of development of the worm found, but as these young stages were found in all of the hosts of this species examined, they appear to be the rule and not the exception.

The absence of segmentation at the posterior end of the young worms could also be explained by a growth sequence in which segmentation from the neck region takes place in a normal way, this being followed by its disappearance at the posterior end. However the short neck with well formed proglottides immediately behind it and the absence of the typical growth zone make this unlikely.

The third possibility is that in the young worms, between the stages represented by the worms shown in Figs. 8–10, segmentation takes place from a diffuse area in the hinder region of the body.

This process is relatively rapid and is complete, no further segments being formed in the later development of the worm.

These young individuals bear a slight resemblance to certain plerocercoid larvae. However, without knowing the whole life cycle of this species it is impossible to say what larval stages it undergoes. It is in fact very unlikely that this species has a plerocercoid larva. What must be emphasised is that the hind end of these young individuals, although being unsegmented at first, remains and eventually becomes segmented and develops to full maturity, whereas the corresponding part of a plerocercoid larva is lost.

Fig. 13 shows the relative positions along the worm of the genital anlage, the onset of maturity, the production of eggs and also the total number of segments in the worm. The positions of the onset of maturity and egg production become nearer to each other as the worm ages and they both approach the genital anlage. Thus in a strobila of length 65 mm. and maximum breadth 1·2 mm., anlage is at the 37th proglottis, the onset of maturity is at the 44th, and eggs are apparent 12 segments further on at the 56th proglottis from the scolex. This contrasts strongly with a young worm of a similar length, 67 mm., but with a smaller maximum breadth of 0·85 mm., which has its anlage at the 47th segment, onset of maturity at the 96th segment and eggs are produced at the 201st segment. Thus after segmentation and a period of growth in which this segmentation becomes asserted we can visualise a period in which the strobila increases in thickness and breadth but of greater importance is the maturation of the genitalia, this taking place at the posterior end first and working forward. The number of mature and gravid proglottides increases and the position of the onset of maturity and the production of eggs moves towards the scolex.

Curiously enough, the position of the anlage relative to the scolex is constant between narrow limits and the anlage does not move towards the scolex as the worm matures as one might expect from the behaviour of the position of the onset of maturity. This constancy of the position of the genital anlage is difficult to account for, but it could possibly be explained on a theory of axial gradients.

Further stages in development were not found in this host bird but examples from second and third hosts indicates what happens later. In appearance the specimens (Figs. 7a, b) are narrow for

40–50 proglottides then rapidly widen out to about 1·5 mm. This wide portion in some examples is very short and the hinder proglottides are lacerated and empty of egg capsules. A specimen such as this is obviously older than those described earlier had has shed most of its ripe proglottides. It may be noted here that even in this older stage there are some 40 or so narrow undeveloped segments. A worm like this has probably reached almost the end of its productive life.

To summarise the different stages in development that I have postulated :—

1. Segmentation, this takes place from a diffuse area in the posterior region of the young worm.

2. A period of material growth in which the worm increases in size, and gains complete external and internal segmentation. The posterior region of the strobila is the last to gain complete external segmentation.

3. Maturation of the sexual organs, this proceeds from the posterior end and works towards the scolex.

4. Loss of gravid segments from the posterior end, until 40–50 segments remain, at this stage the worm nears the end of its productive life.

The growth that I have described for *Capsulata edenensis* n.gen., n.sp. differs greatly from the classical picture of a tapeworm in which segments are produced at the neck region as fast as they are shed, when ripe, from the posterior end. Apolysis takes place in the new species in so much as ripe segments are shed from the posterior end. Its growth, however, differs from the classical picture in that the growth zone is not immediately behind the scolex, but is a diffuse region situated at the posterior end of the young strobila. Segmentation taking place from a region other than in the neck is by no means unknown among tapeworms. It is widespread among pseudophyllideans and has been recorded in some detail by Curtis (1906) in *Crossobothrium laciniatum* Linton, and by Fuhrmann (1925 and 1931) in *Idiogenes nana* (Fuhrmann) and *Haplobothrium globuliforme* Cooper. These last species however have additional complications in that they form primary and secondary individuals and their associated pseudoscolices. It is difficult to compare the new species with very distantly related pseudophyllideans, their anatomy is completely different and their segmentation is generally

not orderly although it also arises from a diffuse growth zone in the posterior region of the body. The growth of *Crossobothrium laciniatum* Linton as described by Curtis (1906) differs from *Capsulata edenensis* n.gen., n.sp. in that its growth zone is somewhere in the middle of the young strobila and gives off "anterior" and "posterior" segments. The strobila of the new species could be compared to the "anterior" segments of *Crossobothrium laciniatum* Linton.

Idiogenes nana (Fuhrmann) is the only other cyclophyllidean tapeworm, as far as I can ascertain, which shows this unusual type of growth. Related to its growth is the production of secondary individuals and the formation of pseudoscolices. If a single individual of this species is compared to a strobila of *Capsulata edenensis* then a certain similarity between the two may be seen. The segmentation of *Idiogenes nana* also appears to work backwards from the scolex end; "La strobilation se fait en effet en partant de l'extrémité qui porte le pseudoscolex et en se propageant de là en arrière (Fig. 3, a, b, c). De ce fait les derniers proglottis de l'extrémité distal seront les plus jeunes et non les plus âgés, comme chez la généralité des cestodes." In Fuhrmann's examples as well as mine the hindermost proglottides are the first to reach maturity, it may be thus questionable to state that the posterior segments are in any way younger than the anterior ones, although the latter may have gained their external segmentation first.

The type of growth that I have described for *Capsulata edenensis* n.gen., n.sp. is rare, at least among cyclophyllidean tapeworms. It does not involve schizogenesis or the production of secondary individuals as in some of the other species mentioned earlier, nor is a pseudoscolex formed. The anterior segmentation may however play a part with the rather small scolex in assisting the worm to remain in position in the gut of the host as many of the worms were found unattached in the intestine. It is difficult to account for this almost unique type of growth ·encountered in this species. It is possible that this type of growth is not as rare as its absence from the literature might suggest, and it may be worth while investigating other species in the same way. It is however unfortunate that it is not often that one finds enough material, with different stages of growth, and also in a good enough state of preservation to enable an investigation of this type to be carried out.

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