ON OESOPHAGOSTOMUM APIOSTOMUM (Willach) AND SOME REMARKS ON THE CLASSIFICATION OF THE STRONGYLIDAE

BY

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UTRECHT.

(With 5 figures)

When the editors of this memorial volume invited me to write a contribution, I was glad to have an opportunity to express my regard and esteem for Prof. MAX WEBER whom I have the privilege to reckon amongst my teachers. When I was a student and afterwards, when I examined material, collected by the Siboga-Expedition, which he led with so much success and the results of which are so exquisitely published, I had plenty of occasion to appreciate WEBER as man, professor and investigator.

My colleague, Prof. J. POELS, director of the Rijksseruminrichting at Rotterdam, provided me with the material for this investigation: 5 worms (2 ♂♂, 3 immature ♀♀), found in nodules of the wall of the intestine of an orang-outan. They proved to belong to *Oesophagostomum apiostomum* (Willach), a species of which it is not superfluous to give a somewhat detailed description.

This species was described by WILLACH (1891) and later on by RAILLIET & HENRY (1906). WALKER (1913) studied the free living larval stages. It is closely related to *O. Brumpti.*

Description. When fixed, the worms have contracted strongly and hence they are coiled. The ♂♂ are 10—12.8 mm. long; the longest, least contracted ♂ has a maximum thickness of 425 μ, the other one a thickness of 565 μ. The ♀♀ are 11.5—15 mm. long; the longest, least contracted ♀ has a maximum thickness of 530 μ, the others a thickness of 650—665 μ. These measurements agree with those of WILLACH and RAILLIET & HENRY (♂ long 10—12.5 mm., broad 400 μ, ♀ long 12—16 mm., broad 450 μ).

In the least contracted ♂ the cuticular striae are 16—17 μ distant from each other, in the least contracted ♀ they are 12.5 μ distant from each other. According to RAILLIET & HENRY this distance is 12—14 μ. Behind the mouth-collar a distinct cuticular swelling (vésicule céphalique RAILLIET) is present. In the ♂♂ the transverse cervical groove (fente ventrale RAILLIET) is 262—270 μ, in the ♀♀ 308 μ from the anterior extremity; according to RAILLIET & HENRY this distance is 250—275 μ. Behind the cervical groove the cuticle is also somewhat swollen; this swelling disappears backwards, before the posterior extremity of the oesophagus is reached.

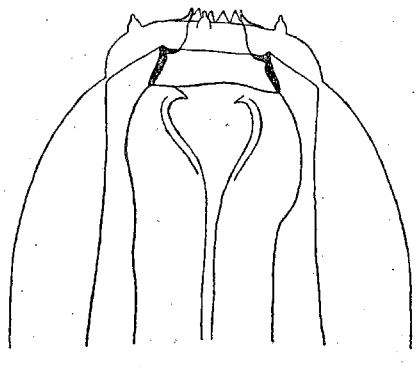

Fig. 1. Anterior extremity with mouth-collar, mouth-capsule and oesophageal funnel. × 270 (× $\frac{3}{4}$).

The mouth-collar is well developed (fig. 1). Its outer margin does not ascend so steeply from the circular groove behind it as in RAILLIET & HENRY's figure (1912, pl. 22, fig. 2, 3) of *O. Brumpti.* The two lateral papillae scarcely protrude. The 4 submedian papillae do not agree with the figure of WILLACH. They are rather short and consist of two parts, the proximal one being the longest and the distal one appearing as a small appendage of the proximal part. The latter tapers in distal direction. According to the figure of RAILLIET & HENRY (l. c.) this part has a cylindrical shape in *O. Brumpti.*

In one of the species examined the external leaf-crown consists of 13 elements, which, seen from before, possess rounded tips and limit a circular opening. RAILLIET & HENRY state: "coronule externe paraissant formée d'une dizaine de dents". The mouth-capsule has the shape of a truncated cone. Its anterior margin forms a short circular fold, protruding towards the body-axis (fig. 1). For this reason the diameter of the entrance to the cavity of the mouth-capsule is only 45—49 μ, the oral diameter of the mouth-capsule, its wall included, being 60—70 μ. The caudal diameter of the mouth-capsule is 78—82 μ, its length is 21 μ. According to RAILLIET & HENRY the anterior diameter averages 48 μ, the posterior diameter 65 μ, the length 20 μ. An internal leaf-crown seems to be absent. The posterior margin of the mouth-capsule is provided with 3 shallow incisions, while in *O. Brumpti* this margin shows 3 incisions reaching the middle of the mouth-capsule.

The oesophageal funnel is well developed; its cuticular wall possesses a small pointed nodule in the dorsal mid-line and latero-ventrally near the posterior margin of the mouth-capsule. This nodule is also mentioned by RAILLIET & HENRY. *O. Brumpti* possesses curved teeth at these places.

The length of the oesophagus is in the ♂ 615 μ, in the ♀ 685—720 μ, according to RAILLIET & HENRY 550—600 μ. The anterior part, containing the oesophageal funnel, is slightly thicker than the following part. Its minimum thickness is 75 μ. Close in front of the posterior extremity the oesophagus has its maximum thickness (170 μ in the ♂, 165—170 μ in the ♀, according to RAILLIET & HENRY 165 μ). The wall of the mesenteron is pigmented, which characteristic is also mentioned by WILLACH and RAILLIET & HENRY.

The median lobe of the bursa copulatrix (fig. 2—4) is somewhat emarginate in the median plane, does not protrude and is separated by a shallow incision from each lateral lobe. The rays have

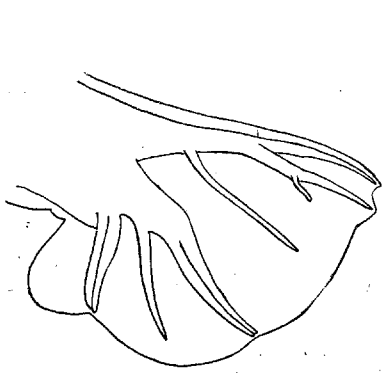

Fig. 2. Bursa copulatrix, lateral view. × 110 (× $\frac{3}{4}$).

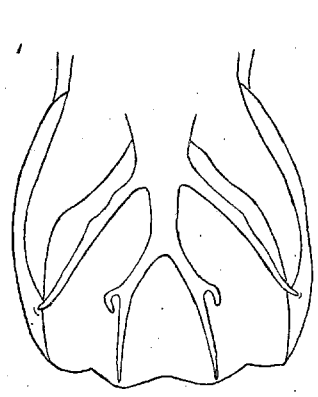

Fig. 3. Bursa copulatrix, dorsal view. × 122 (× $\frac{3}{4}$).

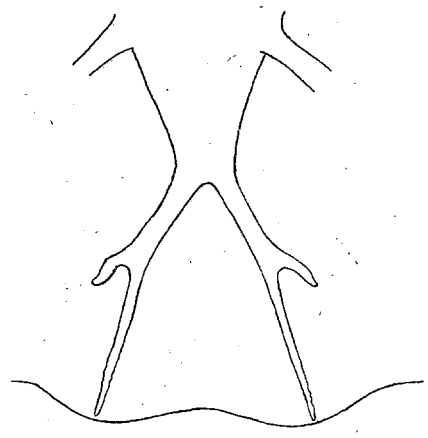

Fig. 4. Dorsal ray of the bursa copulatrix, spread out. × 270 (× $\frac{3}{3}$).

a course typical of *Oesophagostomum*. So each ray D divides into a short lateral ray D_1 and a medial ray D_3, which is the continuation of D [1]). D_0 has a length of 96 μ, measured from the origin of the externo-dorsal ray to the bifurcation. D is 82 μ long, measured from the bifurcation of D_0 to the branching of D in D_1 and D_3. D_1 is 29 μ and D_3 123 μ long. D_1 is directed backwards and somewhat exteriorly. The externo-dorsal ray ends at a rather large distance from the border of the bursa. From the common stem of the lateral rays the externo-lateral ray first comes off and ends at a rather long distance from the border of the bursa, while the medio- and postero-lateral rays, which run parallel, terminate at a short distance from this border. The ventral rays end quite near to the border of the bursa.

In one of the 2 ♂♂ the spicules protrude from the cloacal opening and are somewhat unequal

1) I use a nomenclature previously applied by me (1921, p. 401), in which the median stem of the dorsal ray is called D_0. This one bifurcates into two branches (D) which divide into rays called D_1, D_2 and D_3 from before backwards. In *Oesophagostomum* D_2 is generally lacking apparently. Behind D_1 a short lateral side branch can be present, which is found by CL. LANE (1917, pl. 35) in *O. radiatum trifurcatum* and sometimes in *O. venulosum* and which may be interpreted as D_2. D_3 of *Oesophagostomum* then agrees with D_3 of *Cylicostomum* and allied genera, this ray being the direct continuation of D in these cases. Apparently D_2 is disappearing in *Oesophagostomum*.

in length, resp. 1350 and 1285 μ. The distal ends, situated close to each other, are pointed. According to RAILLIET & HENRY the length of the spicula amounts to 1250—1275 μ.

The posterior extremity of the ♀ (fig. 5) agrees with that of *O. Brumpti.* Already before the vulva the body tapers to end at the level of the anus in a point not always sharply marked off. The vagina is long and directed longitudinally. The distance between vulva and anus is 205—240 μ; the distance between the anus and the tip of the tail is 205—210 μ. According to RAILLIET & HENRY these measures are resp. 240 μ and 180 μ; according to WILLACH 100 and 200 μ. In the specimens examined by me vulva and anus are not salient, contrary to the statements of RAILLIET & HENRY. WILLACH only mentions that the anus protrudes, so that this characteristic is not of much systematic value.

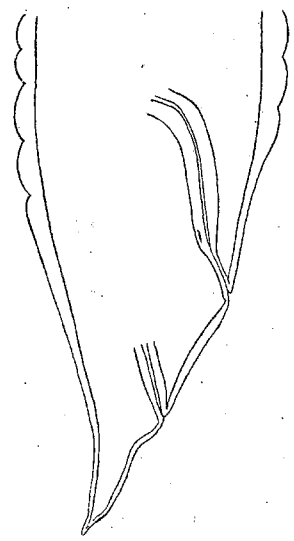

Fig. 5. Posterior extremity of ♀, lateral view, with vulva and anus. × 122 (× ⅔).

Geographical distribution. *O. apiostomum* was described by WILLACH in *Macacus cynomolgus* and found several times by WEINBERG (1909) in *M. cynomolgus* and *M. sinicus*. The specimens collected by him were examined by RAILLIET & HENRY. This species is of common occurrence in the Philippine Islands according to WALKER (1913, p. 501). LEIPER (1911, p. 116; 1913, p. 274) thinks that this species occurs in negroes in Northern Nigeria. The specimens examined by LEIPER were thought to be an independant species by RAILLIET & HENRY (BRUMPT, 1913, p. 456). I agree with this opinion as LEIPER's specimens differ too much from the description of RAILLIET & HENRY and from that given above in shape and measurements of the mouth-capsule, the height of the mouth-collar, the length of the spicules etc. CL. LANE (1916, p. 12) leaves this question undecided. Apart from LEIPER's observation *O. apiostomum* is found only in Asiatic monkeys up to now. This species was not yet found in the orang-outan.

The *Oesophagostomum*-species occurring in Primates. Besides *O. apiostomum* the following species are found in man and monkeys (RAILLIET & HENRY, 1906, p. 448; 1909, p. 168; STILES & HASSELL, 1920, p. 611).

O. Brumpti Railliet et Henry, in man, in Asiatic and African monkeys (RAILLIET & HENRY, 1912, p. 567).

O. Blanchardi Railliet et Henry, in orang-outan, Borneo (RAILLIET & HENRY, 1912, p. 572, note).

O. stephanostomum Stossich, in gorilla, Africa (STOSSICH, 1904, p. 2; RAILLIET & HENRY, 1912, p. 572).

O. stephanostomum var. *dentigera* (Railliet et Henry) = *O. dentigerum* Railliet et Henry, in chimpanzee, Afrika (RAILLIET & HENRY, 1906, p. 448; 1912, p. 572).

O. stephanostomum var. *Thomasi* Railliet et Henry, in man, Brazil (RAILLIET & HENRY, 1912, p. 570).

O. pachycephalum Molin, in *Cercopithecus*, Africa (MOLIN, 1861, p. 450; BRUMPT, 1913, p. 455).

The following species are to be regarded as *species inquirendae.*

O. aculeatum (v. Linstow), in *Macacus cynomolgus*, Asia (v. LINSTOW, 1879, p. 333).

O. attenuatum (Leidy), in *Cynocephalus porcarius*, Africa (LEIDY, 1904, p. 100).

O. bifurcum (Creplin), in *Cercopithecus patos*, Africa (CREPLIN, 1849, p. 54; 1850, p. 480; DIESING, 1861, p. 722).

O. ovatum (v. Linstow), in *Hylobates syndactylus* and *agilis*, Sumatra (H. SMIDT, 1906, p. 646). This species is perhaps identical with *O. apiostomum.*

Key to the well-known species of *Oesophagostomum* in Primates.

1. mouth-collar spherically inflated [1]), ♂ 11.5—21 mm., ♀ 15—27 mm. long . *O. pachycephalum.*
   mouth-collar high but not spherical . . . . . 2.
2. elements of the external leaf-crown numerous (ca. 38), mouth-capsule nearly cylindrical . . . . . 3.
   the elements of the external leaf-crown number less than 20 . . . . . 4.

1) "Caput epidermide sphaerice inflata" (MOLIN, 1861, p. 450).

3. ray D_1 directed obliquely to the exterior . . . . . *O. stephanostomum*
   ray D_1 directed backwards, length of ♂ 18—22 mm., of ♀ 20—26 mm. . *O. steph.* var. *dentigera.*
   ray D_1 directed obliquely to the interior, length of ♂ 17—22 mm., of ♀ 16—20 mm. . . . . *O. steph.* var. *Thomasi.*
4. external leaf-crown consists of 16 elements, spicules up to 1825 μ long. *O. Blanchardi.*
   external leaf-crown consists of 10—13 elements, spicules up to 1350 μ long, the mouth-capsule has the shape of a truncated cone. . . . . 5.
5. length of ♂ 6.7—11 mm., of ♀ up to 12.5 mm. [1]), anterior diameter of the mouth-capsule averages 35 μ, posterior diameter 45 μ, spicules 900—1080 μ in length [2]). D_1 is directed backwards and somewhat to the interior . . *O. Brumpti.*
   length of ♂ 10—12.8 mm., of ♀ 11.5—16 mm., anterior diameter of the mouth-capsule 60—70 μ, posterior diameter 78—82 μ, spicules 1250—1350 μ in length. D_1 is directed backwards and somewhat to the exterior. *O. apiostomum.*

Subgenus *Conoweberia* (n. subg.). RAILLIET & HENRY (1913, p. 507; RAILLIET, HENRY & BAUCHE, 1919, p. 332) have divided the *Oesophagostomum*-species of the Artiodactyla into 3 subgenera. *O. apiostomum* and *O. Brumpti,* closely related to each other, cannot be grouped in one of these subgenera, so that a new subgenus may be created for these species, which in honour of MAX WEBER may be called *Conoweberia.* This name also points to the shape of the mouth-capsule which is a truncated cone. The systematic place of the other *Oesophagostomum*-species occurring in Primates I leave undecided.

The characteristics of the new subgenus of which *O. apiostomum* forms the type, are as follows:

Cuticle of neck inflated between the mouth-collar and the cervical groove. Cervical papillae close behind the middle of the oesophagus. No lateral cuticular membranes. The mouth-capsule has the shape of a truncated cone. Oesophageal funnel with 3 teeth behind the mouth-capsule. Vagina long, from the vulva directed to the front.

The systematic place of the genus *Oesophagostomum* and the classification of the *Strongylidae.* Classifying the *Strongylidae* RAILLIET & HENRY (1912, p. 564; RAILLIET, 1916, p. 518) emphasize the structure of the bursa. LEIPER (1908, p. 190; 1913, p. 276) does not agree with the opinion of the famous French authors and lays stress upon the importance of the structure of the mouth and mouth-capsule for taxonomic purposes. In the family of the *Strongylidae* LEIPER distinguishes amongst others the subfamilies *Strongylinae* (mouth with external leaf-crown) and *Ancylostominae* (mouth-capsule with teeth or cutting plates). CL. LANE (1917, p. 423), TRAVASSOS (1919, p. 65) and myself (in SLUITER, SWELLENGREBEL & IHLE, 1922) have followed this classification. HALL (1916, p. 119) is satisfied neither with RAILLIET & HENRY's arrangement nor with that of LEIPER.

RAILLIET (1916, p. 518) writes in support of his opinion: „HALL critique notre classification des Strongylidés parce qu'elle sépare des formes à bouche semblable; je ne crois cependant pas qu'on puisse nier que les caractères tirés de la bourse caudale (caractères sexuels secondaires) l'emportent sur ceux que fournit la bouche (caractères d'adaption)". I do not believe that we can consider the characteristics of mouth and mouth-capsule simply „caractères d'adaption", as the very uniform conditions of existence in the intestine of mammals could hardly produce the manifold and divergent structures of the mouth and mouth-capsule of the *Strongylidae.* On the other hand we see that some genera (*Triodontophorus* and *Ternidens,* LEIPER, 1913, p. 276) agree in a number of main points of the body-structure, but differ especially in the course of the rays of the bursa, this being a strong argument not to attribute too much systematic importance to the structure of the bursa.

RAILLIET (1916) places *Oesophagostomum* in the subfamily of the *Oesophagostominae* (formerly (1912, 1913) tribus of the *Oesophagostomeae*); moreover the genera *Chabertia, Ternidens, Agriostomum* and *Bourgelatia* (RAILLIET, HENRY & BAUCHE, 1919) are considered to belong to this subfamily. With LEIPER (1913, p. 277) I believe that we have to do with a heterogeneous group. *Agriostomum* belongs

1) According to ELDERS (1917, p. 172, 173) the length of a ♂ measured by him amounts to 12 mm., of a ♀ to 14 mm., but it is not certain whether the specimens examined by him belong to *O. Brumpti* or to *O. apiostomum.*

2) In specimens, considered to belong to *O. Brumpti* by H. J. SMIT (1919) (from a monkey which died on Java) the length of the spicula amounts to 1300 μ.

to LEIPER's *Ancylostominae*; *Chabertia* differs in a mouth-opening which faces antero-ventrally; *Ternidens* is closely related to *Triodontophorus*; to include *Bourgelatia* in the *Oesophagostomeae* RAILLIET, HENRY & BAUCHE (1919, p. 325) had to modify their diagnosis of this group.

It does not seem advisable to divide LEIPER's *Strongylinae* into tribus, because the relations between the genera, belonging to this group, are very intricate, so that some of these genera agree with one genus in a certain group of characteristics (e. g. mouth and mouth-capsule), while they agree with a totally different genus in another group of characteristics (e. g. bursa).

For this reason, even after separating all genera without exterior leaf-crown, we cannot maintain RAILLIET's groups: *Strongyleae*, *Oesophagostomeae* and *Cylicostomeae* (= *Trichonemeae*) as tribes of LEIPER's *Strongylinae*. RAILLIET's classification is based on the course of the rays of the bursa and on the position of vulva and uteri. Some differences between RAILLIET's groups appear to be not well defined, others to be of slight systematic value. E. g. in some cases it is more or less arbitrary whether the externo-dorsal ray is considered to originate independently or to originate together with the dorsal ray, which characteristic forms a difference between *Strongyleae* and *Cylicostomeae*. E. g. in the genus *Bourgelatia*, considered to belong to the *Oesophagostomeae*, there is a distinct space between the medio- and postero-lateral ray (RAILLIET, HENRY & Bauche, 1919, p. 325), which is absent in the other *Oesophagostomeae* and present in *Strongyleae* and *Cylicostomeae*. The splitting up of the ray D in 2 or 3 branches, which characteristic is important in RAILLIET's taxonomy, is of little value, as e. g. CL. LANE (1917, p. 426) described an *Oesophagostomum radiatum trifurcatum*, in which ray D possesses 3 sidebrances, while the typical *Oesophagostomeae* possess only 2 sidebranches here. In connection with this CL. LANE (1914, pl. 52, fig. 19—21; 1917, p. 430) points to the fact that in *Decrusia additicia* ray D_0 bears 4 or 6 branchings at its extremity (ray D is lacking). Neither must too much systematic value be attributed to the course of the uteri. Their course — whether parallel or opposite — is connected with the situation of the vulva, which is very variable and which can be inconstant even in one and the same species (e. g. *Physocephalus sexalatus*, cf. SEURAT, 1920, p. 69).

Neither is TRAVASSOS' (1919, p. 65) division of LEIPER's *Strongylinae* into two tribes satisfactory. He distinguishes: *Strongyleae* (the longitudinal axis of the mouth-capsule is straight) and *Ransomeae* (the longitudinal axis of the mouth-capsule is curved). However, in the latter tribe in the genera *Ransomus* and *Chabertia* the mouth-opening is obliquely directed to the ventral side, in *Choniangium* obliquely to the dorsal side. The structure of the bursa in *Choniangium* also differs from that of *Chabertia* and *Ransomus* in many respects.

Utrecht, April 1922.

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