

# Terrestrial Nematodes from the Galápagos Archipelago II : Redescription of *Aporcelaimellus obtusicaudatus* (BASTIAN, 1865) ALTHERR, 1968, with review of similar species and a nomenclature for the vagina in Dorylaimida (Nematoda)

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## Abstract

*Aporcelaimellus obtusicaudatus* and *A. obscurus* are redescribed on the basis of topotypes, resp. syntypes, and compared with specimens from localities on the Galápagos Islands. *A. obscurus* cannot be differentiated from *A. obtusicaudatus* and is therefore synonymized with it. *A. amylovorus* is also redescribed from syntypes, and can be distinguished from *A. obtusicaudatus* by the shorter odontostyle (16-19  $\mu\text{m}$  vs 19-29  $\mu\text{m}$ ), shorter odontophore (29-35  $\mu\text{m}$  vs 36-48  $\mu\text{m}$ ) and proportionately longer tail ( $c' = 1.07-1.27$  vs 0.52-0.98). A neotype is designated for *A. obtusicaudatus*, as well as lectotypes for *A. obscurus* and *A. amylovorus*. Twenty nominal species very similar to *A. obtusicaudatus* are reviewed; eleven of these are considered *species inquirenda*. The diagnostic (un)reliability of some characters is discussed, and a nomenclatorial scheme for the detailed description of the vagina in Dorylaimida is presented.

**Key-words :** *Aporcelaimellus*, Nematoda, taxonomy, morphology, Galápagos.

## Résumé

*Aporcelaimellus obtusicaudatus* et *A. obscurus* sont redécrits à base de topotypes, resp. syntypes, et comparés avec spécimens de plusieurs localités sur les Iles Galápagos. Comme *A. obscurus* ne peut pas être distingué de *A. obtusicaudatus*, les deux sont synonymisés. *A. amylovorus* est redécrit aussi à base de syntypes, et diffère de *A. obtusicaudatus* par l'odontostyle plus court (16-19  $\mu\text{m}$  vs 19-29  $\mu\text{m}$ ), l'odontophore plus court (29-35  $\mu\text{m}$  vs 36-48  $\mu\text{m}$ ) et la queue relativement plus longue ( $c' = 1.07-1.27$  vs 0.52-0.98). Un néotype est désigné pour *A. obtusicaudatus*, comme aussi des lectotypes pour *A. obscurus* et *A. amylovorus*. Vingt espèces nominaux ressemblantes à *A. obtusicaudatus* sont revues; onze de ces espèces sont considérées d'être *species inquirenda*. L'importance diagnostique de quelques caractères est discuté, et une nomenclature est proposée pour la description détaillée du vagin des Dorylaimida.

**Mots-clefs :** *Aporcelaimellus*, Nematoda, taxonomie, morphologie, Galápagos.

## Introduction

This is the second paper in a series on the terrestrial nematofauna of several of the Galápagos Islands. After the publication of the first paper (DE LEY & COOMANS, 1990) more soil samples were taken, and the organization of the series has therefore been revised to accommodate the additional material. In this publi-

cation we describe specimens of *Aporcelaimellus obtusicaudatus* (BASTIAN, 1865) ALTHERR, 1968, a dorylaimid encountered in many of our samples. As this species is the focal point of a very confusing and much confused group of species, we had to reassess the diagnosis of *A. obtusicaudatus*. We therefore give a redescription based on topotypes, as well as a review of related and possibly synonymous nominal species. Of the latter, *A. obscurus* (THORNE & SWANGER, 1936) HEYNS, 1965 and *A. amylovorus* (THORNE & SWANGER, 1936) HEYNS, 1965 are also redescribed. Syntypes of *A. obscurus* did not exhibit any qualitative difference with the topotypes of *A. obtusicaudatus*, and all quantitative differences were invalidated by the Galápagos material. *A. obscurus* is therefore considered invalid. In addition, a nomenclatorial framework is formulated to provide terminology for more accurate description of the vagina in Dorylaimida.

## Material and Methods

### SAMPLES AND SPECIMENS

Samples from the Galápagos were collected by the third author and Mr. M. COBO in February and March of 1988, and by Dr. K. DESENDER in April and May of 1991. All material of the 1988 expedition was fixed in 4 % formaldehyde solution heated to 70°C. In contrast, only four samples from 1991 were fixed directly after collection, the other eight having been shipped as dry soil to the laboratory and stored in a cooled closet at 4°C for three months. In september 1991, half of each sample was taken out, soaked in distilled water for three hours, and centrifugated in 50 % ludox AS for extraction of live nematodes. All nematodes were then fixed in 4 % hot formaldehyde. As *A. obtusicaudatus* was found in most localities in the Galápagos, a complete list of all samples and their collection data is given in Table 1, while numbers of *A. obtusicaudatus* specimens isolated per sample are given in Table 2. Topotype females of *A. obtusicaudatus* were collected

Table 1:  
Data of the samples collected on the Galápagos Archipelago

Island	Sample n°	Date (d/m/y)	Altitude (m)	Soil type	Vegetation zone*	Details of vegetation and locality
Isla Santa Cruz	1	12/2/88	150	dark brown, stony	arid	moderate cover of shrubs, shoots, <i>Burseria</i> , <i>Passiflora</i> ; N slope, 9.7 km from Itabaca
	2	"	300	dark brown	arid	similar to 1, many shoots; N slope, 12.3 km from Itabaca along road Baltra-Puerto Ayora
	3	"	500	dark brown	transition	forest with <i>Pisonia</i> , <i>Tournefortia</i> ; N slope, 16.4 km from Itabaca along sideway
	4	"	630	brown	<i>Scalesia</i>	clearing in forest with grasses & sedges; N slope, Los Gemelos, 19.1 km from Itabaca
	5	"	630	brown	<i>Scalesia</i>	<i>Scalesia</i> forest; N slope, Los Gemelos, 3 m right from road
	7	15/2/88	875	reddish brown	fern-sedge	grasses, sedges & herbs; Cerro Crocker, 1.5 m N from cabin
	8	"	700	brown	fern-sedge	similar to 7; between Cerro Crocker and Media Luna near pool
	10	"	550	brown	<i>Miconia</i>	<i>Miconia</i> and ferns next to brooklet; Media Luna, S slope
	11	19/2/88	180	dark grey, brown spots	transition	grasses between barracks (Casetas Tortuga) in tortoise reserve, SW slope
	D1	29/4/91	20	brown	arid	dried-up pool near Barranco
	D2	28/4/91	15	dark brown	arid	around roots <i>Cryptocarpus</i> near Charles Darwin Research Station
Isla Floreana	13	21/2/88	350	humid	<i>Scalesia</i>	around roots of grasses, herbs in secondary forest with Guava, <i>Zanthoxylum</i> ; highland
	14	"	350		(farm)	grasses between Guava trees; Finca Claudio Cruz - highland
	15	"	340		<i>Scalesia</i>	<i>Scalesia</i> forest with little undergrowth; highland
	16	"	150		(sediment)	in brooklet (occasionally dry - last drought in 1983), pH=7; near Finca padre Cruz
	F4	?/4/92	640			<i>Lantana</i> , <i>Pisonia</i> , <i>Zanthoxylum</i> , <i>Croton</i> ; summit Cerro Pajas
Isla Fernandina	17	25/2/88	200	relatively humid	arid	soil around roots <i>Zanthoxylum</i> , <i>Bursera</i> ; foot Cerro Verde, SW slope
	18	26/2/88	800	humid	fern-sedge	cover with 50% ferns (20% <i>Pteris</i> ), 40% sedges, 5% <i>Psychotria</i> , some <i>Zanthoxylum</i>
	19	26/2/88	1420	very humid	<i>Scalesia</i> / fern-sedge	<i>Nacraea</i> , <i>Psychotria</i> , scattered <i>Scalesia</i> , sedges, herbs; at edge caldera near fumarole
	D3	10/5/91	2	dark sand+ shell fragm.	littoral	<i>Pennisetum</i> , <i>Scutia</i> , malvaceous tree; Cabo Hammond
Isla Española	20	4/3/88	50	crumbly	arid	<i>Lantana</i> ; along transect from coast to highest point near Punto Cevallos (E slope)
	21	"	150	sticky	arid	<i>Lantana</i> , <i>Gordia</i> ; transect continued
	22	"	160	black	arid	sedges; depression near highest point at Punto Cevallos
	D7	18/4/91	5	mostly shell fragm.	littoral	around roots <i>Cryptocarpus</i> ; Bahía de los Flamencos
	D8	"	15	brown	littoral	<i>Cordia</i> , <i>Lantana</i> , <i>Bursera</i> ; Bahía de los Flamencos
Isla Santa Fé	D4	25/4/91	100	reddish brown	arid	dry pool
	D5	"	5	light sand	littoral	around roots <i>Cryptocarpus</i>
Isla Isabela	D6	25/5/91	10	dark brown	aberrant	Forest with <i>Pisonia</i> , ferns; along transect from Coleta Iguana to Cerro Azul
	F1	25/5/91	200		aberrant	Forest with <i>Pisonia</i> , ferns; along transect from Coleta Iguana to Cerro Azul
	F2	"	850		fern-sedge	Cerro Gavilan (along transect)
	F3	"	1530		fern-sedge	near caldera Cerro Azul

\*: Following WIGGINS & PORTER (1971)

Table 2

Numbers of specimens of *Aporcelaimellus obtusicaudatus* (BASTIAN, 1865) ALTHERR, 1968 isolated from the Galápagos

Island	Sample n°	females	juveniles
Isla Santa Cruz	2	—	1
	3	—	2
	4	15	155
	5	2	36
	7	—	8
	8	3	28
	10	1	5
	11	8	148
Isla Floreana	13	1	4
	14	15	95
	15	—	56
	F4	3	18
Isla Fernandina	17	4	5
	18	18	42
	19	25	103
Isla Isabela	D6	3	3
	F1	9	11
	F2	4	12
	F3	—	5
Total :		111	737

by Dr. D.J. HOOPER in 1967 in Falmouth, UK. A neotype female was selected and is kept on slide WT 2882 at the Landbouwniversiteit, Wageningen, the Netherlands, together with seven other topotypes kept on slides 2883-2885. Three topotypes are kept on slide 3710 in the Nematode Collection of the Instituut voor Dierkunde, Gent, Belgium. Two slides with syntype females of *A. obscurus* were kindly lent by Dr. A.M. GOLDEN. One of these read "Lewiston, Utah - Bullenfield - Dec. 10, 1925" and the other "Ogden, Utah - Beetfield - Sept. 12, 1925". A lectotype was selected from the Lewiston slide and remounted; it is kept as slide T-492t in the USDA Nematode Collection, Beltsville, Maryland, USA, together with paralectotypes on slides T-4375p - T-4380p. One slide with syntype females of *A. amylovorus* was also borrowed from Dr. GOLDEN. This slide was marked with "Buena

Park, Cal. - Tomato field - Nov. 20, 1925"; a lectotype was taken out for remounting and is kept in the USDA Collection as slide T-493t, together with paralectotypes on slides T-4381p - T-4387p.

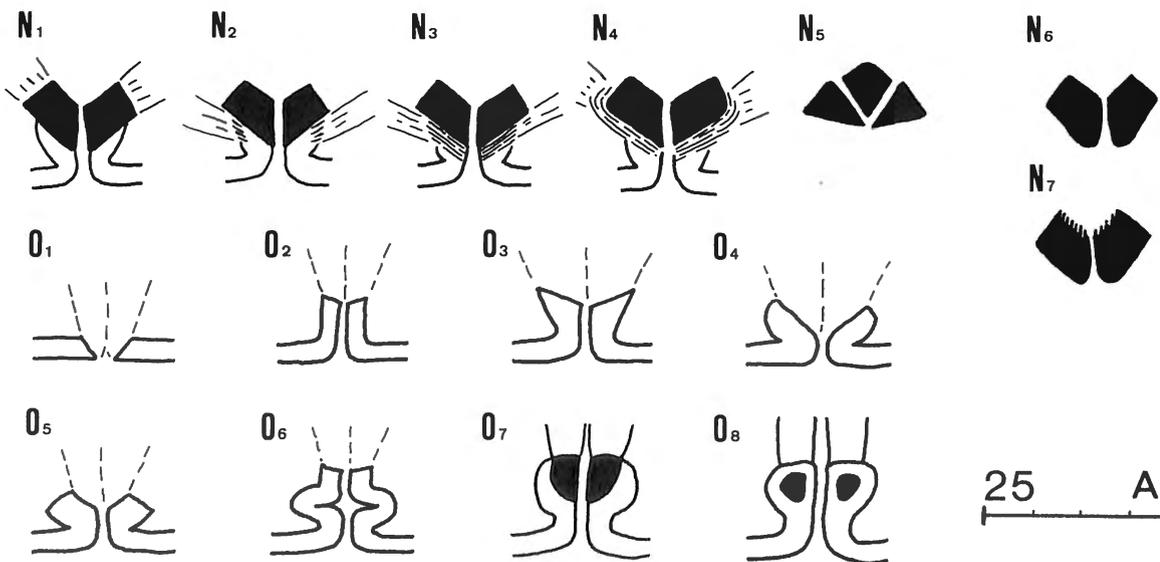
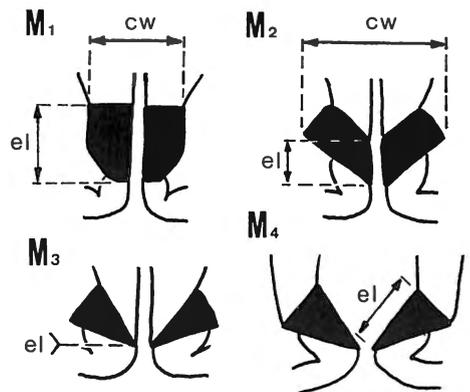
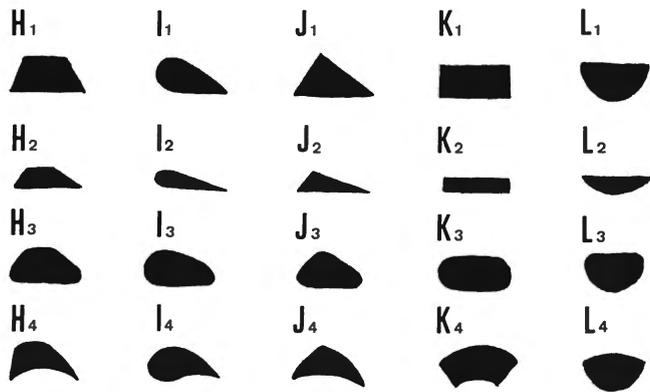
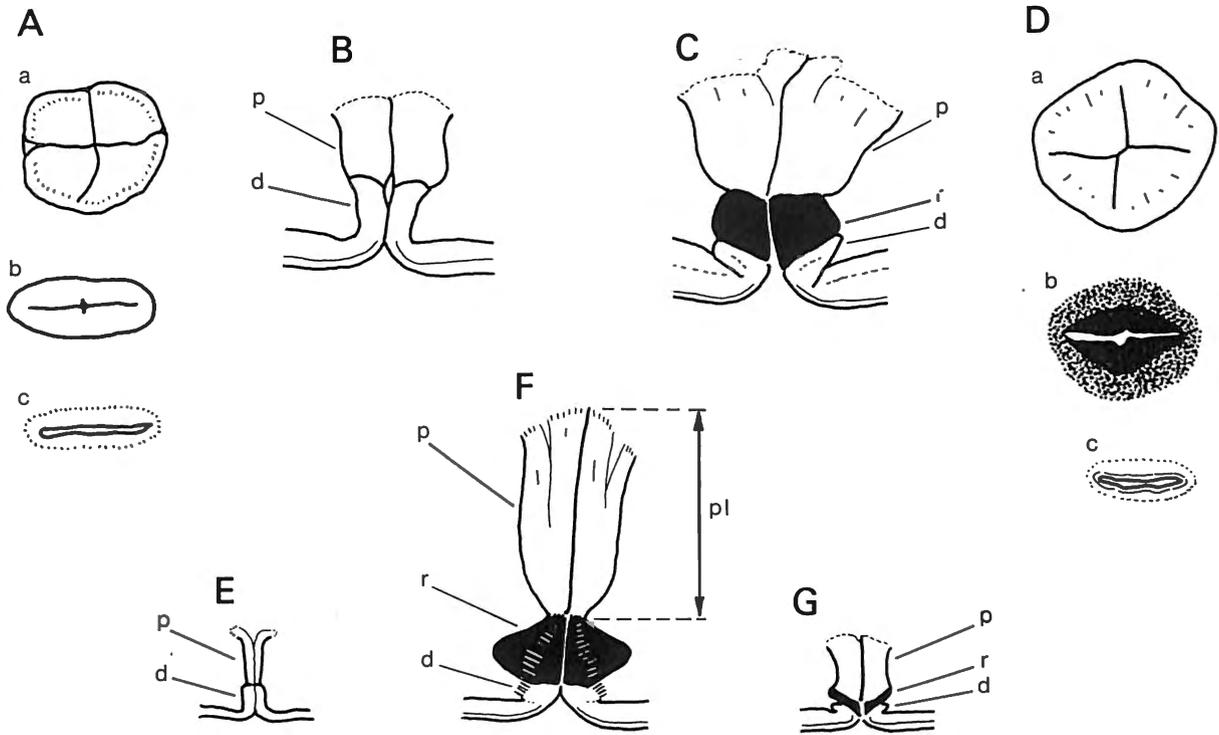
#### DESCRIPTIONS AND TERMINOLOGY

We have followed terminology of tail and lip region as proposed in THORNE & SWANGER (1936) and TJEPKEMA *et al.* (1971). In identifying dorylaims from the Galápagos, the detailed structure of the vagina and odontostyle also proved generally useful, although no standardized descriptive terminologies have as yet been introduced for these organs. We will describe odontostyle shape by specifying the aspect in lateral view of (a) the ventral wall, (b) the dorsal wall and (c) the aperture rims. This allows for a combination of descriptive freedom and detail (see first description below for an example).

Information about vagina structure is often minimal in descriptions and diagnoses of Dorylaimida, despite its great variation within the order (e.g. cf. Fig. 18 in JAIRAJPURI & AHMAD, 1992). We think it should be described in detail, and therefore propose a terminology for the description of new and known forms (Fig. 1). In Dorylaimida observed under light microscope, the channel connecting the uterus, uteri or ovejector with the exterior can be divided in up to three parts: a proximal section with hyaline walls assumed to consist of connective tissue (cf. SEINHORST & KOZLOWSKA, 1974); an intermediate section with often very refractive walls; and a distal section with walls consisting of cuticle continuous with and at least as thick as the body cuticle. These three sections have hitherto been referred to by a variety of terms, often implying that the intermediate and distal section should be considered as part of the vulva. We must therefore first resolve the distinction between the terms "vulva" and "vagina".

There are good reasons to consider both sections distal to the connective tissue as part of the vulva. The external opening of the female reproductive tract is at least part of the vulva; it is then logical to consider the most distal set of dilator muscles surrounding the genital tract as vulval dilators, and in consequence to consider their attachment site on the tract as part of the vulva. Since they may be attached either to the cuticular section or the refractive section, both these structures should therefore be considered as part of the vulva, irrespective of the actual point of attachment in each particular case.

On the other hand, some dorylaims have a proportionately large cuticular section, such as e.g. *Carcharolaimus ramirezi* (Fig. 1B), *Axonchium bulbosum* (cf. Fig. 3G in NAIR, 1972) and *Longidorus macrosoma* (cf. Fig. 1E in SEINHORST & KOZLOWSKA, 1974). It would be awkward to have to consider the vulva of these forms as being a channel as long as, or longer than the vagina



25 A-G

itself. Also, in many non-Dorylaimida the term “vagina” is already generally applied for the whole channel, in spite of being lined along most of its length by invaginating cuticle comparable to and as thick as the body cuticle (cf. e.g. MOUNTPORT *et al.*, 1991).

Weighing these arguments against one another, we think it is best to follow the Shorter Oxford English Dictionary, which restricts the meaning of “vulva” to: “The external organ of generation in the female; esp. the opening or orifice of that organ”. A similar stress is laid in HOLMES (1979) on the fundamental distinction between vulva and vagina as one between respectively the *external opening* of a canal and the *internal canal* itself. In dorylaims, the internal canal consists of the proximal, intermediate and distal sections taken together, and all three are therefore taken to be part of the vagina.

For descriptive purposes, we will now introduce three terms to denote the three subdivisions as seen with light microscope: *pars proximalis vaginae* for the proximal section with hyaline walls, *pars refringens vaginae* for the intermediate section with sclerotized walls, and *pars distalis vaginae* for the distal section with walls continuous with the body cuticle. The *pars proximalis vaginae* was until now frequently referred to as *vagina uterina*, and the *pars refringens* and/or *pars distalis* as *vagina vera* (cf. e.g. Fig. 24 in CAVENESS, 1964). We have decided to depart from this terminology, because it was borrowed incorrectly from usage in certain secernentean zooparasites, where a cuticular, ectodermal true vagina is followed by a uterine, endodermal and non-cuticular tube (SEURAT in CHITWOOD & CHITWOOD, 1950). In longidorids, VAN DE VELDE & COOMANS (unpublished) found that the “vagina uterina” is really lined by cuticle, and the same is by extension very probably true for all Dorylaimida. Continued use

of “vagina vera” and “vagina uterina” in Dorylaimida would therefore mean using the same terms as in zooparasites for structures that are clearly not homologous, and would run counter to their original definitions.

We also think it is more appropriate to distinguish three components than two: while the *pars refringens vaginae* is often absent (Fig. 1B,E) and may well be a derivation of the *pars distalis* (suggested by conditions as in Fig. 1 O<sub>7,s</sub>), it usually has a very distinct appearance and a well-delineated extent when present (Fig. 1C,F,G). We will now lay down some descriptive guidelines for each of the three vagina components as seen in lateral view with light microscope.

The *pars proximalis vaginae* can be described in terms of its length, its width proportional to this length, and the shape and distal convergence of the contours of its walls. Length is measured along the lumen, from *pars refringens vaginae* to the proximal ends of the hyaline walls (where the lumen usually widens out into that of the ovejector); width is estimated (and not measured, as this is too difficult to standardize) at the level of the surrounding sphincter, but excluding the sphincter itself. To illustrate, the *pars proximalis vaginae* of *C. ramirezi* in Fig. 1B is 9 µm long, slightly wider than long, with weakly sigmoid, non-divergent contours; *Aporcelaimellus* sp. (Fig. 1C) has a *pars proximalis vaginae* 15 µm long, wider than long, with weakly sigmoid, convergent contours; *Aquatides* sp. (Fig. 1E) has a *pars proximalis vaginae* 6 µm long, much longer than wide, with straight, parallel contours; *Labronema* cf. *mauritiense* (Fig. 1F) has a *pars proximalis vaginae* 22 µm long, much longer than wide, with contours straight and parallel proximally but curved and converging distally; *Microdorylaimus diminutivus* (Fig. 1G) has a *pars proximalis vaginae* 7 µm long, slightly longer than wide, with concave, non-convergent contours. The *pars*

- ◁ Fig. 1. – Descriptive scheme for the dorylaim vagina: A-G: bi- or tripartite vagina of some dorylaims (*d* = *pars distalis vaginae*, *r* = *pars refringens vaginae*, *p* = *pars proximalis vaginae*, *pl* = length of *pars proximalis vaginae*). *Carcharolaimus ramirezi* THORNE, 1967 – A. optical sections of vagina in ventral view (*a* = through *pars proximalis vaginae*, *b* = through *pars distalis vaginae*, *c* = through *pars distalis vaginae* at vulva). – B. lateral view. *Aporcelaimellus* sp. – C. lateral view of vagina. – D. optical sections in ventral view (*a* = through *pars proximalis vaginae*, *b* = through *pars refringens vaginae*, *c* = through *pars distalis vaginae*). *Aquatides* sp. – E. vagina in lateral view. *Labronema* cf. *mauritiense* WILLIAMS, 1959. – F. vagina in lateral view. *Microdorylaimus diminutivus* (THORNE & SWANGER, 1937) ANDRÁSSY, 1986 – E. vagina in lateral view.
- H-N: shapes and measurements of the *pars refringens vaginae*. H<sub>1</sub>-L<sub>1</sub>: five basic shapes of sclerotizations in lateral view – H<sub>1</sub>. trapezoid. – I<sub>1</sub>. drop-shaped. – J<sub>1</sub>. triangular. – K<sub>1</sub>. bar-shaped. – L<sub>1</sub>. semicircular. – H<sub>2</sub>-L<sub>4</sub>: three transformations of the basic shapes – H<sub>2</sub>-L<sub>2</sub>. flattened. – H<sub>3</sub>-L<sub>3</sub>. rounded. – H<sub>4</sub>-L<sub>4</sub>. arcuate.
- M: measurements of the sclerotizations (*cw* = combined width, *el* = extent along lumen) – M<sub>1,2</sub>. sclerotizations with similar shape but different orientations. – M<sub>3,4</sub>. sclerotizations with similar shape and orientation, but different extent along lumen due to effects of vulva dilators.
- N: additional features of *pars refringens vaginae* – N<sub>1</sub>. none. – N<sub>2</sub>. with striated ring. – N<sub>3</sub>. with striated disk. – N<sub>4</sub>. with striated sheath. – N<sub>5</sub>. three sclerotizations. – N<sub>6</sub>. proximal surfaces smooth. – N<sub>7</sub>. proximal surfaces jagged.
- O: various states of the *pars distalis vaginae* – O<sub>1</sub>. absent. – O<sub>2</sub>. walls straight. – O<sub>3</sub>. walls tapering. – O<sub>4</sub>. walls rounded. – O<sub>5</sub>. walls angular. – O<sub>6</sub>. walls folded. – O<sub>7</sub>. partly enveloping *pars refringens vaginae*. – O<sub>8</sub>. wholly containing *pars refringens*.

proximalis vaginae can be expected to be most prone to deformations, and of the three parts of the vagina it should be the least reliable diagnostically.

The pars refringens vaginae, when present, usually presents itself in lateral view in the form of two sclerotizations, and for simplicity's sake we will refer to these as such. It should be realized, however, that they really form a single sclerotized ring, as e.g. in the *Aporcelaimellus* sp. in Fig. 1C,D. It should also be noted that in some cases (e.g. Fig. 1N<sub>5</sub>, based on Fig. 5D in ANDRÁSSY, 1986) three or more sclerotizations have been described. We have not seen any such specimens ourselves, but we suspect one really sees lateral corners or folds of the sclerotized ring in between the two median sections. The pars refringens vaginae is undoubtedly the most variable vaginal section in structure, at the same time being probably least prone to deformation. This makes it the most promising, but also the most difficult component for characterization. We will distinguish four descriptive aspects: absence versus presence of the pars refringens vaginae; the shape of the sclerotizations; their size; and the appearance of their distal and proximal surfaces. Although the illustrations in Fig. 1 are all of vaginas terminating in a transverse vulva, the proposed terminology for each of these aspects does not depend upon the shape and orientation of the vulva, and can just as well be used when a pore-shaped or longitudinal vulva is present.

a) Determining the presence of the pars refringens vaginae is not as trivial as it seems, for apparently several published descriptions indiscriminately considered as sclerotizations both (what we define as) pars distalis vaginae and pars refringens vaginae, especially when the walls of the former were well-developed. We therefore stress the importance of a *difference in refractiveness* with the body cuticle, and also stress that the attachment sites of the dilators are not relevant to our definition. The dilators may be attached to the pars distalis vaginae, even when a distinct pars refringens vaginae is present.

b) Description of the shape of each sclerotization of the pars refringens vaginae contains two components: the basic geometric shape, and one or more of the possible transformations of this shape. The range of geometric shapes occurring is almost infinite, but the most recurrent appear to be *trapezoid*, *drop-shaped*, *triangular*, *bar-shaped* and *semicircular* (Fig. 1H<sub>1</sub>-L<sub>1</sub>). These shapes can be thought to have undergone one or a combination of three operations: flattening, rounding and bending. Thus, each geometrical shape can be further specified as, respectively, *slender* (Fig. 1H<sub>2</sub>-L<sub>2</sub>), *rounded* (Fig. 1H<sub>3</sub>-L<sub>3</sub>) and/or *arcuate* (Fig. 1H<sub>4</sub>-L<sub>4</sub>).

c) It is difficult to define reference points for measuring the size of the sclerotizations, because of their great diversity in shape. We will give an approximate indication of size by using terms such as "well-developed", "thin", etc., and also by giving two measurements: the greatest width of the sclerotizations together (measured parallel with the body cuticle and at straight angles to the entire vagina lumen: Fig. 1M<sub>1,2</sub>), and the length of sclerotization surface demarcating the lumen (measured vice versa: Fig. 1M<sub>1-3</sub>, except when the sclerotizations have clearly been rotated by the vulval dilators: Fig. 1M<sub>4</sub>). Indirectly, this usually also gives an indication of the orientation of the sclerotizations towards each other and the vagina lumen (compare Fig. 1M<sub>1</sub> and 1M<sub>2</sub>, which both feature trapezoid sclerotizations).

d) The proximal surface of the sclerotizations, i.e. the surface attached to the pars proximalis vaginae, can be *smooth* (Fig. 1N<sub>6</sub>) in appearance or *jagged* (Fig. 1N<sub>7</sub>). This must be observed exactly medially in optical section. The distal surface is usually attached immediately to the pars distalis vaginae walls (Fig. 1N<sub>1</sub>), but can also be separated by a *striated disc* (Fig. 1N<sub>3</sub>), a thin layer different in refringency from both the sclerotizations and pars distalis vaginae walls. When this disc is present, it apparently always functions as attachment site for the vulval dilators (cf. all species described in NAIR, 1973). Sometimes this striated layer does not extend over the whole distal surface of the sclerotizations, in which case we call it a *striated ring* (Fig. 1N<sub>2</sub>), or conversely it can envelope the sclerotizations nearly entirely, which is called a *striated sheath* (Fig. 1N<sub>4</sub>).

Some examples of this scheme for the pars refringens vaginae: in Fig. 1B,E the pars refringens vaginae is absent; in Fig. 1C it consists of two well-developed, rounded-trapezoid sclerotizations having smooth proximal surfaces, a combined width of 13 µm, and an extent along the lumen of 7 µm; in Fig. 1F it consists of two well-developed, rounded-triangular sclerotizations with narrow, finely jagged proximal surfaces, a combined width of 14 µm, an extent along the lumen of 8 µm, and a sclerotized ring; in Fig. 1G it consists of two delicate, very flattened, trapezoid sclerotizations with smooth proximal surfaces, a combined width of 8 µm, and an extent along the lumen of 1 µm.

The pars distalis vaginae, finally, can also vary considerably in shape and size. When the pars refringens vaginae sclerotizations (in this case usually with striated disc) are immediately attached to the body cuticle (cf. e.g. Fig. 5B;6F;8F,G in NAIR, 1973), then the pars distalis vaginae is absent (Fig. 1O<sub>1</sub>). When at least a short distal part of the vagina is formed by straight cuticle no thicker than the body cuticle (measured at straight angles to the vagina lumen), then the

pars distalis vaginae is present and its walls are *straight* (Fig. 1 O<sub>2</sub>). When the walls are thicker than the body cuticle, then we will describe them as *tapering* (Fig. 1 O<sub>3</sub>), *rounded* (Fig. 1 O<sub>4</sub>) or *angular* (Fig. 1 O<sub>5</sub>). When they are shaped in such a way that the lumen is diamond- or cross-shaped in lateral view, we will call them *folded* (Fig. 1 O<sub>6</sub>). Finally, the pars distalis vaginae walls can cover more than just the distal surfaces of the pars refringens vaginae. Depending on the degree of covering, this condition will be called *partly enveloping* (Fig. 1 O<sub>7</sub>) or *wholly containing* (Fig. 1 O<sub>8</sub>) the pars refringens vaginae. The latter two of these conditions are linked to presence of a pars refringens vaginae, the others are not. Applied to the vaginas in Fig. 1B-G, the pars distalis vaginae of Fig. 1B is as long as the pars proximalis vaginae, with slightly tapering walls; those of Fig. 1C,F,G are very short with rounded walls; and that of Fig. 1E is half as long as the pars proximalis vaginae with straight walls.

To conclude this chapter with respect to the descriptions given in this paper, we wish to clarify two more points. TEM-studies of nematode cuticles invariably reveal it to consist of more layers than the two or three seen with light microscope. In this paper, descriptions are based on light microscopy only and we therefore speak of e.g. "three-layered", using parentheses to stress that this is only appearance. Analogously, there probably is no such thing as a duplex amphid (see below; cf. e.g. THORNE, 1974 and BAQRI & KHERA, 1975). We will therefore speak of "duplex" amphids, again using parentheses to stress the deception.

#### ILLUSTRATIONS, MEASUREMENTS AND CHARACTERS

In the drawings, dashed lines are used to delineate contiguous layers (as seen with LM) in the cuticle *only* when these were thick enough to allow drawing on scale. Also, when a "layer" was interpreted as being really a lacuna, it was delineated with solid lines.

Up to ten specimens were measured per sample from the Galápagos, depending on whether enough were in good condition for measuring or not. Measurements were made with *camera lucida* and curvimeter. Mean and standard deviation (SD) were calculated only when  $n \geq 5$  and range interval  $\geq 5 \times \text{AE}$ , and are given in the format mean  $\pm$  SD (range). To prevent superfluous repetition, characters that were completely similar in all specimens studied are mentioned only in the description of the topotypes of *A. obtusicaudatus*. Uterus lengths were measured (from sphincter to proximal end of pars proximalis vaginae lumen), but only when the uteri were straight and contained neither sperm nor eggs.

#### ABBREVIATIONS

- ABW : anal body width.
- LRW : lip region width.
- OL : odontostyle length.
- VBW : vulval body width.

#### Descriptions

##### **Aporcelaimellus obtusicaudatus** (BASTIAN, 1865) ALTHERR, 1968

#### A) TYPE SPECIMENS

(Fig. 2A-J)

*Measurements* :  
Table 3.

#### *Females*

Body with weak ventral curvature that increases towards posterior end. Cuticle 3-6  $\mu\text{m}$  thick on most of body, 1-2  $\mu\text{m}$  wide on the lips, and 4-9  $\mu\text{m}$  wide on tail tip. Depending on the specimen and body region observed, the cuticle appears "two-layered" or "three-layered"; the outer layer is 1  $\mu\text{m}$  thick or less.

Lip region very strongly offset by a deep constriction, moderately sunken in, 20-22  $\mu\text{m}$  wide and 6-10  $\mu\text{m}$  high (from constriction), the lips moderately offset from each other, weakly angular with blunt papillae. Amphids stirrup-shaped, 7-10  $\mu\text{m}$  wide, without median support. A pair of somatic muscle bands ending just posterior to the fovea on the cuticle; their anterior edges distinct, suggesting a "duplex" amphid shape.

Perioral region not offset from lip contour, without visible liplets. Fixed guiding ring single, strongly plicate, at 9-12  $\mu\text{m}$  from anterior end. Odontostyle 1.05-1.25 LRW long and 5-7  $\mu\text{m}$  or 21-32 % of OL wide, its aperture occupying 54-65 % of OL. Dorsal wall and aperture rim of odontostyle straight, at an angle to one another; ventral wall straight posteriorly, obtusely angular opposite posterior of aperture, mildly arcuate anteriorly. Odontophore 1.6-2.0 OL long, with four pairs of retractors attached to it and with distinct base. Slender part of pharynx muscular, encircled by nerve ring at about one third of pharynx length, widening gradually to a posterior expansion at halfway to three-fifths of pharynx. Pharyngeal gland nuclei and orifices located as follows (n = 9) :

DO 51-55 %	S <sub>1</sub> N <sub>1</sub> 64-70 %	S <sub>2</sub> N 81-85 %	K = 58-64
DN 54-58 %	S <sub>1</sub> N <sub>2</sub> 73-76 %	S <sub>2</sub> O 84-86 %	K' = 64-68
DO-DN 2.8-3.6 %	dist. 6.6-8.1 %		

Cardia 23-37  $\mu\text{m}$  long, conical to ovoid, anteriorly encircled by a thin epithelial ring (Fig. 2G-J), posteriorly halfway to completely enveloped by intestinal cells. Vulva transverse. Vagina extending over 25-35 % of

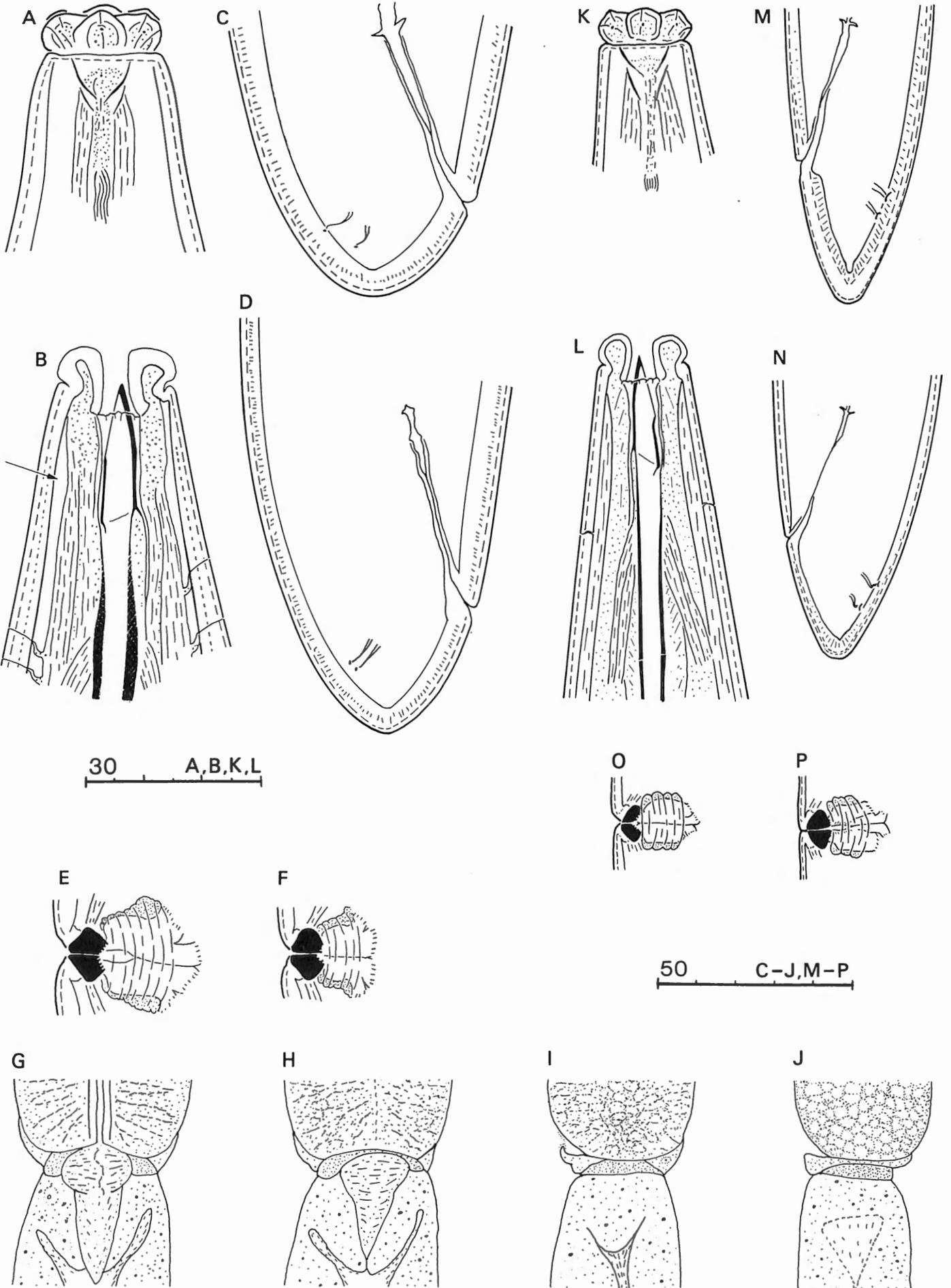


Table 3 :

Measurements (in  $\mu\text{m}$ ) of topotypes of *Aporcelaimellus obtusicaudatus* (BASTIAN, 1865) ALTHERR, 1968 and syntypes of *A. obscurus* (THORNE & SWANGER, 1936) HEYNS, 1965 and *A. amylovorus* (THORNE & SWANGER, 1936) HEYNS, 1965

Species :	A. obtusicaudatus		A. obscurus			A. amylovorus	
	Falmouth, England		Lewiston, Utah		Ogden, Utah	Buena Park, California	
Locality :	Neotype ♀	Topotypes (n=10 ♀♀)	Lectotype ♀	Syntypes (n=7 ♀♀)	Syntypes (n=7 ♀♀)	Lectotype ♀	Syntypes (n=8 ♀♀)
Character							
L ( $\mu\text{m}$ )	2415	2360 $\pm$ 138 (2185-2570)	3164	3325 $\pm$ 123 (3148-3497)	2917 $\pm$ 195 (2585-3325)	1691	1725 $\pm$ 48 (1635-1790)
Body width ( $\mu\text{m}$ )	88	84 $\pm$ 8 (72-92)	116*	121 $\pm$ 7 (113-134)*	100 $\pm$ 9 (92-117)*	55	58 $\pm$ 3 (55-62)
Pharynx ( $\mu\text{m}$ )	626	606 $\pm$ 28 (566-656)	648	697 $\pm$ 41 (649-756)	581 $\pm$ 58 (481-679)	383	392 $\pm$ 9 (382-406)
Tail ( $\mu\text{m}$ )	25	26 $\pm$ 2 (24-30)	40	38 $\pm$ 5 (30-42)	39 $\pm$ 3 (35-43)	32	35 $\pm$ 1 (32-36)
ABW ( $\mu\text{m}$ )	46	45 $\pm$ 3 (41-50)	56*	56 $\pm$ 4 (53-63)*	47 $\pm$ 5 (40-53)*	29	30 $\pm$ 1 (28-31)
a	27	28 $\pm$ 2 (25-31)	27*	28 $\pm$ 2 (26-30)*	29 $\pm$ 2 (25-31)*	31	30 $\pm$ 1 (29-32)
b	3.9	3.9 $\pm$ 0.3 (3.6-4.5)	4.9	4.7 $\pm$ 0.2 (4.5-4.9)	5.2 $\pm$ 0.3 (4.9-5.5)	4.4	4.4 $\pm$ 0.2 (4.2-4.6)
c	97	91 $\pm$ 8 (77-103)	80	88 $\pm$ 10 (78-110)	75 $\pm$ 6.5 (68-82)	53	49 $\pm$ 3 (44-54)
c'	0.54	0.58 $\pm$ 0.06 (0.50-0.67)	0.71*	0.67 $\pm$ 0.08 (0.56-0.79)*	0.86 $\pm$ 0.03 (0.71-0.98)*	1.12	1.17 $\pm$ 0.06 (1.07-1.27)
Odontostyle ( $\mu\text{m}$ )	24	24 $\pm$ 1 (22-26)	28	27 $\pm$ 2 (25-29)	22 $\pm$ 2 (19-24)	18	17-19
Od. aperture ( $\mu\text{m}$ )	15	13-16	14	14-16	11-13	12	11-12
Odontophore ( $\mu\text{m}$ )	43	43 $\pm$ 1.5 (42-46)	46	44 $\pm$ 2 (41-46)	41 $\pm$ 2 (38-43)	34	34 $\pm$ 2 (29-35)
Nerve ring ( $\mu\text{m}$ )	202	190 $\pm$ 9 (177-202)	220	219 $\pm$ 21 (184-248)	191 $\pm$ 10 (176-204)	132	137 $\pm$ 6 (130-146)
Expansion ( $\mu\text{m}$ )	323	292 $\pm$ 21 (258-323)	400	397 $\pm$ 31 (350-435)	324 $\pm$ 23 (290-369)	238	240 $\pm$ 7 (231-249)
Prerectum ( $\mu\text{m}$ )	103	103 $\pm$ 10 (90-114)	?	176-187	168 $\pm$ 40 (103-205)	83	68 $\pm$ 14 (51-84)
Rectum ( $\mu\text{m}$ )	50	47 $\pm$ 4 (40-51)	66	65 $\pm$ 5 (56-67)	51 $\pm$ 4 (47-56)	40	40 $\pm$ 1 (39-42)
Vagina ( $\mu\text{m}$ )	31	26 $\pm$ 3 (22-31)	36	37 $\pm$ 3 (34-43)	28-29	24	23 $\pm$ 1 (22-24)
V (% body)	53	53 $\pm$ 2 (49-56)	46	47 $\pm$ 1 (46-48)	48 $\pm$ 3 (43-52)	51	51 $\pm$ 1 (50-53)
G <sub>1</sub> (% body)	12	13 $\pm$ 2 (9-17)	10	9-13	13 $\pm$ 4 (6-17)	12	12 $\pm$ 3 (7-17)
G <sub>2</sub> (% body)	13	13 $\pm$ 2 (11-17)	9	7-9	15 $\pm$ 4 (10-20)	12	12 $\pm$ 3 (6-16)

\* : influenced by flattening

VBW. Pars distalis vaginae very short with rounded walls. Pars refringens vaginae present, sclerotizations well-developed, rounded-trapezoid to rounded-triangular, lining lumen for 7-9  $\mu\text{m}$  and having a combined width of 11-14  $\mu\text{m}$ , with distinctly jagged proximal surface. Pars proximalis vaginae 11-20  $\mu\text{m}$  long, wider than long to as long as wide, with sigmoid contours, encircled by sphincter over 10-16  $\mu\text{m}$ . Vulval dilators attached both to pars refringens vaginae and pars distalis vaginae. Sphincter present at junction of uterus and oviduct. Ovaries on alternate sides of intestine, with anterior ovary on right side in three females out of ten. Anterior uterus straight in six of the females measured,

111  $\mu\text{m} \pm 18$  (85-128) long, posterior uterus straight in four females, 117  $\mu\text{m} \pm 22$  (95-147) long. No females with sperm. Gravid females with up to three eggs per uterus; dimensions of twenty-one eggs : 91  $\mu\text{m} \pm 9$  (74-108) by 50  $\mu\text{m} \pm 4$  (43-57).

Prerectum of variable length : 2.3  $\pm$  0.3 (1.9-2.7) times ABW (n = 7). Rectum 0.9-1.2 times ABW (n = 9). Tail with two pairs of caudal pores, never longer than two-thirds of ABW, bluntly convex-conoid to nearly hemispherical.

Males :

Not found.

◁ Fig. 2. – *Aporcelaimellus obtusicaudatus* (BASTIAN, 1865) ALTHERR, 1968 topotype females – A. lip region externally. – B. lip region in median view (arrow points at lacuna). – C, D. tail. – E, F. vagina. – G-J. cardia at different focusing levels (G : median; J : peripheral) *Aporcelaimellus amylovorus* (THORNE & SWANGER, 1936) HEYNS, 1965 syntype females – K. lip region externally. – L. lip region in median view. – M, N. tail. – O, P. vagina.

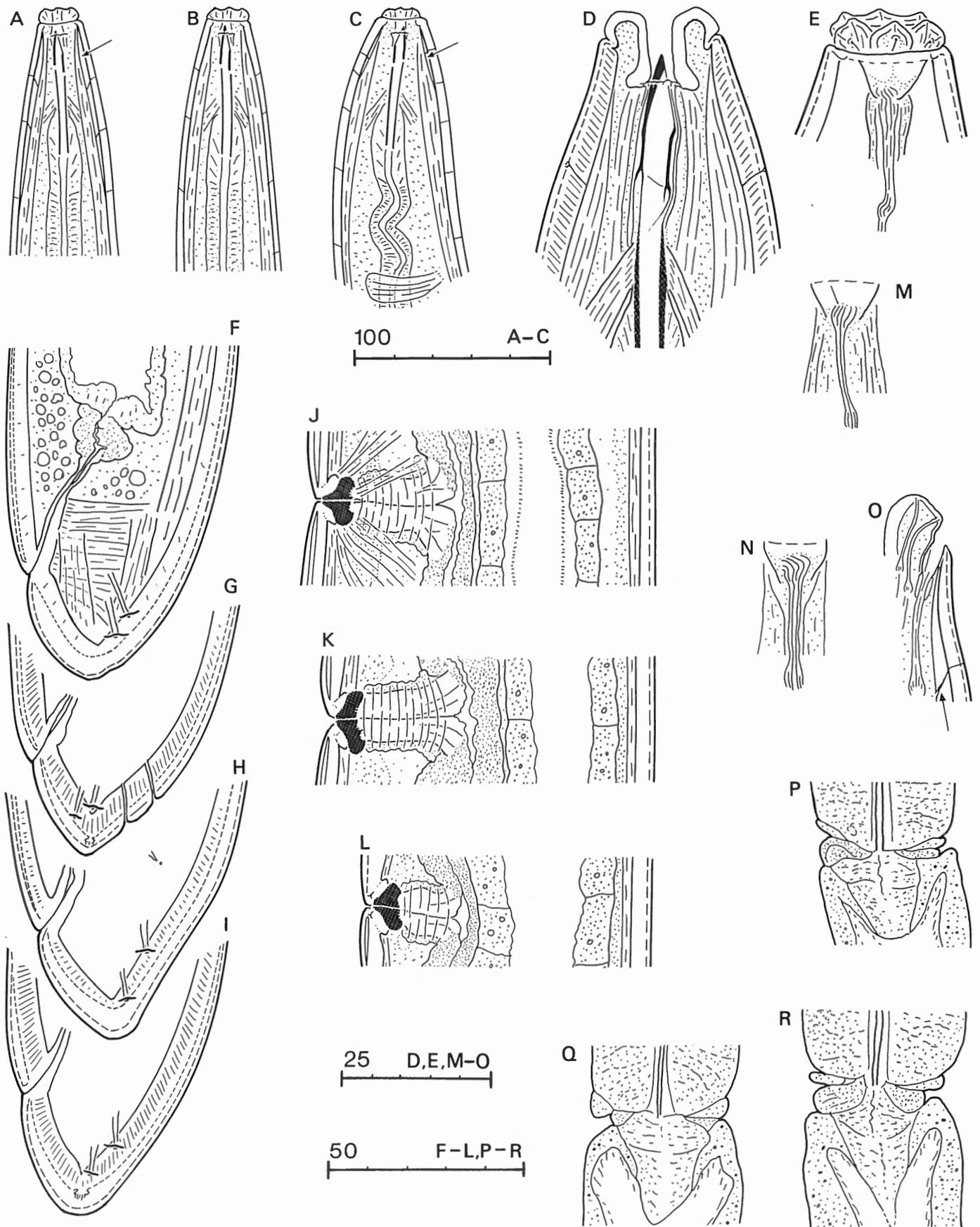


Fig. 3. – *Aporcelaimellus obtusicaudatus* (BASTIAN, 1865) ALTHERR, 1968 from the Galápagos Archipelago – A-C. influence of cervical extension or labial retraction on cuticle (arrows point at lacunae). – D. lip region in median view. – E. lip region in external view. – F-I. tails. – J-L. vaginas. – M, N. amphids in lateral view. – O. amphid in ventral view (arrow points at stretched somatic sensorial nerve in lacuna). – P-R. cardiae.

## B) SPECIMENS FROM THE GALÁPAGOS

(Fig. 3)

*Measurements :*

Table 4.

*Females*

Body weakly to very strongly ventrally curved, occasionally slightly dorsally curved towards either end of body. Cuticle "three-layered", 3-7  $\mu\text{m}$  thick on most of body, 5-13  $\mu\text{m}$  thick on tail tip. Internal layer more or less distinctly radially striated. Lip region 16-23  $\mu\text{m}$  wide and 3-8  $\mu\text{m}$  high from constriction. Amphids stirrup-shaped, 8-12  $\mu\text{m}$  wide, usually without median support, but sometimes with a very faint one (Fig. 3E) and in two cases with a distinct support in asymmetrical position (Fig. 3M). Anterior edges of lateral somatic muscle bands sometimes suggesting a "duplex" amphid shape (Fig. 3N), but usually not (Fig. 3E,M). Fixed guiding ring at 10-15  $\mu\text{m}$  from anterior end. Odontostyle 0.95-1.32 LRW long and 4-6  $\mu\text{m}$  or 19-28 % of OL wide, its aperture occupying 49-67 % of OL. Odontophore 36-48  $\mu\text{m}$  or 1.6-2.2 OL long. Pharyngeal gland nuclei and orifices located as follows (n = 40) :

DO 48-57 %       $S_1N_1$  64-72 %     $S_2N$  82-90 %    K = 55-69  
 DN 52-61 %       $S_1N_2$  72-80 %     $S_2O$  84-93 %    K' = 61-74  
 DO-DN 1.9-4.6 %    dist. 6.6-12 %

Cardia 20-43  $\mu\text{m}$  long, with anterior epithelial ring sometimes swollen dorsally (Fig. 3P), and posteriorly usually largely enveloped by intestinal cells, but sometimes only partly or not at all (Fig. 3P-R). Vagina extending over 17-46 % of VBW. Pars refringens vaginae sclerotizations strong, lining lumen for 5-9  $\mu\text{m}$  and having a combined width of 12-18  $\mu\text{m}$ , of very variable shape (more or less rounded, from trapezoid to triangular, drop-shaped or almost bar-shaped, distal edge straight or concave), with distinctly jagged proximal surface. Pars proximalis vaginae 15-29  $\mu\text{m}$  long, longer than wide, with sigmoid or straight contours, encircled by sphincter over 11-22  $\mu\text{m}$ .

Ovaries both left of intestine (n = 1), or alternating and with anterior one on left side (n = 31), or alternating and with anterior one on right side (n = 25). Anterior uterus 78  $\mu\text{m} \pm 16$  (54-121) long (n = 41), posterior uterus 79  $\mu\text{m} \pm 15$  (48-110) long (n = 37). One female with its uteri packed with sperm. Gravid females with up to two eggs per uterus; dimensions of fourteen eggs : 117  $\mu\text{m} \pm 10$  (100-135) by 53  $\mu\text{m} \pm 8$  (40-66). Prerectum of variable length : 2.1  $\pm 0.8$  (0.7-5.4) times ABW (n = 48). Rectum 1.2  $\pm 0.2$  (0.8-1.5) times ABW (n = 57). Tail never longer than one ABW, bluntly rounded but rather variable in exact shape.

*Males :*

Not found.

**Aporcelaimellus obscurus**  
 (THORNE & SWANGER, 1936) HEYNS, 1965

## A) TYPE SPECIMENS FROM LEWISTON

(Fig. 4A-F)

*Measurements :*

Table 3.

*Females*

Specimens clearly flattened, affecting VBW and ABW, but otherwise fairly well-preserved. Body with ventral curvature that increases towards posterior end. Cuticle 4-7  $\mu\text{m}$  thick on most of body (n = 6 for this and subsequent measurements, unless stated otherwise), "three-layered", 8-11  $\mu\text{m}$  thick on tail tip. Inner layer finely radially striated. Lip region 19-22  $\mu\text{m}$  wide and 6-8  $\mu\text{m}$  high (from constriction). Amphids stirrup-shaped, 9-10  $\mu\text{m}$  wide (n = 3), without median support. Anterior edges of somatic muscle bands usually distinct, suggesting a "duplex" amphid shape. Fixed guiding ring at 10-13  $\mu\text{m}$  from anterior end. Odontostyle 1.24-1.35 LRW long (n = 5) and 5-6  $\mu\text{m}$  or 22-24 % of OL wide, its aperture occupying 56-60 % of OL. Odontophore 1.7-2.0 OL long. Pharyngeal gland nuclei and orifices located as follows :

DO 49-54 %       $S_1N_1$  65-69 %     $S_2N$  84-86 %    K = 59-65  
 DN 51-57 %       $S_1N_2$  74-76 %     $S_2O$  86-87 %    K' = 65-69  
 DO-DN 2.4-3.4 %    dist. 6.8-8.6 %

Cardia 40-57  $\mu\text{m}$  long, posteriorly enveloped by intestinal cells for one to two thirds of its intra-intestinal length. Vagina extending over 31-36 % of VBW (n = 5 for this and other vaginal measurements). Pars refringens vaginae sclerotizations well-developed, trapezoid, lining lumen for 8-10  $\mu\text{m}$  and having a combined width of 16-18  $\mu\text{m}$ , with distinctly jagged proximal surface. Pars proximalis vaginae 22-32  $\mu\text{m}$  long, wider than long to as long as wide, with sigmoid contours, encircled by sphincter over 13-22  $\mu\text{m}$ . Ovaries on alternate sides of intestine, with anterior one on right side (n = 4). Anterior uterus 134-140 long (n = 4), posterior uterus 131  $\mu\text{m} \pm 7$  (123-140) long (n = 5). No females with sperm or eggs. Prerectum of variable length : 3.0  $\pm 0.6$  (1.9-3.7) times ABW. Rectum 1.2-1.5 times ABW (n = 9). Tail never longer than three-fifths of ABW, bluntly convex-conoid.

*Males :*

Not seen.

## B) TYPE SPECIMENS FROM OGDEN

(Fig. 4G-L)

*Measurements :*

Table 3.

Table 4:

Measurements (in  $\mu\text{m}$ ) of *Aporcelaimellus obtusicaudatus* (BASTIAN, 1865) ALTHERR, 1968 from the Galápagos

Character	Total range	Isla Santa Cruz			Isla Floreana		
		Sample: 4	5	10	11	13	F4
n	58	10	2	1	6	1	1
L	1530-3180	2140 $\pm$ 219 (1820-2480)	2040-2355	1975	2430 $\pm$ 334 (2015-3040)	2140	1550
Body width	67-117	83 $\pm$ 10 (67-101)	82-90	92	99 $\pm$ 9 (81-107)	89	95
Pharynx	437-697	587 $\pm$ 65 (480-662)	525-672	515	636 $\pm$ 48 (586-697)	571	501
Tail	23-43	34 $\pm$ 5 (27-41)	24-40	28	36 $\pm$ 6 (31-43)	27	29
ABW	36-65	47 $\pm$ 4 (40-54)	42-47	50	53 $\pm$ 4 (46-57)	52	50
a	18-31	26 $\pm$ 2.5 (22-31)	25-26	21	25 $\pm$ 3 (22-30)	24	16
b	3.1-4.6	3.7 $\pm$ 0.3 (3.1-4.0)	3.5-3.9	3.8	4.0 $\pm$ 0.3 (3.5-4.4)	3.7	3.1
c	42-87	63 $\pm$ 5 (53-68)	59-85	71	68 $\pm$ 9 (56-80)	79	53
c'	0.52-0.90	0.73 $\pm$ 0.08 (0.62-0.84)	0.57-0.85	0.56	0.68 $\pm$ 0.11 (0.54-0.83)	0.52	0.58
Odontostyle	20-26	22-25	22-24	24	24-25	26	21
Od. aperture	10-16	13-15	14-16	14	14-16	16	15
Odontophore	36-48	43 $\pm$ 3 (39-48)	41-45	42	46 $\pm$ 1 (44-48)	42	45
Nerve ring	133-232	178 $\pm$ 17 (153-201)	184-202	164	193 $\pm$ 15 (181-209)	183	171
Expansion	183-363	292 $\pm$ 39 (236-363)	253-306	225	311 $\pm$ 23 (275-335)	312	211
Prerectum	39-220	114 $\pm$ 38 (64-164)	74-132	58	99 $\pm$ 31 (61-150)	131	81
Rectum	39-76	57 $\pm$ 10 (42-72)	55-71	49	67 $\pm$ 6 (59-76)	63	58
Vagina	20-38	30 $\pm$ 3 (26-33)	30-32	28	35 $\pm$ 2 (33-38)	38	38
V (% body)	44-58	51 $\pm$ 2 (47-54)	52-54	46	50 $\pm$ 3 (47-55)	50	56
G <sub>1</sub> (% body)	5.8-16.9	8.3 $\pm$ 1.3 (6.4-10.5)	6.5-10.0	9.1	8.2 $\pm$ 0.5 (7.7-8.9)	10.0	8.8
G <sub>2</sub> (% body)	6.2-15.6	8.6 $\pm$ 1.4 (6.7-11.0)	6.4-9.8	9.5	8.3 $\pm$ 1.2 (6.2-9.9)	10.5	13.1
		Isla Fernandina			Isla Isabela		
		17	18	19	F1	F2	D6
n	3	10	10	10	8	3	3
L	1960-2210	2009 $\pm$ 102 (1860-2190)	2100 $\pm$ 175 (1813-2310)	1725 $\pm$ 147 (1530-1919)	2370-3180	1655-2090	
Body width	72-80	79 $\pm$ 7 (67-88)	87 $\pm$ 9 (74-104)	83 $\pm$ 7 (74-94)	98-117	80-91	
Pharynx	473-550	503 $\pm$ 20 (468-530)	511 $\pm$ 26 (473-555)	460 $\pm$ 18 (437-487)	555-692	437-510	
Tail	23-32	31 $\pm$ 4 (24-35)	28 $\pm$ 3 (23-32.5)	37 $\pm$ 5 (27-42)	30-41	25-38	
ABW	38-44	40 $\pm$ 3 (36-44)	39 $\pm$ 2 (36-43)	45 $\pm$ 3 (40-49)	54-65	39-46	
a	26-28	26 $\pm$ 1.7 (24-30)	24 $\pm$ 2.5 (21-29)	21 $\pm$ 1.6 (18-24)	24-29	21-23	
b	3.9-4.1	4.0 $\pm$ 0.2 (3.8-4.3)	4.1 $\pm$ 0.3 (3.4-4.6)	3.8 $\pm$ 0.3 (3.4-4.2)	4.3-4.8	3.8-4.5	
c	65-87	66 $\pm$ 9 (57-83)	75 $\pm$ 8 (63-85)	47 $\pm$ 5 (42-57)	77-79	55-65	
c'	0.61-0.79	0.77 $\pm$ 0.08 (0.63-0.90)	0.72 $\pm$ 0.08 (0.63-0.86)	0.82 $\pm$ 0.11 (0.61-0.95)	0.55-0.75	0.65-0.83	
Odontostyle	21-23	21.5-24	20-22	20-21	25	21-22	
Od. aperture	10-14	12-14	10-13	12-13	14-15	11-12	
Odontophore	39-40	41 $\pm$ 2.5 (37-45)	41 $\pm$ 2 (36-45)	41 $\pm$ 3 (36-46)	44-48	41-43	
Nerve ring	151-182	159 $\pm$ 9 (149-172)	161 $\pm$ 8 (149-177)	151 $\pm$ 9 (133-161)	182-232	155-167	
Expansion	242-263	275 $\pm$ 20 (247-303)	255 $\pm$ 19 (237-298)	225 $\pm$ 26 (183-265)	289-347	198-218	
Prerectum	81-82	79 $\pm$ 21 (50-103)	73 $\pm$ 21 (40-115)	134 $\pm$ 46 (90-220)	39-77	82-130	
Rectum	51-55	50 $\pm$ 4 (42-56)	50 $\pm$ 4 (45-56)	45 $\pm$ 3 (39-48)	60-72	54-56	
Vagina	23-30	29 $\pm$ 2 (26-33)	28 $\pm$ 3 (23.5-32)	31 $\pm$ 2.5 (27-35)	20-29	27-39	
V (% body)	53-58	53 $\pm$ 2 (51-56)	52 $\pm$ 2 (49-55)	47 $\pm$ 2 (44-51)	48-50	50-55	
G <sub>1</sub> (% body)	8.0-16.2	8.6 $\pm$ 1.9 (6.5-13.0)	8.5 $\pm$ 1.3 (7.1-11.0)	11.0 $\pm$ 2.8 (7.1-16.9)	5.8-14.3	10.3-11.7	
G <sub>2</sub> (% body)	5.1-9.2	10.6 $\pm$ 2.5 (6.7-14.7)	8.8 $\pm$ 1.4 (7.2-11.0)	10.6 $\pm$ 1.8 (7.1-13.2)	8.6-15.6	7.0-13.2	

*Females*

Specimens covered by droplets and clearly flattened, affecting VBW and ABW, but otherwise fairly well-preserved. Cuticle 3-5  $\mu\text{m}$  thick on most of body ( $n = 8$  for this and subsequent measurements, unless stated otherwise), 4-9  $\mu\text{m}$  thick on tail. Lip region 17-21  $\mu\text{m}$  wide and 4-8  $\mu\text{m}$  high. Amphids 8-10  $\mu\text{m}$  wide ( $n = 5$ ), with or without median support. Fixed guiding ring at 9-12  $\mu\text{m}$  from anterior end. Odontostyle 0.95-1.16 LRW long and 4-5  $\mu\text{m}$  or 21-25 % of OL wide, its aperture occupying 53-65 % of OL. Odontophore 2.0-2.4 OL long. Pharyngeal gland nuclei and orifices located as follows :

DO 49-60 %  $S_1N_1$  67-74 %  $S_2N$  84-90 %  $K = 56-64$   
 DN 55-63 %  $S_1N_2$  75-81 %  $S_2O$  86-92 %  $K' = 65-70$   
 DO-DN 2.4-4.1 % dist. 6.8-8.4 %

Cardia 17-49  $\mu\text{m}$  long. Vagina extending over 31-38 % of VBW ( $n = 4$  for this and other vaginal measurements). Sclerotizations of pars refringens vaginae well-developed, trapezoid or rounded-trapezoid, lining lumen for 6-8  $\mu\text{m}$  and having a combined width of 13-16  $\mu\text{m}$ , with distinctly jagged proximal surface. Pars proximalis vaginae 19-23  $\mu\text{m}$  long, longer than wide to as long as wide, with straight or sigmoid contours, encircled by sphincter over 12-17  $\mu\text{m}$ . Ovaries on alternate sides of intestine, with anterior ovary on right side in three females out of eight. Anterior uterus 105-112  $\mu\text{m}$  long ( $n = 2$ ), posterior uterus 106  $\mu\text{m}$  long ( $n = 1$ ). No females with sperm, seven females with one to eight eggs each, 25 eggs measuring  $103 \pm 14$  (78-122) by  $61 \pm 10$  (46-76)  $\mu\text{m}$ . Prerectum of variable length :  $2.3 \pm 0.6$  (1.6-3.4) times ABW. Rectum 0.9-1.4 times ABW. Tail never longer than one ABW.

*Males :*

Not seen.

**Aporcelaimellus amylovorus**

(THORNE & SWANGER, 1936) HEYNS, 1965

## TYPE SPECIMENS

(Fig. 2K-P)

*Measurements :*

Table 3.

*Females*

Specimens sometimes clearly flattened (VBW and ABW probably variously affected), otherwise well-preserved. Body almost straight to weakly ventrally curved. Cuticle 2-3  $\mu\text{m}$  thick on most of body ( $n = 7$  for this and subsequent measurements, unless otherwise stated), "three-layered", 5-7  $\mu\text{m}$  thick on tail tip. Inner layer finely radially striated.

Lip region 15-17  $\mu\text{m}$  wide and 5-7  $\mu\text{m}$  high (from

constriction). Amphids stirrup-shaped, 8-10  $\mu\text{m}$  wide, with median support. Anterior edges of somatic muscles usually fairly distinct, suggesting a "duplex" amphid shape. Fixed guiding ring at 8-9  $\mu\text{m}$  from anterior end. Odontostyle 0.94-1.16 LRW long and 4-5  $\mu\text{m}$  or 21-25 % of OL wide, its aperture occupying 58-63 % of OL. Odontophore 1.7-2.3 OL long. Pharyngeal gland nuclei and orifices located as follows ( $n = 8$ ) :

DO 61-62 %  $S_1N_1$  74-75 %  $S_2N$  88-89 %  $K = 59-68$   
 DN 64-65 %  $S_1N_2$  80-81 %  $S_2O$  90-91 %  $K' = 65-72$   
 DO-DN 2.2-3.3 % dist. 5.5-6.5 %

Cardia 21-27  $\mu\text{m}$  long, posteriorly enveloped by intestinal cells for one to two thirds of its intra-intestinal length. Vagina extending over 35-41 % of VBW. Pars refringens vaginae sclerotizations well-developed, rounded-trapezoid to rounded-triangular, lining lumen for 4-6  $\mu\text{m}$  and having a combined width of 8-11  $\mu\text{m}$ , with distinctly jagged proximal surface. Pars proximalis vaginae 14-16  $\mu\text{m}$  long, wider than long to as long as wide, with sigmoid contours, encircled by sphincter over 9-11  $\mu\text{m}$ . One female with anterior ovary on right side of intestine, 45  $\mu\text{m}$  long, and posterior uterus on left side, 41  $\mu\text{m}$  long. No females with sperm. Six females with eggs, none with more than one egg per uterus; dimensions of nine eggs :  $116 \mu\text{m} \pm 6$  (110-123) by  $47 \mu\text{m} \pm 2$  (44-49). Prerectum of variable length :  $2.4 \pm 0.6$  (1.6-3.1) times ABW ( $n = 5$ ). Rectum 1.3 times ABW ( $n = 6$ ). Tail never shorter than one ABW, bluntly convex-conoid.

*Males :*

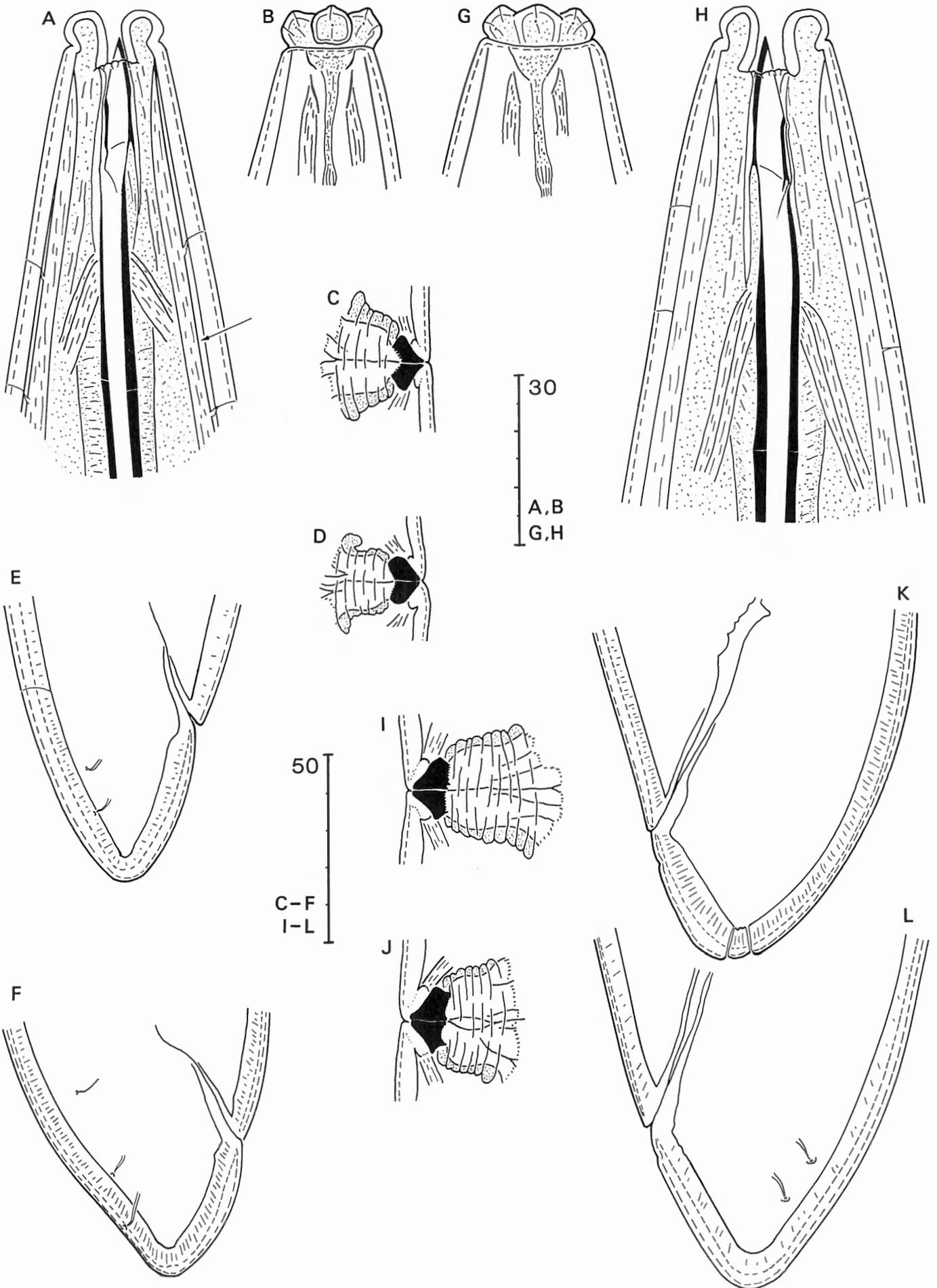
Not found.

**Discussion**

## A) VARIABILITY OF SOME CHARACTERS

Before discussing the identification and validity of species, some remarks must be made on variability. Very wide variation in a number of measurements was already reported for *A. obscurus* by TJEPKEMA *et al.* (1971), particularly for tail shape, L, a, b, c, V, odontostyle length, odontophore length and spicule length. Similar plasticity is now also apparent in the material from the Galápagos, and we furthermore found different qualitative character states — supposedly typical for different species — co-occurring within the Galápagos populations. In particular, this occurred for amphid shape, intestinal cell overlap of the cardia, and appearance of the cuticle close to the lip region. We considered these three characters to be unreliable, for the following reasons.

The structure of the cuticle in the sublabial region was used by THORNE (1974) to distinguish several species (see below) from *A. obscurus*, reporting that under



light-microscope these species have a distinctly thickened, "three-layered" cuticle in the sublabial region, compared to a "two-layered", very gradually thickening cuticle of *A. obscurus*. TEM studies of the cuticle of *A. obscurus* and/or *A. obtusicaudatus* have revealed the local presence of an infracuticle: an extra internal layer extending from the middle of the retracted odontophore to just below the amphidial aperture (LIPPENS *et al.*, 1974; GROOTAERT & LIPPENS, 1974). However, even with this additional layer the cuticle was only 5-6  $\mu\text{m}$  thick (measured on Fig. 1 in LIPPENS *et al.*, 1974), about the same as in most of our specimens, where the infracuticle was not distinguishable with the light-microscope. Furthermore, we repeatedly found specimens in several populations with the cuticle detached to varying degrees from the epidermis and somatic musculature in the sublabial region, yielding the aspect of cuticle "thickening" as drawn by THORNE (1974: compare his Figs 5C,E; 6A,D with our Fig. 3A-C).

We are confident that in our specimens this "thickening" really is a lacuna and not a layer, from several indications. Firstly, from its hollow aspect under the light microscope. Secondly, from the fact that it occurs in specimens with maximally extended neck (Fig. 3A) and again in those with contracted neck (Fig. 3C), but not in the great number of specimens in intermediate condition (Fig. 3B). This corresponds with the behaviour expected of a less contractile layer (the cuticle) enveloping a more contractile cylinder (the nematode body minus cuticle). Thirdly, the presence of a cavity between cuticle and epidermis in those specimens with "thickened" cuticle was betrayed by the innervation of the body pores in the sublabial region, each nerve being stretched out between the epidermis and the cuticle at an angle to its course in the cuticle itself (Fig. 3 O). In most of the cited figures in THORNE (1974) the body pore nerves make the tell-tale angle at the transition from "inner layer" to "middle layer". These three indications were also apparent in the topotypes of *A. obtusicaudatus* and the types of *A. obscurus* and *A. amylovorus* (Fig. 2B; 4A), and the sensitivity of the cuticle to fixation is well known (e.g. LIPPENS & GROOTAERT, 1974). From all this, we conclude that THORNE's observations were probably erroneous, mistaking lacunae for an additional layer.

Another character used by THORNE (1974) in distinction of a species (*A. porcus*) from *A. obscurus*, is the extent of overlap of the intestinal cells over the intestinal part of the cardia. This was quite variable in our specimens, especially those from the Galápagos

(Fig. 3P-R), and is rejected as diagnostic feature. It must be noted that the cardia of *Aporcelaimellus* is described with cardiac disc, but that we always found a ring instead of a true disc (Fig. 2G-J; 3P-R).

The third dubious character is the "duplex" amphid reported in some species. In all specimens examined by us, the cuticle just posterior to the fovea was attached to by a somatic muscle band on each side of the fovea. This pair of muscles can lie close against the fovea and canalis as broad bands (Fig. 3M), or the muscles can be fixed as narrow cords (Fig. 3E), neither case suggesting a "duplex" amphid shape. However, the anterior edges of the muscles can also lie slightly posterior and parallel to the rims of the fovea, resulting in a distinct "duplex" amphid shape (Fig. 3N, which is the same specimen as Fig. 3A; also Fig. 2A,K; 4B,G), and intermediate conditions occur. One specimen in ventral view revealed presence of a faintly visible "chamber" just posterior to the fovea (Fig. 3 O). Confirmation from ultrastructural studies is needed, but we strongly have the impression that the difference between "duplex" and simple shape of the amphid is due to fixation effects on the somatic muscles, rather than to the presence or absence of a true postfoveal chamber. Fig. 4B in THORNE (1974) pictures a "duplex" amphid of *A. obscurus* with the transition fovea-canalised contained in a separate chamber.

#### B) PROPOSAL OF A NEOTYPE FOR *A. OBTUSICAUDATUS*

In accordance with Article 75 of the International Code of Zoological Nomenclature (1985), designation of a neotype must be explicitly justified. The determination of the identity of *A. obtusicaudatus* is essential in clarifying the systematics of *Aporcelaimellus* because of the species' seniority, widespread occurrence and very close proximity to *A. obscurus*, type of the genus. Since no type material remains of *A. obtusicaudatus*, the requirements listed in Art. 75(b) are therefore met. Furthermore, the qualifying conditions listed in Art. 75(d) are fulfilled as follows:

- (1) – A short differential diagnosis cannot be given for *A. obtusicaudatus* because of the large number of poorly described nominal species that are similar to it. These are all listed and discussed below in section (D), which functions as an extended differential diagnosis.
- (2) & (6) – The neotype is kept separately on slide WT 2882 in the Nematode Collection of the Landbouwniversiteit, Wageningen, the Netherlands.
- (3) – There is no evidence at all to suggest that BASTIAN (1865) kept type specimens of the species he

◁ Fig. 4. – *Aporcelaimellus obscurus* (THORNE & SWANGER, 1936) HEYNS, 1965 syntype females (A-F: from Ogden; G-L: from Lewiston). – A, H. lip region in median view (arrow points at lacuna). – B, G. lip region externally. – C, D, I, J. vagina. – E, F, K, L. tail.

described. Even if he did so, these cannot have been preserved intact for well over a century.

(4) – The topotypes do not agree perfectly with the measurements given in BASTIAN (1965), who reported  $L = 2.8$  mm (vs 2.2-2.6), body  $145\ \mu\text{m}$  wide (vs 72-92), pharynx  $508\ \mu\text{m}$  long (vs 566-656) and anus  $51\ \mu\text{m}$  from posterior end (vs 24-30). However, considering both the optics available in BASTIAN's time and the large variability known to occur in species of *Aporcelaimellus* (cf. e.g. the specimens from the Galápagos and TJEPKEMA *et al.*, 1971), these differences are not considered significant.

(5) – The topotypes were collected in the autumn of 1967 from forest litter in Falmouth, Great Britain.

#### C) SPECIES ALLOCATION OF THE SPECIMENS STUDIED PROPOSED SYNONYMY OF *A. OBTUSICAUDATUS* AND *A. OBSCURUS*

Upon comparison of the different populations of *Aporcelaimellus* described here, it is evident that they are all quite closely related to one another, having a very similar cuticle, lip region, odontostyle, pharynx, cardia and female reproductive system. Allocation to separate species is much less clear, due to the variability encountered in many characters. Most measurements are quite variable in the Galápagos specimens, and there is also considerable variation in the exact vagina and tail tip morphology.

The type specimens of *A. amylovorus* differ narrowly from all others (even from Galápagos specimens with comparable body size) in three measurements: they have a shorter odontostyle ( $16-19\ \mu\text{m}$  vs  $19-26\ \mu\text{m}$ ), shorter odontophore ( $29-35\ \mu\text{m}$  vs  $36-48\ \mu\text{m}$ ) and slenderer tail ( $c' = 1.07-1.27$  vs  $0.52-0.98$ ) — although it must be noted that both the *A. amylovorus* and *A. obscurus* specimens were flattened. They also exhibit slightly smaller sclerotizations in the vagina (compare Fig. 2O,P with Fig. 2E,F; 3J-L; 4C,D,I,J), and have usually assumed a less arcuate body posture upon fixation (although there is occasional overlap with *A. obtusicaudatus*). In combination, all these slight differences suggest *A. amylovorus* to be a valid species that is extremely close to, but nevertheless separate from *A. obtusicaudatus* and *A. obscurus*. Contrary to the diagnosis of *A. amylovorus* in TJEPKEMA *et al.* (1971), there is no evidence of a significant difference in egg size.

The remaining material studied shows only the slightest of differences between populations. Thus, the topotypes of *A. obtusicaudatus* tend to have somewhat more triangular-rounded sclerotizations of the pars refringens vaginae (in the other populations more trapezoid shapes prevail) and the cuticle usually has a somewhat different aspect, without clear separation into a middle and inner layer. Also, the *A. obscurus* specimens from Lewiston have the largest odontostyles, on average, and

the animals of the Galápagos sometimes exhibit less regularly rounded tails. But on the whole, upon comparison of all these specimens with each other, and taking into account the variability reported by TJEPKEMA *et al.* (1971), we cannot find any satisfactory grounds for dividing these animals further into consistent groupings. We therefore consider *A. obscurus* to be a junior synonym of *A. obtusicaudatus*, the latter thus becoming the type species of *Aporcelaimellus*.

#### D) REVIEW OF NOMINAL SPECIES SIMILAR TO *A. OBTUSICAUDATUS*

The group of nominal species around *A. obtusicaudatus* epitomizes identification problems encountered to a lesser degree in many other nematode genera. Because no less than twenty nominal species are involved, it is quite likely that several are invalid. But on the other hand it is equally likely that some descriptions do pertain to valid species, with distinctive features that were overlooked by their discoverers. A solution to this impasse requires the re-examination of type material of all species concerned, which in this instance constitutes a formidable task. Furthermore, this group of species may well contain one or more species complexes, and some populations may be simply impossible to classify satisfactorily.

Below, a list is given of species possibly synonymous with *A. obtusicaudatus*, with a short discussion per species of the characters used in the original descriptions to differentiate them from known species. Each of these discussions is ended with an evaluation of the likelihood of (in)validity of the species concerned. As these evaluations are based solely on descriptions and not (with exception of *A. obtusicaudatus*, *A. obscurus* and *A. amylovorus*) on type specimens, we can only assess the *diagnostic* validity, i.e. whether the nominal species as described can be distinguished from *A. obtusicaudatus*. Because of this, we refrain from synonymizing species even when their descriptions do not contain any significant difference, proposing instead that in such cases the junior species be considered *species inquirenda*. Thus, while our review of the many doubtful nominal species cannot provide definite solutions, we hope that it will at least establish the extent of the diagnostic problems involving *A. obtusicaudatus* and relatives, and provide a point of departure for a re-assessment of this group. A last remark: it must be noted that, unfortunately, ranges are often omitted in TJEPKEMA *et al.* (1971), many values apparently being presented as mean + SD. This complicates comparison of their data with those of others.

##### 1) *A. amylovorus* (THORNE & SWANGER, 1936) HEYNS, 1965

As redescribed here, *A. amylovorus* can be distinguished from *A. obtusicaudatus* by the usually shorter

odontostyle (16-19  $\mu\text{m}$  vs 19-24  $\mu\text{m}$ ) and odontophore (29-35  $\mu\text{m}$  vs 36-48  $\mu\text{m}$ ), and by the proportionally longer tail ( $c' = 1.07-1.27$  vs  $0.52-0.98$ ). AHMAD & JAIRAJPURI (1982) reported a male of *A. amylovorus*, with spicules 66  $\mu\text{m}$  or 1.7 ABW long, which seems to fall at the lower end of the spicule lengths reported in TJEPEKEMA *et al.*, 1971 for *A. obscurus* (= *A. obtusicaudatus*): 98  $\mu\text{m} \pm 32$  (see also discussion of *A. obscuroides*).

Status : considered valid and distinct from *A. obtusicaudatus* on the basis of type specimens.

2) *A. duhouxi* (ALTHERR, 1963) BAQRI & KHERA, 1975 Differs from the other species of this group in the posterior vulva ( $V = 62\%$ ), the dorsally indented tail and the presence of 15 male supplements (10-11 in *A. obtusicaudatus* according to MEYL, 1960). The tail shape described by ALTHERR (1963) is rather suspect, however, because it matches the shape observed in subventral view in two of the specimens seen by us (Fig. 3G, 4K), with the "dorsal indentations" actually being the caudal pores (compare with Fig. 10c in ALTHERR, 1963).

Status : distinguishable from *A. obtusicaudatus* on the basis of published description, but re-examination desirable.

3) *A. krygeri* (DITLEVSEN, 1928) HEYNS, 1965

Based on its original description, this species differs from *A. obtusicaudatus* in its extremely squat body ( $a = 13.4$  vs  $21-40$ ) and extremely short tail ( $c = 175$  vs  $42-110$ ). Both these differences could well be due to flattening, however. The population identified as *A. krygeri* in THORNE (1974) is, as far as can be judged from its description, in no way different from *A. obtusicaudatus*.

Status : diagnostically suspect, probably synonymous with *A. obtusicaudatus* - *sp. inq.*

4) *A. microhystera* ALTHERR, 1972

This species was described (from females only) by ALTHERR (1976) as different from *A. obtusicaudatus* and *A. obscurus* because : "La forme de la queue et les dimensions de la vulve et de l'utérus s'y opposent" (p. 831 in ALTHERR, 1976). In effect ALTHERR (1976) describes a very short uterus ("25-30 % du corps au maximum" - p. 833) : in comparison, the topotypes and Galápagos specimens of *A. obtusicaudatus* have longer uteri (112-163 %, resp. 61-144 % of VBW). However, it would appear from several indications that ALTHERR actually uses the term "utérus" for what we denote as pars proximalis vaginae! Thus, calculation from the values of  $a$ ,  $G_1U$  and  $G_2U$  given for *A. microhystera* in Table 10 in ALTHERR (1976) yields uterus lengths of at least 100 % of VBW. Also, the vagina is never referred to as such, but appears to be denoted with "vulve-utérus" in his Table 10,

and "utérus" is repeatedly referred to in a context of ventro-dorsal extent in the body throughout the other descriptions in his paper. Finally, a uterus less than one third as long as a VBW seems an unlikely feature for any dorylaim, and the distinction on the basis of the "uterus" is therefore probably erroneous (the entire vagina occupies 25-35 % of the VBW in the topotypes).

With respect to the other differentiating characters mentioned by ALTHERR (1976), neither the tail shape nor the "vulva dimensions" (the latter apparently corresponding with our pars refringens vaginae) allow distinction from *A. obtusicaudatus* topotypes. While ALTHERR (1976) found considerable variation in tail shape in *A. microhystera* (with  $c' = 0.4-0.7$ ), this does include shapes encountered in the topotypes (compare his Fig. 12f,g with our Fig. 2C,D). Also, we measure an extent of 7-14  $\mu\text{m}$  and a combined width of 10-18  $\mu\text{m}$  of the sclerotizations depicted by ALTHERR (1976 : Fig. 12b-d), encompassing the dimensions and shapes found by us in *A. obtusicaudatus* topotypes (Fig. 2E,F).

Status : diagnostically indistinguishable from *A. obtusicaudatus* - *sp. inq.*

5) *A. micropunctatus* BOTHA & HEYNS, 1990

According to the diagnosis of BOTHA & HEYNS (1990), this species "can be distinguished from *A. obscurus* by the presence of radial striae over the entire body, vs very weak radial striae in the cuticle of *A. obscurus* as well as by the apparent absence of males, although males are also very rare in *A. obscurus*". The latter criterion clearly does not carry any diagnostic weight (THORNE & SWANGER, 1936 found only four males among several thousand specimens). The clarity of radial striae (and the corresponding punctations seen in the tangential plane of the cuticle) is also very suspect because this feature was quite variable within our populations from the Galápagos. In the types of *A. obscurus* and the topotypes of *A. obtusicaudatus*, radial striae were clear only in the inner layer of the tail cuticle, but in some specimens they could vaguely be seen more anteriorly.

TEM-study of *A. obtusicaudatus* revealed presence of radial, relatively electron-dense stripes in layer 6 of the cuticle (Fig. 23 in LIPPENS *et al.*, 1974; Fig. 2 in GROOTAERT & LIPPENS, 1974). These were at the time identified as lacunae, and in our opinion they may well be the ultrastructural equivalent of the radial striae under light microscope. This supports our assumption that radial striae occur generally in these *Aporcelaimellus* species, but are not always distinct with light microscope. It is likely that the visibility of the striae generally depends on conditions of preservation.

Status : diagnostically indistinguishable from *A. obtusicaudatus* - *sp. inq.*

6) *A. obscuroides* ALTHERR, 1968

According to the description of both species in ALTHERR (1968), *A. obscuroides* differs from *A. obscurus* (= *A. obtusicaudatus*) in its longer odontostyle on average (20-25  $\mu\text{m}$  vs 17-22  $\mu\text{m}$  in ALTHERR, 1968), relatively shorter tail ( $c' = 0.5-0.75$  vs 0.6-1.0), more posterior vulva ( $V = 52-56\%$  vs 46-54%) and more clearly in the males having an odontostyle 23-26  $\mu\text{m}$  long, four pairs of caudal pores (two in *A. obscurus* in Fig. 151d in THORNE & SWANGER, 1936), supplements beginning at level of proximal end of spicules (60% of spicule length further anterior in *A. obscurus* according to ALTHERR, 1968) and longer spicules (90-100  $\mu\text{m}$  "à la corde" in ALTHERR, 1968 vs 50  $\mu\text{m}$  "à la corde" in Fig. 151d in THORNE & SWANGER, 1936 according to ALTHERR, 1968). According to p.14 in THORNE (1974), *A. obscuroides* is distinctive in its "massive two-layered cuticle near the head and form of tail". Judging by his Fig. 5C, this probably should have read three-layered cuticle, because it clearly shows three cuticular layers near the lip region.

Our specimens from the Galápagos agree with *A. obscuroides* females in all measurements and in nearly all morphological characters. They resemble *A. obscurus* more in their cuticle near the lip region, with its thin middle layer, and in their exact odontostyle shape (Fig. 4A in THORNE, 1974), but the tail cuticle is clearly more reminiscent of *A. obscuroides* (compare Fig. 3b in ALTHERR, 1968 and Fig. 5D in THORNE, 1974 with Figs. 4F, M, N in THORNE, 1974).

Bringing together information from the different sources mentioned with our data, not one of the reported differences remains wholly acceptable as distinctive character between *A. obscurus* and *A. obscuroides*. Firstly, the already largely overlapping ranges of odontostyle length,  $c'$  and  $V$  lose significance upon consideration of TJEPKEMA *et al.*'s data ( $\text{♀}$  odontostyle 23.8  $\mu\text{m} \pm 2.1$ ;  $\text{♀}$  tail length 27-52  $\mu\text{m}$ , ABW 46  $\mu\text{m} \pm 8$ ;  $V = 42.1-54.7\%$ ), our measurements ( $\text{♀}$  odontostyle 19-29  $\mu\text{m}$ ;  $c' = 0.50-0.98$ ;  $V = 43-58\%$ ) and those of THORNE (1974) for his *A. obscuroides* ( $V = 47\%$ ). Secondly, the reported differences between the males are contradicted in the other papers: TJEPKEMA *et al.* (1971) report a male odontostyle length of 28.4  $\mu\text{m} \pm 3.2$ ; ALTHERR (1968) draws only two pairs of caudal pores himself (Fig. 3d,e); and Figs 151b-c in THORNE & SWANGER (1936) show that the row of supplements begins variously between 0-60% of spicule length anterior to it in *A. obscurus*. Also, these illustrations are not furnished of any scale, so that it is unclear how ALTHERR (1968) measured spicule length correctly in them, and in fact in both the illustrations of *A. obscurus* in THORNE & SWANGER (1936: Fig. 151d) and THORNE (1974: Fig. 4C) the spicule length "à la corde" is 1.5 times the ABW, while it is 1.6 times the ABW in ALTHERR (1968: fig. 3d,e) in *A. obscuroides*. TJEPKEMA *et al.* (1971) report spicule length =

98  $\mu\text{m} \pm 32$ . Thirdly, we consider the apparent differences in cuticular structure in the sublial region to be artefacts (see above). Finally, the variation in tail shape in our material and that of TJEPKEMA *et al.* (1971) greatly exceeds the reported difference between *A. obscurus* and *A. obscuroides*.

Status: diagnostically indistinguishable from *A. obtusicaudatus* - *sp. inq.*

7) *A. obscurus* (THORNE & SWANGER, 1936) HEYNS, 1965

As originally described, *A. obscurus* was fairly clearly different from *A. obtusicaudatus* in its longer, convex-conoid tail ( $c' = 0.8-1.1$  vs 0.5) and "duplex" amphid. We also calculate a greater body width from the original description of *A. obtusicaudatus* than that found in e.g. the *A. obscurus* material of TJEPKEMA *et al.* (1971) and the *A. obscurus* syntypes (145  $\mu\text{m}$  vs 59-115  $\mu\text{m}$ , resp. 92-134  $\mu\text{m}$ ), but the gap is rather small, and furthermore the topotypes of *A. obtusicaudatus* had body widths of 72-92  $\mu\text{m}$ . In fact, comparison of the types of *A. obscurus* with the topotypes of *A. obtusicaudatus* invalidates all the differences noted, and we did not find any new characters to justify retention of *A. obscurus*.

DAS (1962) described specimens identified as *A. obscurus* by Dr. THORNE, which had  $L = 1.95-2.6$  mm, odontostyle 18-24  $\mu\text{m}$ , cuticle with faint transverse striae and tail with three pairs of caudal papillae and a terminal hyaline core in the cuticle. The latter three characters do not fit with our observations, and perhaps these specimens were not really *A. obscurus*.

Status: synonymized with *A. obtusicaudatus* on the basis of type material.

8) *A. papillatus* (BASTIAN, 1865) BAQRI & KHERA, 1975

According to its original description, this species has the vulva "near the commencement of the middle third of body". This would represent a clear difference from the other species discussed here, if it were not for THORNE & SWANGER (1936), who redescribed the species on the basis of specimens with  $V = 49\%$ . No clear difference with *A. obtusicaudatus* can be found in this redescription, but this evidently does not affect the possibility that the original material belonged to quite a different species.

Status: distinguishable from *A. obtusicaudatus* on the basis of original description, but re-examination desirable.

Status of THORNE & SWANGER's material: considered to be *A. obtusicaudatus*.

9) *A. porcus* THORNE, 1974

This species "is distinctive because of the intestinal cells surrounding the cardia, and strong radial striae of the dorsally arcuate rounded tails" (THORNE, 1974).

Both the degree of cardia overlap and striation of inner cuticular layer are very variable in our specimens, and cannot be considered reliable diagnostic features.

Status : diagnostically indistinguishable from *A. obtusicaudatus* - *sp. inq.*

10) *A. pycnus* (THORNE, 1939) BAQRI & KHERA, 1975  
The male of this species is characterized by L-shaped, very long spicules (2.8 ABW in Fig. 23b in THORNE, 1939) and a row of 15, slightly spaced supplements, which allows differentiation from the males of *A. obscurus* (spicule normal, 1.6 ABW in Fig. 151d in THORNE & SWANGER, 1936; 7-13 supplements). The female, however, is not clearly distinguishable.

Status : valid, but as far as known only males distinguishable from *A. obtusicaudatus*.

11) *A. quietus* (KIRJANOVA, 1951) BAQRI & KHERA, 1975

This species appears to differ greatly from *A. obtusicaudatus* in the presence of 25 longitudinal ridges on the cuticle and in having a triangular odontostyle hardly longer than the lip region is high, i.e. 6  $\mu\text{m}$  (KIRJANOVA, 1951 : Fig. 18-5). These distinctive features are extremely suspect, however, since KIRJANOVA (1951) reports longitudinal ridges and draws triangular odontostyles for two other species, *Eudorylaimus stilus* (KIRJANOVA, 1951) ANDRÁSSY, 1959 and *A. submissus* (KIRJANOVA, 1951) BAQRI & KHERA, 1975, without reporting examination of transverse sections or mentioning odontostyle aperture. Since cuticular ridges are unknown in other *Aporcelaimellus* and *Eudorylaimus* species, it is quite probable that they did not occur in these specimens either, and that the almost-longitudinal striation pattern of the somatic musculature was interpreted as representing longitudinal ridges. The odontostyle shape was either mistaken too, or it might be resembling that of *Sectonema* species, in which case the species (though relatively very small) would have to be transferred to that genus.

Status : diagnostically very suspect - *sp. inq.*

12) *A. subsimilis* (COBB, 1893) BAQRI & KHERA, 1975  
Neither the measurements nor the description in COBB (1893a) reveal any difference between this species and *A. obtusicaudatus*. On the other hand, so few relevant data are given, that the species might just as well be synonym to several other species not belonging to the *obtusicaudatus*-group. As far as we know, no detailed description was ever given of a population determined as *A. subsimilis*.

Status : diagnostically indistinguishable from *A. obtusicaudatus* among others - *sp. inq.*

13) *A. taylori* YEATES, 1967 apud THORNE (1974)

This population probably was not *A. taylori*. THORNE's description (females only) differs from the original des-

cription (based on one female and four males) in several respects : sclerotizations present in vagina (absent in holotype), pharyngeal expansion near middle (at one third its length in types), cardia with disc (without in holotype), and muscular pharyngeal wall beginning at two odontostyle lengths posterior to odontostyle (in Fig. 5E in THORNE, 1974; at two thirds odontostyle length in type in Fig. 4A in YEATES, 1967). A fifth point is the structure of the lateral field, which was reported to contain glandular bodies (85-95 in the males) by YEATES (1967), but is not mentioned by THORNE (1974). Except for the distinctly "widened" cuticle near the lip region, no feature in his description allows distinction of THORNE's specimens from *A. obtusicaudatus*, and this character is considered artefactual. Since it was not described as a new species, we feel safe to consider THORNE's population as *A. obtusicaudatus*.

Status : considered to be *A. obtusicaudatus*.

14) *A. vanderlaani* (MEYL, 1957) HEYNS, 1965

As originally described, this species would differ from *A. obtusicaudatus* only in the simple amphid (MEYL, 1957 : Abb. 30), and as already noted we do not attach diagnostic significance to this feature. The spicules measure 60  $\mu\text{m}$  ("à la corde" ?; see discussion of *A. obscuroides*) or 1.2 ABW (measured "à la corde" in MEYL, 1957 : Abb. 32), and the male has four pairs of caudal pores (see discussion of *A. obscuroides*). The fixed guiding ring is said to be absent (MEYL, 1957) but this is evidently structurally impossible.

Status : diagnostically indistinguishable from *A. obtusicaudatus* - *sp. inq.*

15) *A. vitrinus* (THORNE & SWANGER, 1936) BAQRI & KHERA, 1975

As originally described, this species only differs clearly from *A. obtusicaudatus* in its less distinctly offset lips and lip region, while it is rather small (L = 1.6 mm), slender (a = 36) and has a short pharynx (b = 5.6) compared to the ranges of *A. obscurus* (= *A. obtusicaudatus*) in TJEKEMA *et al.* (1971 : L = 1.50-3.50 mm, a = 19.7-35.5 and b = 3.48-5.50). From *A. amylovorus* it was said to differ, again, "in the less angular lips and simple amphid" (THORNE & SWANGER, 1936). As the egg was described as nearly as long as two body widths (*ibid.*), or nearly 90  $\mu\text{m}$  (recalculated from L and a), this might also constitute a difference (eggs 110-123  $\mu\text{m}$  long in types of *A. amylovorus*). A population identified as *A. vitrinus* has also been described in TJEKEMA *et al.* (1971), but with substantial quantitative differences with the original description (cf. their discussion). They found an odontostyle length of 13.4  $\mu\text{m} \pm 0.2$ , which would constitute a clear difference with *A. obtusicaudatus*, but unfortunately the discrepancies with THORNE & SWANGER (1936) cast some doubt on their identification.

Status : distinguishable from *A. obtusicaudatus* on the basis of published descriptions, but re-examination desirable.

16) *A. williamsi* HEYNS, 1965

This species was originally described by WILLIAMS (1959), who determined it at the time as *Aporcelaimus spiralis* (COBB, 1893) THORNE & SWANGER, 1936 and did not give many details about it. The differences with *A. spiralis* were pointed out by both WILLIAMS (1959) and HEYNS (1965), the latter transferring the population as a separate species to *Aporcelaimellus*. The differences with *A. obtusicaudatus* are neither stated nor apparent from the description, with the exception of the amphid, which is simple and shallow with a distinct median support (WILLIAMS, 1959 : Fig. 15) and the cheilostome, which is apparently 8 µm wide (*ibid.*). We only have our specimens to compare the latter character with (cheilostome 4-5 µm wide), and do not consider the noted differences in amphid structure reliable.

Status : diagnostically indistinguishable from *A. obtusicaudatus* - *sp. inq.*

17) *Aporcelaimus bestiarius* IZATULLAEVA, 1967

According to the differential diagnosis, *Aporcelaimus bestiarius* differs from *Aporcelaimellus obscurus* (= *A. obtusicaudatus*) only in having a single guiding ring and proportionately shorter tail. These distinctions are erroneous, but *Aporcelaimus bestiarius* also differs in being larger (females 3.69-4.00 mm and males 4.60-5.00 mm long, versus 2.48-3.50 mm in syntypes of *Aporcelaimellus obscurus*) and in having males with 25 supplements (7-13 in *A. obscurus* according to THORNE & SWANGER, 1936). While it is not likely that this species is another synonym of *A. obtusicaudatus*, it does point towards an additional problem : the difficulties of distinguishing the genera *Aporcelaimus* THORNE & SWANGER, 1936 and *Aporcelaimellus* HEYNS, 1965.

Status : distinguishable from *A. obtusicaudatus*, mainly by males.

18) "*Dorylaimus domus Glauci*" COBB, 1893

The very brief original description of this species does not allow distinction from *A. obtusicaudatus* and other species with similar overall dimensions. THORNE & SWANGER (1936) synonymized it with *A. papillatus*, but on the basis of material that may well have misled them as to the characters of that particular species (see above).

Status : diagnostically suspect - *sp. inq.*

19) *D. ornatus* FUCHS, 1930

FUCHS (1930) assumed that *A. obtusicaudatus* and *D. ornatus* have a different lip shape and cuticle, but his drawings and description do not bear this out. His measurements (from one female) differ slightly from ours in two respects : the eggs of *D. ornatus* are 65-

67 µm long (versus 74-108 µm long in topotypes of *A. obtusicaudatus*; 78-124 µm long in syntypes of *A. obscurus*), and the pharynx is shorter ( $b = 5.9$  versus 3.6-4.5 in topotypes of *A. obtusicaudatus* and 4.5-5.5 in syntypes of *A. obscurus*). The gaps are quite narrow, and synonymy of the two species as proposed by ANDRÁSSY (1960) is probably justified.

Status : synonymized with *A. obtusicaudatus* by ANDRÁSSY (1960).

20) *D. perfectus* COBB, 1893

In general characters and measurements, no distinction can be found between the females of this species as originally described, and those of *A. obtusicaudatus*. However, a curious reference was made by COBB (1893b) to "two unicellular glands ... ; each of these was as long as the neck was wide and emptied laterally (or sublaterally) by means of an indistinct ampulla and short narrow distinct chitinous [*sic*] pore", these pores apparently being located at 5 % of the total length, or 117.5 µm, from the anterior end, i.e. well before the nerve ring (cf. Plate VI, top fig. 2 in COBB, 1893b). Also, the male was described with twenty-three supplements instead of the usual numbers reported for *A. obtusicaudatus* (10-11 in MEYL, 1960) and *A. obscurus* (7-13 in THORNE & SWANGER, 1936). Finally, males were said to be very common, while only one female was found, which is also quite aberrant from "typical" populations of *A. obtusicaudatus*. *D. perfectus* was synonymized with *A. obtusicaudatus* by ANDRÁSSY (1960), but in view of the three differences noted, this does not seem evident.

Status : distinguishable from *A. obtusicaudatus* on the basis of original description, but re-examination desirable.

21) *Eudorylaimus latus* (COBB, 1891) ANDRÁSSY, 1959

The original description of this species does not allow distinction from *A. obtusicaudatus* in general proportions and morphology, but it was described with a peculiar protrusible lip region that would, if correctly observed by COBB (1891), undoubtedly warrant a wholly separate position of this species. The current position of the species is, therefore, quite unsatisfactory : either this unlikely character was an artefact, in which case *E. latus* is probably invalid, or it was not, in which case it certainly does not belong in any described genus.

Status : diagnostically suspect - *sp. inq.*

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## References

- AHMAD, W. & JAIRAJPURI, M.S., 1982. Some new and known species of Dorylaimoidea. *Nematologica*, 28:39-61.
- ALTHERR, E., 1963. Contribution à la connaissance de la faune des sables submergés en Lorraine - Nématodes. *Annales de Spéléologie*, 18 : 54-98.
- ALTHERR, E., 1968. Nématodes de la nappe phréatique du réseau fluvial de la Saale (Thuringe) et psammiques du Lac Stechlin (Brandebourg du nord). *Limnologia*, 6 : 247-320.
- ALTHERR, E., 1972. Contribution à la connaissance des nématodes rithrostygosammiques et rithrostygoséphiques de Suède. *Revue Suisse de Zoologie*, 79 : 881-902.
- ALTHERR, E., 1976. Nématodes des eaux stygorhitrals des Alpes autrichiennes. *Revue Suisse de Zoologie*, 83 : 779-847.
- ANDRÁSSY, I., 1986. The genus *Mesodorylaimus* Andrassy, 1959 and its relatives (Nematoda : Dorylaimidae). *Acta Zoologica Hungarica*, 32 : 207-261.
- ANDRÁSSY, I., 1960. Taxonomische Übersicht der Dorylaimen (Nematoda). II. *Acta Zoologica Academiae Scientiarum Hungaricae*, 6 : 1-28.
- BAQRI, Q.H. & KHERA, S., 1975. Two new species of the genus *Aporcelaimellus* Heyns, 1965 with some remarks on the relationship of *Aporcelaimellus* with *Eudorylaimus* Andrassy, 1959 (Dorylaimoidea : Nematoda). *Dr. B.S. Chauhan Commemorative Volume* : 171-180.
- BASTIAN, H.C., 1865. Monograph on the Anguillulidae, or free nematoids, marine, land and freshwater; with descriptions of 100 new species. *Transactions of the Linnean Society of London - Zoology*, 25 : 73-184.
- BOTHA, A. & HEYNS, J., 1990. Aporcelaimidae (Nematoda : Dorylaimida) from the Kruger National Park. *Koedoe*, 33 : 27-46.
- CAVENESS, F.E., 1964. A glossary of nematological terms. Nigeria, 83 pp.
- COBB, N.A., 1893a. Plant diseases and their remedies III : Nematode worms found attacking sugar-cane. *Agricultural Gazette of New South Wales*, 4 : 808-833.
- COBB, N.A., 1893b. Nematodes, mostly Australian and Fijian. Department of Agriculture, New South Wales - Miscellaneous Publications, F. Cunninghame & Co., Sydney, 59 pp.
- COBB, N.A., 1891. *Onyx* and *Dipeltis* : new nematode genera, with a note on *Dorylaimus*. *Proceedings of the Linnean Society of New South Wales*, 6 : 143-158.
- DAS, V.M., 1962. Studies on the morphology of female *Eudorylaimus obscurus* (Thorne and Swanger, 1936) Andrassy, 1959. *Canadian Journal of Zoology*, 40 : 747-754.
- DE LEY, P. & COOMANS, A., 1990. Terrestrial Nematodes of the Galápagos Archipelago I : Three Rhabditida from Isla Fernandina. *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Biologie*, 60 : 5-22.
- DITLEVSEN, H., 1928. Land- and freshwater nematodes. Zoology of the Faroes, Copenhagen, 28 pp.
- FUCHS, G., 1930. Neue an Borke- und Rüsselkäfer gebundene Nematoden, halbparasitische und Wohnungseinmieter. Freilebende Nematoden aus Moos- und Walderde in Borke- und Rüsselkäfergängen. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere*, 59 : 505-646.
- GROOTAERT, P. & LIPPENS, P.L., 1974. Some Ultrastructural Changes in Cuticle and Hypodermis of *Aporcelaimellus* during the First Moulting (Nematoda : Dorylaimoidea). *Zeitschrift für Morphologie der Tiere*, 79 : 269-282.
- HEYNS, J., 1965. On the morphology and taxonomy of the Aporcelaimidae, a new family of dorylaimoid nematodes. *Department of Agricultural Technical Services, Entomology Memoirs*, 10 : 1-51.
- HOLMES, S., 1979. Henderson's Dictionary of Biological Terms - Ninth Edition. Longman, London, 710 pp.
- IZATULLAEVA, R.I., 1967. [New nematode species on ornamental plants in Kazakhstan]. *Izvestia Akademii Nauk Kazakhskoi SSR, seria biologicheskaya*, 2 : 45-50.
- JAIRAJPURI, M.S. & AHMAD, W., 1992. Dorylaimida - Free-living, Predaceous and Plant-parasitic Nematodes. E.J. Brill, Leiden, 458 pp.
- KIRJANOVA, E.S., 1951. Nematody pochvy kholkovogo polja i theliny v Golodnoj step (Uzbekistan). *Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR*, 9 : 625-657.
- LIPPENS, P.L., COOMANS, A., DE GRISSE, A.T. & LAGASSE, A., 1974. Ultrastructure of the anterior body region in *Aporcelaimellus obtusicaudatus* and *A. obscurus*. *Nematologica*, 20 : 242-256.
- LIPPENS, P.L. & GROOTAERT, P., 1974. A routine method for mounting nematodes in resin with high refractive index. *Nematologica*, 19 (1973) : 562-563.
- MEYL, A.H., 1957. Beiträge zur freilebenden Nematodenfauna Brasiliens. II. Weitere neue oder wenig bekannte Nematodenarten. *Kieler Meeresforschungen*, 13 : 125-133.
- MEYL, A.H., 1960. Die freilebenden Erd- und Süßwasser-nematoden (Fadenwürmer). Die Tierwelt Mitteleuropas I, Verlag von Quelle & Meyer, Leipzig, 164 pp.
- MOUNPORT, D., BAUJARD, P. & MARTINY, B., 1991. Ultrastructure de la cuticule et de la région vaginale de *Scutellonema bradys*, *S. cavenessi* et *S. clathricaudatum* (Nematoda : Hoplolaimidae). *Revue de Nématologie*, 14 : 261-275.
- NAIR, P., 1972. The genus *Axonchium* (Nematoda : Belondiriidae) II. Typical species. *Nematologica*, 18 : 514-554.
- NAIR, P., 1973. The genus *Axonchium* (Nematoda : Belondiriidae) III. Species with vaginal sclerotization (part 1). *Nematologica*, 19 : 169-189.
- SEINHORST, J.W. & KOZLOWSKA, J., 1975. The muscles of the vagina and the ovejector in *Longidorus caespiticola*. *Nematologica*, 20 (1974) : 308-322.
- THORNE, G., 1939. A Monograph of the Nematodes of the Superfamily Dorylaimoidea. *Capita Zoologica*, 8 : 1-261.
- THORNE, G., 1974. Nematodes of the Northern Great Plains - Part II - Dorylaimoidea in part (Nematoda : Adenophorea). *Technical Bulletin, South Dakota State University, Agricultural Experiment Station*, 41 : 1-120.

THORNE, G. & SWANGER, H.H., 1936. A Monograph of the Nematode Genera *Dorylaimus* Dujardin, *Aporcelaimus* n.g., *Dorylaimoides* n.g. and *Pungentus* n.g. *Capita Zoologica*, 6 : 1-225.

TJEPKEMA, J.P., FERRIS, V.R. & FERRIS, J.M., 1971. Review of the Genus *Aporcelaimellus* Heyns, 1965 and Six Species Groups of the Genus *Eudorylaimus* Andr assy, 1959 (Nematoda : Dorylaimida). *Research Bulletin, Purdue University, Agricultural Experiment Station*, 882 : 1-52.

WILLIAMS, J.R., 1959. Studies on the nematode soil fauna of sugar cane fields in Mauritius. 3. Dorylaimidae (Dorylaimoidea, Enoplida). *Occasional Papers, Mauritius Sugar Industry Research Institute*, 3 : 1-28.

YEATES, G.W., 1967. Studies on nematodes from dune sands 6. Dorylaimoidea. *New Zealand Journal of Science*, 10 : 752-784.

ZIEGLER, H.E., 1909. Zoologisches W rterbuch. Gustav Fischer, Jena, 645 pp.

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