A reappraisal of Tylenchina (Nemata). 3. The family Tylenchidae Örley, 1880 (1)

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SUMMARY

The family Tylenchidae contains those tylenchs with the relatively shortest, not overlapping oesophagus and shortest, delicate stylet. Female reproductive system predominantly monodelphic, prodelphic, rarely amphidelphic. Tail long, conoid to filiform. Caudal alae adanal, small. It is the only family where amphidial apertures can be on the lateral side of the head and where the anterior conical part of the stylet can be much shorter than the posterior cylindrical part. As subfamilies we recognize : Tylenchinae, Ecphyadophorinae, Tylodorinae; Atylenchinae and Boleodorinae. Four families are synonymized with the Tylenchidae and ten subfamilies are synonymized with the five subfamilies mentioned.

RÉSUMÉ

Réévaluation des Tylenchina (Nemata). 3. La famille des Tylenchidae Örley, 1880

La famille des Tylenchidae comprend les Tylenchides présentant : un œsophage très court et ne recouvrant pas distalement l'intestin, un stylet fin et très court, un système reproducteur femelle très généralement monodelphique, prodelphique, plus rarement amphidelphique; queue longue, conoïde à filiforme; ailes caudales adanales, peu développées. C'est la seule famille où les ouvertures amphidiennes peuvent être situées sur le côté de la région labiale et où le cône du stylet peut être nettement plus court que la hampe. Les sous-familles reconnues valides par les auteurs sont : Tylenchinae, Ecphyadophorinae, Tylodorinae, Atylenchinae et Boleodorinae. Quatre familles sont synonymisées avec les Tylenchidae et dix sous-familles avec les cinq sous-familles citées.

An historical review of the Tylenchidae was published in 1983 (Raski & Maggenti, 1983) which traced the changing concepts of that taxon from the time Örley (1880) first proposed it. There were few subfamilies and genera in Tylenchidae until recent years. In fact Thorne's (1949) proposal for Tylenchida had three subfamilies in the Tylenchidae only one of which, Tylenchinae, remains in this family. There were, of course, some more genera and subfamilies in the Neotylenchoidea that are now being transfered to the Tylenchidae, but even taking those into account there were few such high categories in those days.

Since the 1940's there has been a tremendous increase in proposals for new genera, subfamilies and families taxa. These have been proposed in Tylenchidae as well as in other families which must be reviewed as possible members of Tylenchidae. As examples, Antarctenchinae was proposed by Spaull (1972) as a subfamily in the Dolichodoridae and later transfered to Boleodoridae (Brzeski & Sauer, 1982); Campbellenchinae in the Tylodoridae (Wouts, 1977); Pleurotylenchinae first placed in the Atylenchidae (Andrássy, 1976) later transfered to Tylodoridae (Wouts, 1977); Psilenchinae originally placed in Tylenchidae (Paramonov, 1968) later transfered to Boleodoridae (Brzeski & Sauer, 1983); similarly Boleodorinae first proposed in Neotylenchidae (Khan, 1964) transfered to Tylenchidae (Geraert, 1971) and finally to Boleodoridae (Brzeski & Sauer, 1983); Ecphyadophorinae and Atylenchinae each had separate family status as well.

(1) This article is part of a study on the classification of Tylenchina by the present authors and R. Fortuner (CDFA, Sacramento), M. Luc (ORSTOM, Paris) and A. R. Maggenti (University of California, Davis).

Family Tylenchidae Örley, 1980

= Atylenchidae Skarbilovich, 1959
= Ecphyadophoridae Skarbilovich, 1959
= Boleodoridae Khan, 1964
= Tylodoridae Paramonov, 1967

TYPE SUBFAMILY :

Tylenchinae Örley, 1880
= Dactylotylenchinae Wu, 1969
= Duosulciinae Siddiqi, 1979 syn. n.

OTHER SUBFAMILIES :

Atylenchinae Skarbilovich, 1959
= Aglenchinae Siddiqui & Khan, 1983 syn. n.
= Antarctenchinae Spaull, 1972 syn. n.
= Pleurotylenchinae Andrássy, 1976
Ecphyadophorinae Skarbilovich, 1959
= Ecphyadophoroidinae Siddiqi, 1986 syn. n.
= Epicharinematinae Maqbool & Shahina, 1985 syn. n.
Boleodorinae Khan, 1964
= Basiriinae Decker, 1972
= Leipotylenchinae Sher, 1974 syn. n.
= Psilenchinae Paramonov, 1967
Tylodorinae Paramonov, 1967
= Campbellenchinae Wouts, 1978
= Eutylenchinae Siddiqi, 1986 syn. n.

Description of the family Tylenchidae

Small (from 0.33 mm) to medium (up to 1.3 mm) sized, a few much larger; most always slender, vermiform in shape. Body marked with many transverse striae (some species appear smooth when seen by light microscopy but some striae have been found in every case where study by SEM has been possible). Lateral field with 0, 2, 3, 4, 6 or multiple longitudinal lines (sometimes so delicate or shallow to be seen only by SEM). Lip region usually elevated, rounded; transverse striae usually extend up onto labial region, some species with smooth labial region. Labial framework delicate, weakly developped (moderately developed in *Antarctenchus*). Stylet mostly small (3 µm-20 µm), delicate, with distinct basal knobs (rarely without knobs, a few species with long to very long stylet). Conical part of stylet shorter, as long as or longer than posterior part. Amphid apertures quite variable; mostly elongated slits extending posteriad laterally, or arc-shaped to rounded pits on labial plate; rarely small oblique slits on labial plate. Four cephalic sensillae or remnants thereof present on some species. Oral disc or plate sometimes distinctly elevated, rounded; rarely six-lobed *(Basiria)* with evidence of six (inner?) labial papillae. Deirids present or absent. Phasmid-like structures present on some species, usually advulval and dorsad near lateral field; small, rounded, covered by cuticle, not an aperture; rarely pore-like, on tail *(Antarctenchus, Atetylenchus)*. Procorpus elongate; median bulb slender-spindle-shaped, apparently non-muscular in many; rounded, muscular well-developed in others; valvular apparatus variously developed. Isthmus long, slender; oesophageal glands, symmetrically swollen, usually pyriform rarely with short irregularly-lobed overlap of intestine (except *Epicharinema* and some *Cephalenchus*). Small cardia usually projecting into intestine. Excretory pore usually near hemizonid and nerve ring at isthmus, rarely more posteriad; occasionally exceptional in prominent cuticularization. Spermatheca small or large, rounded, ovate or elongated; axial or offset; sperms small (less than 2 µm), rounded. Female reproductive system single, anteriorly directed; rarely two, amphidelphic *(Antarctenchus, Atetylenchus, Psilenchus)*. Uterus quadricolumellar. Post-uterine branch usually present, shorter than one vulval body diameter (VBD); sometimes lacking. Spicules slender, ventrally arcuate, cephalated; gubernaculum simple, trough-shaped. Caudal alae usually adanal; never extending to terminus; rarely asymmetrical (one side, usually the right one, shorter than other); occasionally reduced *(Polenchus)* or totally lacking *(Miculenchus)*. Tail elongate-conoid, mostly narrowing to long slender, filiform, even hair-like outline, similar in both sexes. Sexual dimorphism on labial plate and amphidial apertures sometimes present.

Diagnosis

Tylenchoidea. Usually slender, elongate, small species. Sexes similar. Stylet usually small, delicate. Oesophagus with slender procorpus, median bulb more or less developed; long, slender isthmus, oesophageal glands symmetrically arranged, pyriform, rarely with slight overlapping of intestine. One female genital branch, anteriorly developed; rarely two branches; columned uterus with four rows. Tail long, conoid to filiform. Caudal alae adanal, small, occasionally lacking.

Relationships

Most of the characteristics of the species of Tylenchidae conform with the definition of primitivity as covered in Luc *et al.* (1987) : small stylet; delicate labial framework; amphid openings from small to elongate, sinuous or straight extending posteriad longitudinally; median bulb spindle shaped, small, delicate or rounded, muscular; oesophageal glands symmetrically arranged, pyriform; tail elongate, long. Little is known of the life history of most species but in so far as known they have no specialized cycles, resting or resistant stages. Yet it is one of the most diverse of the Tylenchina; apparently

actively evolving in some characters such as the amphid moving from large elongate post labial varying to arc-shaped or oval pits limited to the labial plate or even small elliptical apertures near the oral opening *(Miculenchus, Ecphyadophora)* with many links and relationships with other groups (i.e. *Tylodorus* to the dolichodorids; *Filenchus* to the anguinids, etc.).

It is most closely related to the Anguinidae which were considered part of the Tylenchidae until recent years (Siddiqi, 1971) and differ by the small elliptical amphids in Anguinidae, which also have elongated, axial spermatheca, sperms large with prominent cytoplasm, long post-uterine branch (more than two body diameters at vulva level).

Comments on morphology of Tylenchidae

LIP AREA (Fig. 1)

All studies on the sensillae in the Tylenchida head have proved that within the Tylenchida the same basic pattern (De Coninck, 1942) as in all nematodes is present : six internal labial, six external labial, four cephalic and two amphids. In most Tylenchida, however, several of these sensillae have no opening to the outside but the nerve endings are found close to or within the head cuticle (De Grisse, 1977). We can assume that the prototylench had the four circles of sensillae all showing at the outside and with the amphidial apertures as the most external ones : a situation present in most free-living nematodes. None of the tylenchs shows that pattern, in all tylenchs that have been studied the six external labial sensillae end within the head cuticle or close to it. The tylenchs closest to the original pattern are found within the Tylenchidae : *Macrotrophurus, Psilenchus, Atetylenchus, Basiria* and relatives with large slit-like apertures on the lateral side of the head.

The remaining Tylenchidae show a different arrangement and by the SEM pictures some grouping can be proposed (Fig. 1).

I. A first group shows a laterally elongated, undivided front plate that carries all the sensillae; the amphidial apertures are entirely within the plate and the four cephalic papillae (if visible) are more towards the outside. In a few species the six internal labial papillae (apparently without pores) can be observed in a symmetrical arrangement around the central mouth opening (= a very small dorsoventral slit). Mid-dorsal and mid-ventral the plate is more or less constricted.

Such an oral plate (here identical to labial plate) is only found in the Tylenchidae, in no other tylench does the front plate contain the amphidial apertures and if the front plate is elongated, then the elongation is dorsoventral (*Triversus* Sher, 1974 and *Amplimerlinius icarus*, " belonolaimids ", have, however, a somewhat similar en-face view).

Genera with this labial plate are : *Aglenchus, Coslenchus, Antarctenchus, Atylenchus* (with large cephalic setae).

II. A second group differs because the amphidial apertures are not confined to the oral plate but continue on the lateral side as longitudinal slits; in some these slits are only on the lateral side *(Irantylenchus).* The region immediately surrounding the mouth opening can be slightly raised but there is no oral disc. The end-on view can be quadrangular or dorso-ventrally flattened.

Genera belonging to this group : *Irantylenchus, Tylenchus, Malenchus* (the entire head is dorso-ventrally flattened), *Filenchus* (several species now included in *Filenchus* have the amphidial apertures within the oral plate).

III. A third group has slit-like amphidial apertures confined to the oral plate but the slits are dorso-ventrally directed.

Genus *Miculenchus* and some species of *Filenchus* belong to this group.

IV. A fourth group has an offset oral disc, the head is dorso-ventrally flattened; the amphidial aperture is very long and mostly sinuous, it starts immediately or close to the oral disc and continues longitudinally on the narrow lateral side of the head.

Genera belonging to this group : *Lelenchus, Ecphyadophoroides, Epicharinema.*

V. A fifth group has also an offset oral disc, the amphidial slits start immediately at the oral disc, they are laterally directed but are only found on the front end of the head, the amphidial apertures are surrounded by a plate that bears the four cephalic papillae (if visible), that plate is constricted dorso-ventrally to a varying degree, the constriction is extreme in *Cephalenchus* so that four separate lobes are formed, in *Eutylenchus* there is a cleft and in *Tylodorus* there is only a shallow constriction.

Genera belonging to this group : *Cephalenchus, Tylodorus, Eutylenchus* (with large cephalic setae), *Campbellenchus. Dolichodorus* species of which SEM pictures are available show a similar head. *Gracilancea* differs slightly from the foregoing ones because the amphidial apertures are rounded.

VI. A sixth group, quite distinct, is that of the Boleodorinae. Labial plate undivided, more or less quadrangular; four prominent cephalic papillae dome-shaped, outside of anterior surface, usually surrounded by a depression. Amphidial apertures start between or outside the four cephalic papillae and are simple oblique slits or have an inverted V-shape. There is a perioral depression bearing six papillae. [Genera included : *Boleodurus, Neopsilenchus, Basiria, Psilenchus* and *Basirienchus;* also included : *Atetylenchus* and *Neothada* (amphidial apertures smaller)].

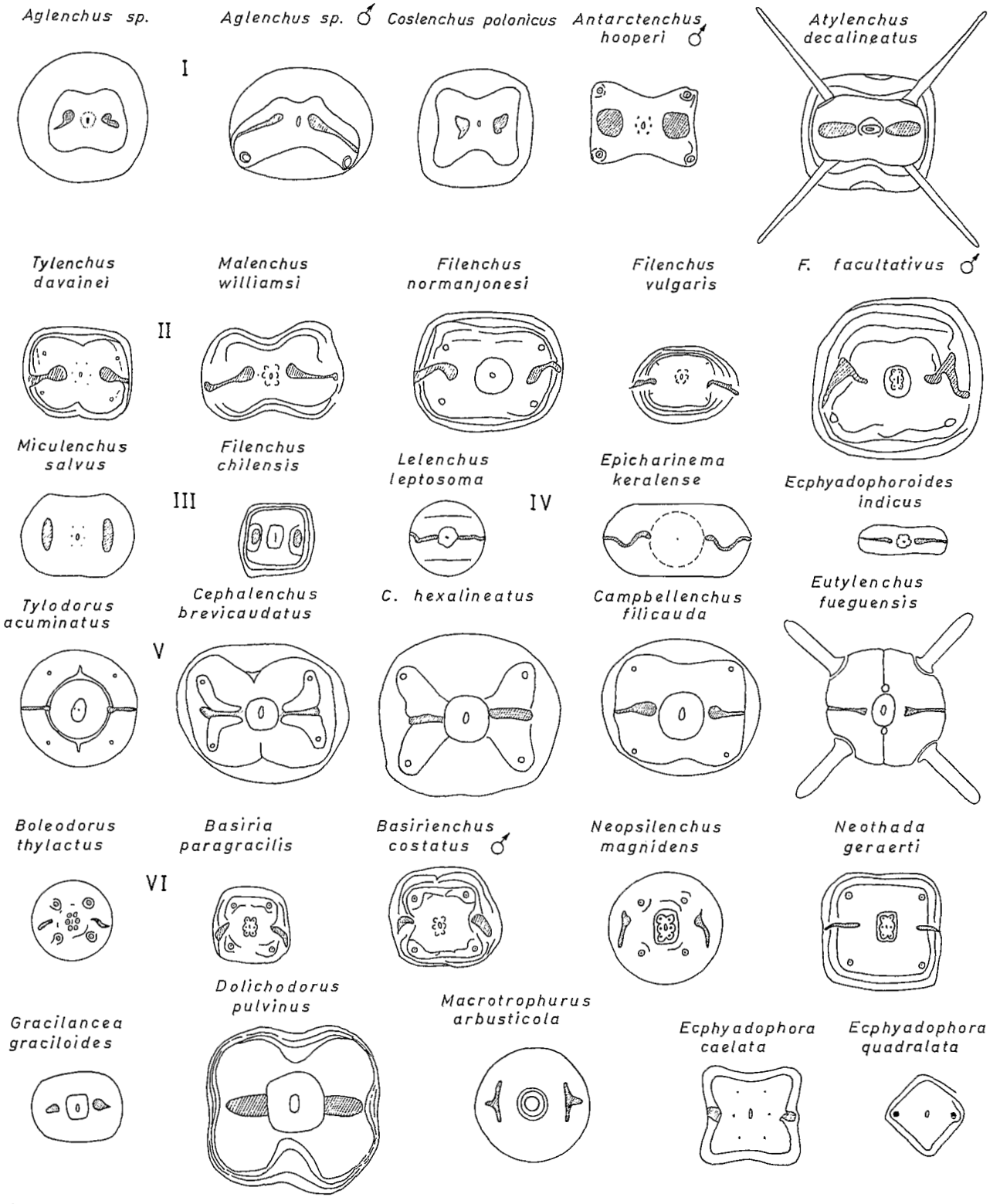

Fig. 1. Comparison of *en-face* views of several Tylenchidae; drawings are made from published SEM-photographs, some of them are schematised so scales have not been added. All head arranged the same way, where known, the ventral side is downwards, amphidial apertures are dashed.

VII. Standing apart are *Macrotrophurus* with a ring-like disc and large T-shaped amphidial apertures (Sher & Bell, 1975; De Grisse, 1977) and *Ecphyadophora* with very small pore-like amphidial apertures.

On the anterior end of several males belonging to various genera *(Atetylenchus, Tylenchus, Filenchus, Aglenchus, Coslenchus)* two papillae on the ventral side are extremely well developed. These are probably two of the four cephalic ones.

Morphometric relations

A. *The oesophagus length-body length relationship*

Geraert and Crappé (1981) pointed out that the Tylenchidae can be characterized by a proper oesophagus/body relationship (not ratio b), significantly different from the other families of the Tylenchida; it was also shown that *Antarctenchus, Gracilancea, Atetylenchus, Macrotrophurus, Sauertylenchus* and *Tylodorus* are within the prolongation of the Tylenchidae line (from the SEM view *Sauertylenchus* is considered to belong to the " belonolaimids ").

A closer examination of the genera usually considered as Tylenchidae revealed that most genera have indeed a very similar relationship with one exception : *Malenchus. Malenchus* has a slightly longer oesophagus than species of other genera with a similar body length; for species with a body length below 0.5 mm the b-value can even be expressed as a ratio, for *Malenchus* this ratio is 4.82 ± 0.47 and for *Aglenchus* and *Coslenchus* it is 5.60 ± 0.32.

B. *The stylet*

Geraert and Crappé (1981) found that the Tylenchidae and Anguinidae form a distinct group within the Tylenchida when the relationship body length/stylet length was considered : they have the shortest stylets.

Study of the relationship between the two stylet parts (for which the symbol m is used) revealed that all species of a certain, well established genus have a similar relationship and that a definite grouping of genera can be done :

— *genera with the conical part much smaller than the cylindrical part* (conical part about 1/3 of total stylet length : m = 30-40 %) : the genera of the Boleodorinae, *Lelenchus, Ecphyadophora, Ecphyadophoroides, Malenchus, Irantylenchus, Filenchus, Miculenchus.*

— *genera with the conical part about equal to the cylindrical part* i.e. m = 40-55 % : closer to 40 % in *Atylenchus, Aglenchus, Coslenchus,* and closer to 50 % in *Tylenchus, Gracilancea, Cephalenchus, Eutylenchus, Epicharinema.*

— *genera with conical part larger than cylindrical part* i.e. m more than 55 % : *Macrotrophurus, Tylodorus.*

C. *The V'-relationship*

In Geraert (1979) it was concluded that in some long-tailed species the vulva position is better correlated with the distance from head to anus (V') than with the body length (V).

The study of V' in several genera with many species revealed that this V' is rather constant within a genus and different among the genera.

Tylenchus has a V' of 76.8 ± 3.1; *T. butteus* Thorne & Malek, 1968 and *T. sandneri* Wasilewska, 1965 have much higher V' values of 82 and 85 %; they were considered by Andrássy (1979) as *Tylenchus* species but because of their short conical stylet part they are transferred to *Filenchus.*

Malenchus has a V' of 79.9 ± 1.7; *M. piauhyensis* Monteiro, 1974 considered by Brzeski (1982) as a synonym of *Ottolenchus facultativus* (Szczygiel, 1964) Brzeski, 1982, was the only one in Andrássy's (1981) list with an exceptionally high V'-value of 83.5 %.

Aglenchus and *Coslenchus* have a V' of 80.6 ± 1.4.

Cephalenchus has a much more posterior V' of 83.6 ± 2.0; in Geraert (1968) a V' of approximately 84 was calculated.

So it is obvious that the afore mentioned genera can be characterized by their V' value; unfortunately not every genus has a typical relation : the species with a body length above 0.5 mm have generally a more anterior V' (78.2 ± 2.1) while the shorter species have a more posterior V' (82.5 ± 2.8).

Female reproductive system (Fig. 2)

In all females where the arrangement of the several cells of the female reproductive system could be studied we found the " crustaformeria " cells of the uterus in four rows, the so-called quadricolumella of Wu (1958, 1967). The very thin Ecphyadophorinae could have a different arrangement but because of this thinness we could not make a definite statement.

Observations by Geraert (1981) mentioned that in *Filenchus* the uterus is tricolumellar, but these observations have not been confirmed.

The arrangement of uterus and spermatheca cells can be used to group some genera :

1) in *Eutylenchus, Cephalenchus, Campbellenchus* and *Tylodorus* we find a long post-vulval and pre-vulval uterine sac, a distinct transition zone of several cells, the crustaformeria-part of the uterus with about five or six cells in each of the four rows, another transition zone of several cells, a non-offset elongated spermatheca, oviduct, ovary.

A similar arrangement is found in the didelphic *Psilenchus.*

2) in most other genera we find a generally smaller structure with three or four cells in each of the four

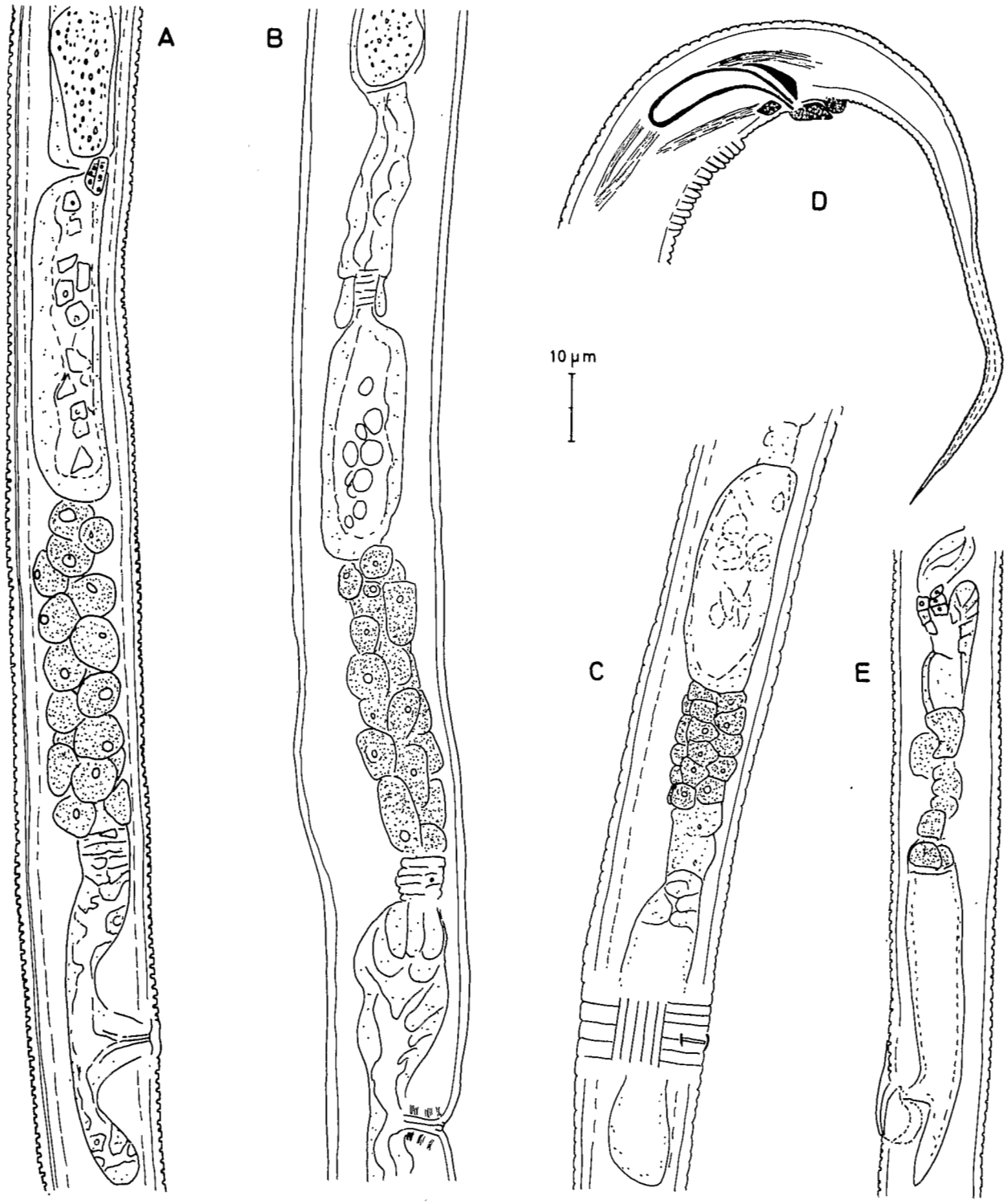

Fig. 2. Genital system of some Tylenchida. A-C : Comparison of the female system of *Eutylenchus fueguensis* (A), *Tylodorus acuminatus* (B) and *Cephalenchus brevicaudatus* (C); D-E : *Atylenchus decalineatus* : D : male with large cloacal protuberances; E : female with longitudinal vulval flap, large pre-vulval uterine sac, empty, offset spermatheca. In the drawings of the female genital system the columned cells of the uterus have been stippled.

uterus rows and with a spermatheca usually offset, sometimes in line.

Vulva and vagina also give useful characteristics :

— a thick vaginal wall, a vulva with epiptygmata and lateral flaps (" dikes " when smaller; see Andrássy, 1981) is found in *Aglenchus, Coslenchus* and *Malenchus;*

— a longitudinal flap covering the vulva is found in *Pleurotylenchus* and in *Atylenchus;*

— a vulva outside the mid-ventral line is found in many *Cephalenchus* species.

Usually the vulva is a simple transverse slit, and the vagina a thin walled structure.

Subfamilies and genera in Tylenchidae

Many of the about 30 genera can be easily grouped into a few subfamilies; as usual others are more difficult to place. This is particularly true for the type subfamily Tylenchinae : the genera left in this subfamily do not have any particular character(s) that unite them except that they do not have any particular character(s) at all.

The type-genus of the Ecphyadophorinae is *Ecphyadophora,* a genus with a quite unique end-on view, *Ecphyadophoroides* has a different head; *Lelenchus* has been considered to belong in this subfamily because its head is very similar to that of *Ecphyadophoroides. Lelenchus* shares, however, many characteristics with *Filenchus* from the Tylenchinae.

The Tylodorinae, Atylenchinae and Boleodorinae are distinct groupings based on many characteristics.

Genera difficult to include are : *Gracilancea* (perhaps belonging to the Atylenchinae), *Macrotrophurus* and *Luella.*

The subfamily Tylenchinae Örley, 1880

= Dactylotylenchinae Wu, 1969
= Duosulciinae Siddiqi, 1979

This subfamily contains the Tylenchidae that are most similar to the type genus *Tylenchus.* The genus *Filenchus* is not always easy to distinguish from *Tylenchus* and several species considered to be *Tylenchus* by Andrássy (1979) belong to *Filenchus* (cf. Raski & Geraert, 1987); moreover not all species considered to be *Filenchus* are well known. In that recent review we synonymize several genera with *Filenchus,* amongst them *Ottolenchus. Ottolenchus* and *Malenchus* have not been easy to differentiate and several transfers have been made between them. Other genera that can be included are *Miculenchus, Irantylenchus, Polenchus* and *Allotylenchus.* All these genera show, however, characteristics that separate them from the rest, moreover our knowledge about some of these genera is rather restricted.

So, we will not add a detailed diagnosis (mentioning the exceptions) but only a short one.

DIAGNOSIS

Tylenchidae. Head not or slightly offset, amphidial openings variously shaped (with two major types, a longitudinal and a transverse slit), usually no distinct oral disc. Stylet small to very small, usually with knobs. Female genital tract short with only three or four cells in each of the four rows of the crustaformeria part of the uterus, spermatheca offset or not. Tail elongated, top variously formed.

TYPE GENUS : ***Tylenchus*** Bastian, 1865.
= *Aerotylenchus* Fotedar & Handoo, 1979
(*Areotylenchus* in Fortuner, 1984)
Type species :
T. davainei Bastian, 1865
Other species :
T. arcuatus Siddiqi, 1963
T. capitatus Andrássy, 1979
T. elegans de Man, 1876
T. hayati Khan, 1985
T. kashmirensis Mahajan, 1973
T. kirjanovae Andrássy, 1954
T. maius Andrássy, 1979
T. neoandrassyi nom. nov.
= *T. andrassyi* Fotedar & Kaul, 1985
nec *T. andrassyi* Szczygiel, 1969
T. neodavainei Wu, 1969
T. rex Andrássy, 1979
T. ritae Siddiqi, 1963
T. rohtangus Khan, 1985
T. safroni (Fotedar & Handoo, 1979) Siddiqi, 1986
T. sherianus Andrássy, 1981
T. stylolineatus Wu, 1969
T. subdavainei Mukhina, 1981
T. tortus Andrássy, 1979

OTHER GENERA

Filenchus Andrássy, 1954
= *Dactylotylenchus* Wu, 1968
= *Discotylenchus* Siddiqi, 1980
= *Duosulcius* Siddiqi, 1979
= *Lambertia* Brzeski, 1977
= *Ottolenchus* Husain & Khan, 1965
= *Zanenchus* Siddiqi, 1979
Type species :
F. vulgaris (Brzeski, 1963) Lownsbery & Lownsbery, 1983
Species list in Raski and Geraert (1987)

Miculenchus Andrássy, 1951
Type species :
Miculenchus salvus Andrássy, 1959
Other species :
M. elegans Raski & Geraert, 1985

Irantylenchus Kheiri, 1972
Type species :
I. clavidorus Kheiri, 1972
Other species :
I. vicinus (Szczygiel, 1970) Brzeski & Sauer, 1983
Both species are probably synonyms.

Malenchus Andrássy, 1968
= *Neomalenchus* Siddiqi, 1979
Type species :
M. machadoi (Andrássy, 1963) Andrássy, 1968
Species list in Geraert and Raski (1986*b*)

Allotylenchus Andrássy, 1984
Type and only species :
A. excretorius Andrássy, 1984

Polenchus Andrássy, 1980
Type and only species :
P. politus Andrássy, 1980
This genus is probably synonymous with *Tylenchus.*

Cucullitylenchus Huang & Raski, 1986
Type and only species :
C. amazonensis Huang & Raski, 1986

The subfamily Ecphyadophorinae Skarbilovich, 1959

= Epicharinematinae Maqbool & Shahina, 1985
= Ecphyadophoroidinae Siddiqi, 1986

This subfamily was reviewed by Raski *et al.* (1980) and again by Raski, Koshy and Sosamma (1982). It was of major significance to this taxon that Raski and Geraert (1986*a*) established with certainty the true nature of the oesophageal morphology. Until now species of *Ecphyadophora* and *Ecphyadophoroides* have been characterized with an irregularly tubular oesophagus without a median bulb, glands in a lobe overlapping the intestine and oesophago-intestinal junction indistinct or obscure. Despite this variance from typical Tylenchidae, the Ecphyadophorinae appeared related to members of that family and were transferred to it (Raski, Koshy & Sosamma, 1982). The œsophageal structure gives further indication of close relationship of *Lelenchus* spp. to *Ecphyadophora, Ecphyadophoroides* and *Epicharinema.* The long, extremely slender body shape (high " a " values), configuration of cephalic region as high, smooth, dorsoventrally narrowed with long amphidial apertures, somewhat sinuous in shape, and exceptionally long tail — all link *Lelenchus* with *Ecphyadophoroides* and *Epicharinema* and in part with *Ecphyadophora.* The character mostly relating *Lelenchus* to Tylenchinae is the typical slender, elongate, low caudal alae quite distinct from the flap-like alae of the Ecphyadophorinae. Considering *Lelenchus* as a link between Tylenchinae and Ecphyadophorinae we judge the morphology of the cephalic region including amphidial structure and the slender bodies with long, almost filamentous tails are indicative of closer relations with the latter. It is also preferable to place a linking group with the more derived to emphasize the direction of change.

Ecphyadophora is inconsistent with the elongate head and long, slit-like amphids of the other three genera by virtue of its small, oval amphids located close to the anterior end of its symmetrically-shaped cephalic region annulated almost to oral plate or aperture. However, considering all the other similarities linking these four genera, it seems best to consider *Ecphyadophoroides, Epicharinema* and *Lelenchus* as most closely related to *Ecphyadophora* in this subfamily.

A subfamily Ecphyadophorinae and family Ecphyadophoridae were proposed by Skarbilovich (1959). Allen and Sher (1967) accepted the subfamily taxon but placed it in the Neotylenchidae. Jairajpuri and Siddiqi (1969) restored the family Ecphyadophoridae within a new superfamily Neotylenchoidea which was accepted by Andrássy (1976). Raski *et al.* (1980) added the genus *Epicharinema* to the subfamily Ecphyadophorinae but transferred it to the Tylenchidae. To these is added the genus *Lelenchus* as discussed earlier.

Maqbool and Shahina (1985) proposed a new generic taxon *Karachinema* as a monotypic genus based on a new species, *K. elongatum.* That species was described with a prominent stylet, well-developed median bulb with valvular apparatus, a long slender isthmus and a glandular region symmetrically arranged in a bulb-like structure set off from intestine, not overlapping. They considered this species related to *Epicharinema* by virtue of its valvate metacorpus and tylenchoid oesophagus. The report of Raski and Geraert (1986) indicates the vague nature of the oesophagus of *Ecphyadophora* and *Ecphyadophoroides* is attributed to fixative artifact and indeed both genera have a tylenchoid oesophagus with variously valvated metacorpus. *K. elongatum* is judged most closely related to *Ecphyadophora teres* Raski, Koshy & Sosamma, 1982 and differs by its shorter stylet (8 µm *vs* 9-12 µm for *E. teres*) and smaller size (L = 0.68 — 0.71 mm *vs* 0.83 — 1.00 mm for *E. teres*). *Karachinema* is proposed as a new synonym of *Ecphyadophora. K. elongatum* belongs to *Ecphyadophora* and transferred to that genus as *Ecphyadophora elongatum* (Maqbool & Shahina, 1985) comb. n. (= *Karachinema elongatum* Maqbool & Shahina, 1985).

Epicharinematinae is judged a synonym of Ecphyadophorinae as syn. n.

DIAGNOSIS

Tylenchidae. Moderate-sized; very slender (" a " values range from 37-176) cephalic region with fine annuli present up to labial plate which bears small, ovate amphidial apertures *(Ecphyadophora, Mitranema)* or cephalic region high, dorso-ventrally narrowed, smooth, amphidial apertures long slits *(Ecphyadopho-*

roides, Epicharinema, Lelenchus). Males with flap-like caudal alae (except *Lelenchus*); tail narrows markedly after cloacal opening; tail long, filiform.

TYPE GENUS : ***Ecphyadophora*** de Man, 1921
= *Karachinema* Maqbool & Shahina, 1985

Type species :
E. tenuissima de Man, 1921
Other species :
E. caelata Raski & Geraert, 1986
E. elongata (Maqbool & Shahina, 1985) comb. n.
= *Karachinema elongatum* Maqbool & Shahina, 1985
E. quadralata Corbett, 1964
= *E. goodeyi* Husain & Khan, 1965
= *E. acuta* Husain & Khan, 1968
= *E. basiri* Verma, 1972
= *E. tritici* Verma, 1972
E. teres Raski, Koshy & Sosamma, 1982
E. vallipuriensis Husain & Khan, 1968
Species inquirenda :
E. tarjani Husain & Khan, 1965

OTHER GENERA

Ecphyadophoroides Corbett, 1964
= *Tenunemellus* Siddiqi, 1986
Type species :
E. annulatus Corbett, 1964
Other species :
E. graminis Husain & Khan, 1968
E. indicus Verma, 1972
E. leptocephalus Raski, Koshy & Sosamma, 1982
E. macrocephalus Raski, Koshy & Sosamma, 1982
E. sheri Raski, Koshy & Sosamma, 1982
E. tenuis Corbett, 1964
E. theae Eroshenko & Nguen Vu Thank, 1981
Species inquirenda :
Ecphyadophoroides eurycephalus (de Man, 1921) Raski, Koshy & Sosamma, 1982
= *Tylenchus eurycephalus* de Man, 1921

Epicharinema Raski, Maggenti, Koshy & Sosamma, 1982
Type and only species :
E. keralense Raski, Maggenti, Koshy & Sosamma, 1982

Lelenchus Andrássy, 1954
= *Tylenchus (Lelenchus)* Andrássy, 1954
Type species :
L. leptosoma (de Man, 1880) Andrássy, 1954
Other species :
L. elegans Raski & Geraert, 1986
L. filicaudatus Raski & Geraert, 1986

Mitranema Siddiqi, 1986
Type and only species :
M. mitrum Siddiqi, 1986

The subfamily Tylodorinae Paramonov, 1967
= Campbellenchinae Wouts, 1978
= Eutylenchinae Siddiqi, 1986 syn. n.

The study of the female reproductive system and the anterior head end with SEM showed that the genera *Eutylenchus* Cobb, 1913 (Fig. 3), *Tylodorus* Meagher, 1963 (Fig. 4) and *Cephalenchus* Goodey, 1962 (syn. *Imphalenchus*) show many charcateristics in common. *Campbellenchus* Wouts, 1977 can also be included.

Eutylenchus and *Atylenchus* Cobb, 1913 were considered to belong to the same family Atylenchidae by Skarbilovich (1959); Sher, Corbett and Colbran (1966), Golden (1971) and Siddiqi (1986) while Thorne (1961) and Goodey (1963) did not accept this proposal and stressed the dissimilarities.

Tylodorus was originally placed in the Tylenchidae, Tylenchinae (Meagher, 1963) and compared with *Tylenchus, Psilenchus, Dolichodorus* and *Macrotrophurus.* The subfamily Tylodorinae Paramonov, 1967 was raised to family level by Siddiqi (1976) to contain Tylodorinae and Antarctenchinae. Dhanachand and Jairajpuri (1980) included the Tylodorinae in the Tylenchidae containing *Cephalenchus, Imphalenchus* and *Tylodorus.*

Campbellenchus was together with its subfamily included in the Tylodoridae by Wouts (1977).

It is noteworthy that the type species of three of the four genera have been described from Australia and New Zealand and that *Tylodorus* and *Campbellenchus* have not been found outside this continent.

DESCRIPTION

Tylenchid with body small to moderate size (from 0.37 mm in *Cephalenchus* to 1.86 mm in *Tylodorus*). Head slightly or not offset, internal sclerotization faint. End-on view as seen by SEM with oral disc (with dorso-ventral slit as oral opening and without indication of six papillae. Amphidial slits longitudinally oriented, starting at the oral disc and confined to a labial plate which forms the front end except for *Tylodorus* where it continues posteriorly. Dorsally and ventrally this labial plate shows a constriction or a smaller or longer cleft. In the four sectors so formed the four cephalic papillae *(Cephalenchus, Campbellenchus)* or setae *(Eutylenchus)* are found; in *Tylodorus* no papillae have been discovered. Cuticle ornamented with longitudinal ridges in *Eutylenchus* and *Campbellenchus,* with lateral field ridges different in *Campbellenchus; Tylodorus* and most *Cephalenchus* species have six lateral lines and fine or coarse transverse annulation.

Stylet longer than usual in Tylenchidae : from 15-24 µm in *Eutylenchus* and *Cephalenchus* over 23-36 µm in *Campbellenchus* and 88-104 µm in *Tylodorus;* the anterior part is about equal to the posterior part except for *Tylodorus* where it is mainly the anterior

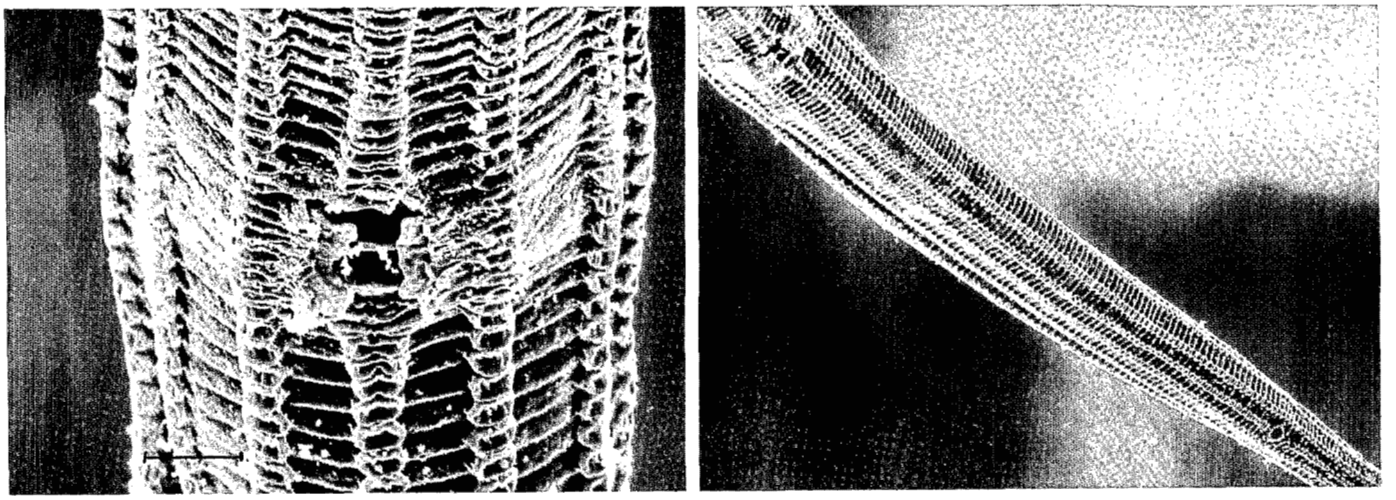

Fig. 3. *Eutylenchus fueguensis.* Female : A : vulva (Bar = 3 µm); B : body vulva to anus (Bar = 10 µm).

part that is elongated. Stylet always with rounded or oval knobs. The median bulb is well developed and anteriorly situated (except for *Tylodorus*), oesophageal glands elongated, symmetrically arranged, only exceptionally overlapping. The first intestinal cells are not always well distinguished to form an oesophago-intestinal valve (a central valve is apparently absent).

Female reproductive system : vulva a transverse slit with slight modifications in each genus; vagina simple; only the anterior side of the tract is fully developed, posteriorly a long post-vulval uterine sac is found; the uterus is subdivided in a few cells forming the transition zone with the uterine sac, a crustaformeria part with five or six cells in each of the four rows, another transition zone of several cells, and is followed by a non-offset elongated spermatheca, oviduct and ovary (in *Campbellenchus* the ovary shows a double curvature).

Males are known in all the genera and almost all the species, there is no sexual dimorphism; spicules are only slightly curved, caudal alae are always well developed.

Tails elongated with terminus acute to finely rounded. Phasmids on tail in *Tylodorus*, ad- or postvulval in the remaining genera.

DIAGNOSIS

Tylodorinae can be characterized by their head end with an oral disc, slit-like amphid apertures longitudinally oriented in a lobed or slightly divided labial disc or ring; stylet long to very long, the female reproductive system with more than twenty crustaformeria cells in the uterus and an elongated spermatheca in line.

TYPE GENUS : ***Tylodorus*** Meagher, 1963

Type and only species :
T. acuminatus Meagher, 1963

OTHER GENERA :

Campbellenchus Wouts, 1977
Type species :
C. poae Wouts, 1977
Other species :
C. filicauda Wouts, 1977
This genus is discussed in a separate paper (Geraert & Raski, 1986*a*).

Cephalenchus Goodey, 1962
= *Imphalenchus* Dhanachand & Jairajpuri, 1980
Type species :
C. hexalineatus (Geraert, 1962) Geraert & Goodey, 1964
This genus is discussed in a separate paper (Raski and Geraert, 1986*b*).

Eutylenchus Cobb, 1913
Type species :
E. setiferus (Cobb, 1893) Cobb, 1913
Other species :
E. africanus Sher, Corbett & Colbran, 1966
= *E. orientalis* Husain & Khan, 1968
E. excretorius Ebsary & Eveleigh, 1981
E. fueguensis Valenzuela & Raski, 1985
E. vitiensis Orton Williams, 1979

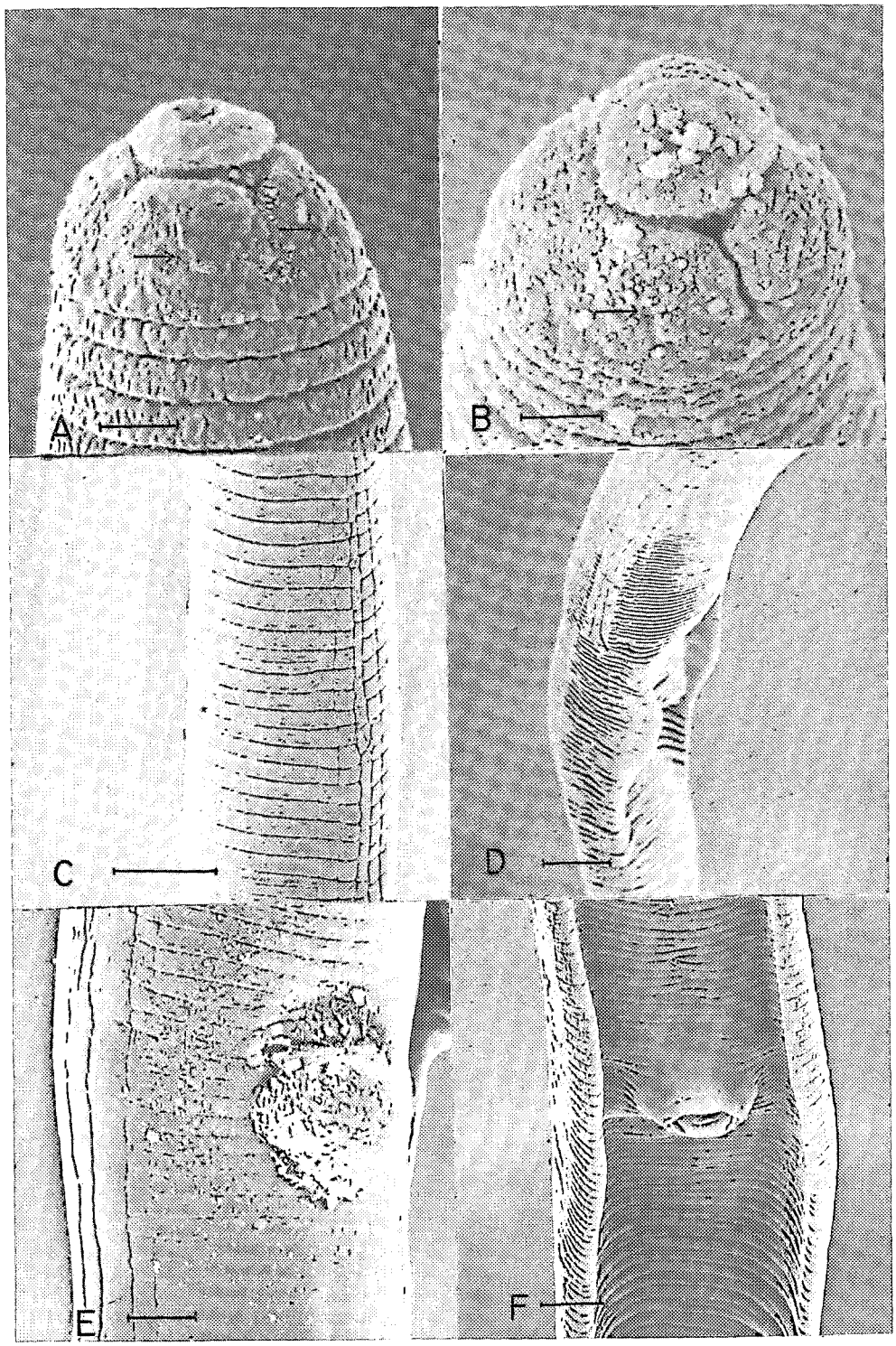

Fig. 4. *Tylodorus acuminatus.* Female : A : head, lateral view; C : lateral field and excretory pore; E : vulva. Male : B : head, lateral view; D : lateral field ending at caudal ala; F : cloacal opening. (Bar on A, B = 2 µm; C, D = 10 µm; E, F = 5 µm). (Arrows on A and B indicate cephalic sensillae).

Macrotrophurus Loof, 1958
Type and only species :
M. arbusticola Loof, 1958
This genus and species are tentatively included in this subfamily.

The subfamily Atylenchinae Skarbilovich, 1959

= Antarctenchinae Spaull, 1972 syn. n.
= Pleurotylenchinae Andrássy, 1976
= Aglenchinae Siddiqui & Khan, 1983 syn. n.

Skarbilovich (1959) was the first to propose a subfamily and family for *Atylenchus* Cobb, 1913 and *Eutylenchus* Cobb, 1913. Sher, Corbett and Colbran (1966) revised and accepted the family taxon but rejected the subfamily. Golden (1971) raised Atylenchidae to superfamily rank Atylenchoidea for these two genera in the single subfamily.

Tylenchus sachsi Hirschmann, 1952 was described from specimens collected in Germany. Szczygiel (1969) redescribed *T. sachsi* from specimens collected in Poland and proposed a separate genus, *Pleurotylenchus* for that species. Andrássy (1976) proposed a subfamily Pleurotylenchinae for this monotypic genus and transfered the taxon to Atylenchidae. Raski *et al.* (1980) accepted the relationship of *Atylenchus, Eutylenchus* and *Pleurotylenchus* but placed them all in one subfamily Atylenchinae in the family Tylenchidae.

Eutylenchus differs in many characteristics from the other two genera and shares many characteristics with the Tylodorinae and is dealt with under that heading.

Atylenchus decalineatus Cobb, 1913, the single species of this genus, shows some interesting characteristics in female and male reproductive system that have not been reported before : the vulva is backwardly covered by a longitudinal flap and the cloacal opening in the male is bordered by large papilla-like structures (Figs 5, 2). The same longitudinal flap is described for *Pleurotylenchus*, the same cloacal ornaments are found in *Coslenchus polonicus* and *Antarctenchus hooperi* Spaull, 1972. As explained before, *Atylenchus, Aglenchus, Coslenchus* and *Antarctenchus* have also a very similar en-face view; unfortunately it has not been possible to obtain SEM pictures of *P. sachsi*.

DESCRIPTION

Body small to moderate size (from 0.33 mm in *Coslenchus* to 1.29 mm in *Antarctenchus*). Head slightly or not offset, internal sclerotization faint. End on view as seen by SEM consists of one large, laterally elongated plate more or less constricted dorso-ventrally containing the large, more or less rounded amphidial apertures (with lateral offshoot in the male of *Aglenchus* sp.); around the dorso-ventral mouth slit six papillae are sometimes distinct; the four cephalic papillae are usually indistinct except in *Atylenchus* (setae) and in the male of *Aglenchus* sp. where only two of them are well developed. Lateral field with two, three, four or six lines; cuticle provided with longitudinal ridges in *Atylenchus, Pleurotylenchus* and *Coslenchus* species. Cuticle distinctly annulated with wide annuli.

Stylet medium sized, moderately developed with rounded knobs : from 7 µm in *Aglenchus* to 22 µm in *Antarctenchus;* the anterior part is slightly smaller than to about equal to the posterior part.

Median bulb well developed, in the middle or slightly anterior to the middle of the oesophagus, the posterior bulb short rounded or elongate.

Female reproductive system : vulva with inner lips (epiptygmata) and lateral flaps covering the transverse vulval slit slightly or partly *(Aglenchus, Coslenchus, Antarctenchus)* or vulva covered by flap-like anterior lip directed backwards *(Atylenchus, Pleurotylenchus).* Vaginal wall usually distinctly thickened at the vulval side in *Aglenchus, Coslenchus* and *Antarctenchus. Antarctenchus* is didelphic, the remaining genera have only the anterior genital tract developed : in *Pleurotylenchus* and *Atylenchus* the post-vulval uterine sac is well developed, in *Aglenchus* and *Coslenchus* this sac is rudimentary or absent. Uterus short (cells probably always in four rows with three or four cells in a row), spermatheca usually offset.

Males present in all genera, but most *Coslenchus* species appear to be parthenogenetic. Bursa well developed in *Antarctenchus, Aglenchus* and *Coslenchus,* very poorly developed in *Atylenchus* and *Pleurotylenchus.* In *Atylenchus, Antarctenchus* and *Coslenchus polonicus* the cloacal opening is provided with large hypoptygmata; in *Aglenchus* and remaining *Coslenchus* species a cloacal tube is present.

Tail long, attenuated, tail tip setose, acute or finely rounded. Phasmids ad-vulval or post-vulval in *Aglenchus* and *Coslenchus,* on the tail in *Antarctenchus.*

DIAGNOSIS

Tylenchidae. Undivided laterally elongated front plate of the head with large, roundish amphidial apertures; stylet with about equal parts, vulva covered by lateral or longitudinal flaps; males often with large hypoptygmata.

TYPE GENUS : ***Atylenchus*** Cobb, 1913

Type and only species :
Atylenchus decalineatus Cobb, 1913

OTHER GENERA

Aglenchus Andrássy, 1954
Type species :
A. agricola (de Man, 1921) Andrássy, 1954.
The genus is discussed in a separate paper (Geraert & Raski, 1987).

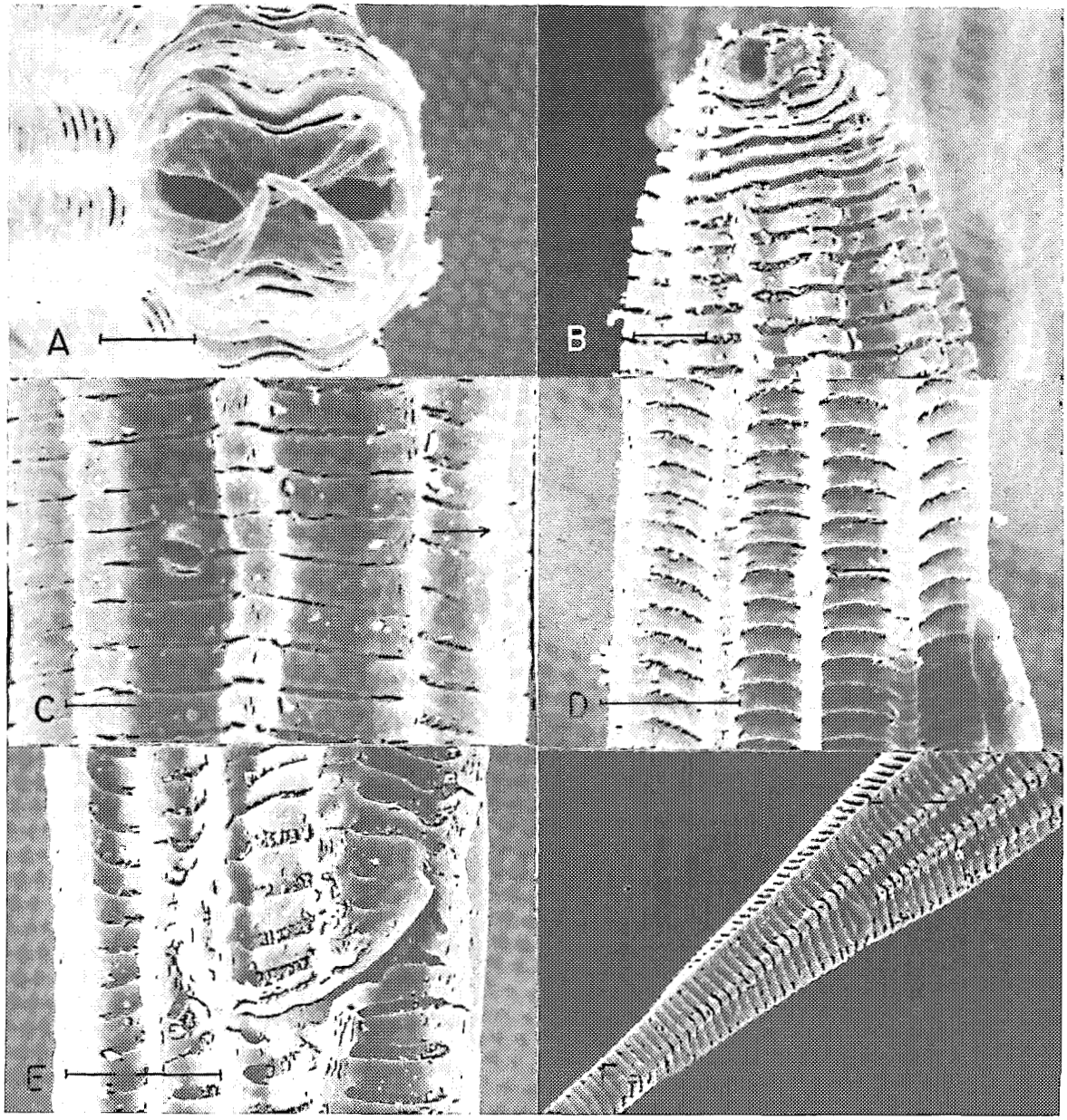

Fig. 5. *Atylenchus decalineatus.* Female : A : En-face; B : head end, lateral view; C : excretory pore (arrow indicates deirid (?)); D : lateral field at deirid (?); E : vulva; F : anus. (Bar on A, B, C = 2 µm; D, E = 5 µm; F = 10 µm).

Antarctenchus Spaull, 1972
Type and only species :
A. hooperi Spaull, 1972

Coslenchus Siddiqi, 1978
= *Cosaglenchus* Siddiqui & Khan, 1983
= *Paktylenchus* Maqbool, 1983
Type species :
C. costatus (de Man, 1921) Siddiqi, 1978.

This genus is discussed in a separate paper (Geraert & Raski, 1987).

Pleurotylenchus Szczygiel, 1969
Type and only species :
P. sachsi (Hirschmann, 1952) Szczygiel, 1969
This species shows no differences with *Atylenchus decalineatus* except for the absence of the long cephalic setae.

Gracilancea Siddiqi, 1976

Type and only species :

G. graciloides (Micoletzky, 1925) Siddiqi, 1976.

In the original description *Gracilancea* was considered to belong to the Tylodorinae, Tylodoridae (Siddiqi, 1976); in Brzeski and Sauer's (1984) redescription the similarities with *Cephalenchus* (on one hand) and *Aglenchus* (on the other hand) are stressed. The perioral disc being well set off makes it difficult to include *Gracilancea* in the Atylenchinae but the structure of the amphidial apertures within the labial plate, of stylet, vulva and vagina shows some relationship with Tylodorinae and is tentatively included here.

The subfamily Boleodorinae Khan, 1964

= Psilenchinae Paramonov, 1967
= Basiriinae Decker, 1972
= Leipotylenchinae Sher, 1973 syn. n.

The family Boleodoridae has been treated in Brzeski and Sauer (1984), including the Boleodorinae with *Boleodorus* Thorne, 1941, *Basiria* Siddiqi, 1959 and *Neopsilenchus* Thorne & Malek, 1968 and the Psilenchinae with *Psilenchus* de Man, 1921 and *Antarctenchus* Spaull, 1972. *Antarctenchus* is now treated under a different subfamily (Atylenchinae); *Psilenchus* differs from the remaining gene'a by a paired female genital system a character that we consider has not sufficient merit to sustain a separate subfamily and so we synonymize the Psilenchinae with the Boleodorinae.

A genus that we have also to consider is *Atetylenchus* Khan, 1973 (= *Leipotylenchus* Sher, 1974). This genus was based on a single species, originally described as *Tetylenchus abulbosus* Thorne, 1949.

Sher (1974) differentiated it from *Psilenchus* by the absence of slit-like amphid apertures on the lip region and the low flat lip region. He could also have added the difference in the position of the median bulb : in *A. abulbosus* the median bulb is slightly anterior to the middle while in the usual *Psilenchus* species it is distinctly behind the middle.

Restudy of the material used by Sher (1974) revealed that large slit-like amphid apertures are present together with six papillae around the oral opening (Fig. 6). In the male two of the four cephalic papillae are very distinct. As for the median bulb position the recently described *Psilenchus graminus* Bajaj, Kaushit & Bhatti, 1982 has also an anterior position; Siddiqi (1986), after studying a paratype, transfeŕed it to *Atetylenchus.*

Leipotylenchus amiri Maqbool & Shahina, 1984 was described unaware of the synonymy of the genus with *Atetylenchus* and unaware of the description of *P. graminus :* from the descriptions both species can hardly be distinguished.

The study of a paratype slide of *L. amiri* revealed that *i)* the stylet cone measured 4 µm; i.e. about 1/3 (and not 1/2) of the stylet length (12.5 µm); *ii)* the opening of the dorsal oesophageal gland is at about 5 µm posterior to the stylet knobs (and not less than 2 µm); *iii)* the lateral field is indistinct : the original description gives four lines, the accompanying Fig. 1 E five lines; Siddiqi (1986) transfered the species to *Merlinius* suggesting there are six lines. In our study of *A. abulbosus* the lateral field is shown to be slightly variable and weakly expressed (cf. Fig. 6 E, F).

Although the end-on view is not available we prefer to consider *L. amiri* as a representative of *Atetylenchus,* differing from the described species by the small, flange-like stylet knobs (absent in the other two species).

The genus *Neobasiria* Javed, 1982 was synonymized with *Basiria* by Hashim (1985) and with *Boleodorus* by Siddiqi (1986); we follow Hashim (1985) as we consider a weakly developed median bulb (*vs* a normally developed bulb) not a genus character. Geraert and Raski (1986*a*) proposed a new genus *Basirienchus* and underlined the similarity of *Neothada* with the remaining Boleodorinae.

The genus *Duotylenchus* Saha & Khan, 1982 probably belongs to this group (Siddiqi, 1986); its single species could be a *Basiria* species.

DIAGNOSIS (cf. Brzeski & Sauer, 1983)

Tylenchidae. Small to medium size nematodes. Oral opening surrounded by six papillae, a second circle of four papillae on the edges of anterior surface. Amphidial apertures in form of open V or oblique, on lateral side of head, usually partially covered by a flap. Stylet delicate, anterior part about half the posterior part, knobs small, often flange-like, stylet sometimes without knobs. Median bulb with or without thickenings of lumen walls. Oesophageal glands symmetrically arranged, offset from intestine. Female reproductive system paired or unpaired; usually with few cells in uterus and spermatheca except for *Psilenchus;* spermatheca offset or in line. Bursa small, adanal. Tail elongated, often rounded at the end, seldom spicate.

TYPE GENUS : ***Boleodorus*** Thorne, 1941

Type species :

B. thylactus Thorne, 1941

Other species :

B. abnormus Khan & Basir, 1964
B. acurvus Jairajpuri, 1982
B. acutus Thorne & Malek, 1968
B. brevistylus Khera, 1970
B. citri Edward & Rai, 1978
B. clavicaudatus Thorne, 1941
B. cynodonti Fotedar & Mahajan, 1974
B. filiformis Husain & Khan, 1977
B. flexuosus Eroshenko, 1982
B. hyderi Husain & Khan, 1965

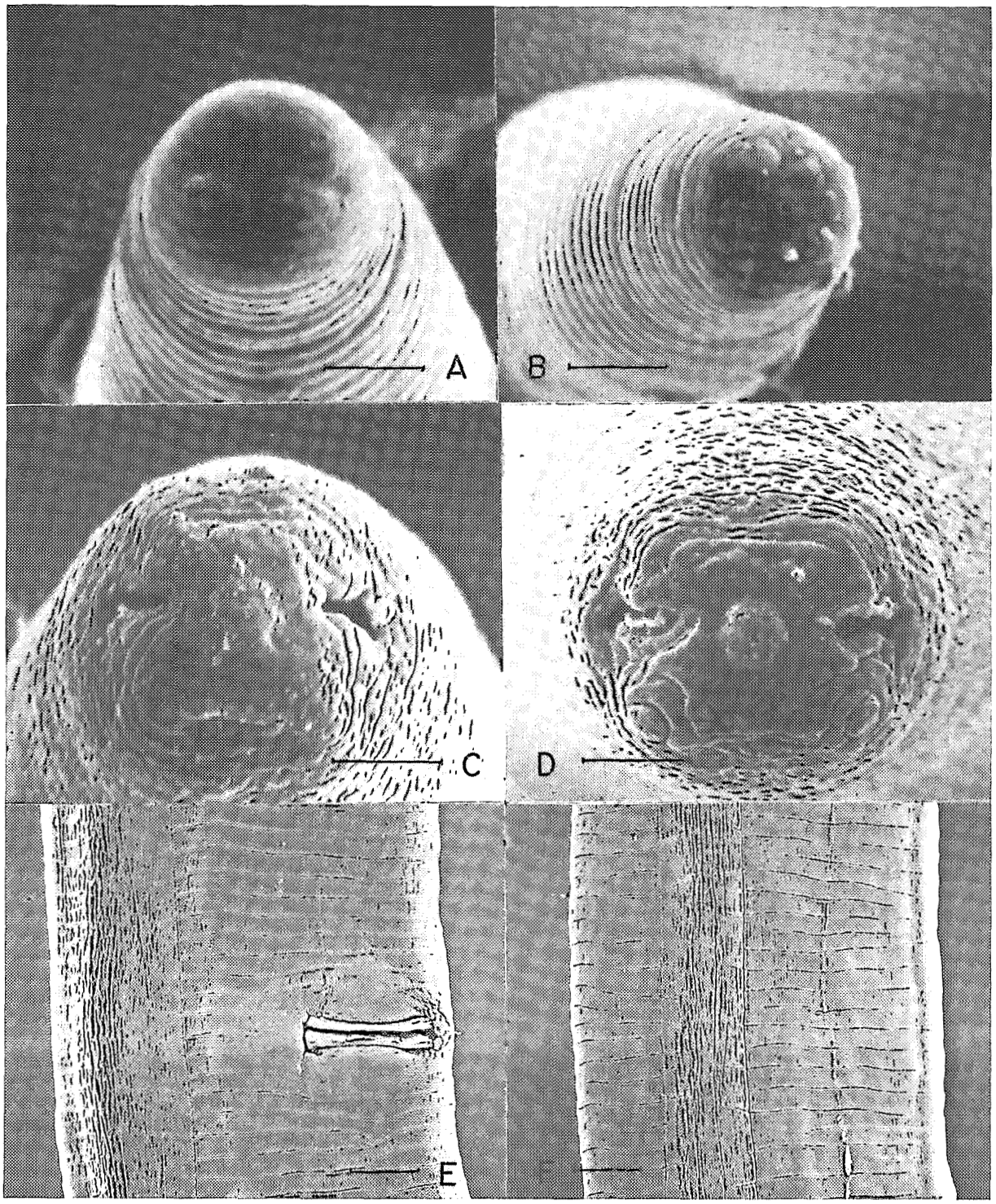

Fig. 6. *Atetylenchus abulbosus.* Female : A : En-face (by S. A. Sher & A. Bell. Utah specimen); C. En-face (Oregon specimen); E. vulva (Oregon specimen). Male : B : En-face (by S. A. Sher & A. Bell. Utah specimen); D : En-face (Oregon specimen); F : lateral field (Oregon specimen). (Bar on A, B = 4 µm; C, D = 2 µm; E, F = 5 µm).

B. impar Khan & Basir, 1964
B. innuptus (Andrássy, 1961) Siddiqi, 1963
B. mirus Khan, 1964
B. neosimilis Geraert, 1971
B. pakistanensis Siddiqi, 1963
B. rafiqi Husain & Khan, 1965
B. similis Khan & Basir, 1963
B. spiralis Egunjobi, 1968
B. volutus Lima & Siddiqi, 1963
B. zaini Maqbool, 1982

OTHER GENERA

Basiria Siddiqi, 1959
= *Clavilenchus* Jairajpuri, 1966
= *Basiroides* Thorne & Malek, 1968
= *Neobasiria* Javed, 1982
Type species
B. graminophila Siddiqi, 1954
Other species : cf. Hashim (1985)

Basirienchus Geraert & Raski, 1986
Type species
B. uncinatus Geraert & Raski, 1986
Other species : cf. Geraert & Raski (1986*a*)

Duotylenchus Saha & Khan, 1982
Type and only species
D. bilineatus Saha & Khan, 1982
Probably junior synonym of *Basiria.*

Neopsilenchus Thorne & Malek, 1968
Type species :
N. magnidens (Thorne, 1949) Thorne & Malek, 1968
Other species : cf. Siddiqi (1986)

Neothada Khan, 1973
Type species
N. tatra (Thorne & Malek, 1968) Khan, 1973
Other species
N. cancellata (Thorne, 1941) Khan, 1973
N. geraerti (Andrássy, 1982), Siddiqi, 1986

Psilenchus de Man, 1921
Type species
P. hilarulus de Man, 1921
Other species : cf. Kheiri (1970)

Atetylenchus Khan, 1973
= *Leipotylenchus* Sher, 1971
Type species
A. abulbosus (Thorne, 1949) Khan, 1973
Other species
A. amiri (Maqbool & Shahina, 1984) n. comb.
A. graminus (Bajaj, Kaushik & Bhatti, 1982) Siddiqi, 1986

This genus is tentatively included under the Boleodorinae because it shares many characteristics with *Psilenchus;* the *en-face* view is, however, more *Filenchus*–like.

Genus *incertae sedis* : *Luella* Massey, 1974

This taxon was proposed by Massey (1974) as a monotypic new genus for a new species, *Luella luculenta,* found in association with *Ips pini* in red pine. The description was based on a single female and male and the taxon judged to be a member of Nothotylenchinae.

The revision of Neotylenchidae (Fortuner & Raski, 1987) has found most members of Nothotylenchinae to belong to the Anguinidae. *Luella* does not entirely fit the definition of the Anguinidae because of the very short post uterine sac (about 46 % of VBD as measured from Massey's drawing - Fig. III, C), and the small sperms without surrounding cytoplasm.

Other characteristics given by Massey include : *i)* cuticle finely striated, without lateral incisures; *ii)* stylet without knobs; *iii)* oesophageal glands slightly overlapping intestine; *iv)* ovary single, reflexed; *v)* terminus filiform; *vi)* spicules and gubernaculum tylenchoid; *vii)* caudal alae adanal. The median bulb is illustrated as spindle-shaped but no suggestion of musculature or valvular thickenings.

None of the above are diagnostic for a particular genus, most can be found in various unrelated genera. Nothing is known about the anterior morphology as to amphids, labial plate, the four cephalic papillae, oral disc or the six labial papillae.

The description by Massey limited by the above uncertainties and lack of knowledge lead to the conclusion *Luella* is most probably related to Tylenchidae but cannot be assigned with confidence to any of the subfamilies as presently defined. Therefore it is proposed *Luella* be designated genus *incertae sedis* in the family Tylenchidae.

Key to the genera (sometimes to species) of *Tylenchidae*

1 - Females didelphic 2
- Females monodelphic 5

2 - Tail short, subcylindrical, rounded; stylet very long (90-110 µm) ..... *Macrotrophurus arbusticola* Loof, 1958
- Tail elongated, attenuated; stylet small (less than 20 µm) 3

3 - Cephalic framework moderately sclerotized; vulva provided with lateral vulval membranes; male cloaca provided with large hypoptygmata ..... *Antarctenchus hooperi* Spaull, 1972
- Cephalic framework not sclerotized; vulva without lateral vulval membranes; male without hypoptygmata 4

4 - Head high with distinct amphidial slit on the lateral side; median bulb usually behind middle of oesophagus ..... *Psilenchus*

- Head low with indistinct amphidial slit; median bulb anterior to middle of oesophagus .... *Atetylenchus*

5 - Stylet = 76-104 µm ..... *Tylodorus acuminatus* Meagher, 1964
- Stylet = 38-52 µm ..... *Epicharinema keralense* Raski *et al.*, 1980
- Stylet = 22-34 µm 6
- Stylet less than 22 µm 7

6 - Cuticle with longitudinal ridges ..... *Campbellenchus*
- Cuticle without ridges ..... *Gracilancea*

7 - Head provided with setae 8
- Head without setae 9

8 - Vulva covered by longitudinal flap, male without caudal alae; cloaca provided with large hypoptygmata ..... *Atylenchus decalineatus* Cobb, 1913
- Vulva with lateral vulval flaps; male with caudal alae; cloaca raised ..... *Eutylenchus*

9 - Cuticle provided with longitudinal ridges 10
- Cuticle without longitudinal ridges 14

10 - Conus about 1/3 of stylet length 11
- Conus slightly less to about 1/2 of stylet length .. 13

11 - The longitudinal ridges mask the transverse body annulation; no distinct lateral field (the midlateral ridge appears slightly larger than the others) ..... *Basirienchus elenae* Geraert & Raski, 1986
- The longitudinal ridges divide the transverse annulation into blocks, lateral field with 4 lines 12

12 - Head with 2-3 annuli; stylet without knobs ..... *Neothada*
- Head with 6-7 annuli; stylet with delicate knobs ..... *Basirienchus costatus* Geraert & Raski, 1986

13 - Vulva covered by longitudinal flap; stylet = 17-19 µm ..... *Pleurotylenchus sachsi* (Hirschmann, 1952)
- Vulva with lateral vulval flaps; stylet less than 15 µm ..... *Coslenchus*

14 - Conus about 1/3 of stylet length 15
- Conus slightly less to about 1/2 of stylet length .. 28

15 - Head high with distinct amphidial slit on the lateral side (monodelphic Boleodorinae) 16
- Head variously shaped, amphidial slit longitudinally orientated or only present on the front 19

16 - Body ventrally curved, sometimes in a spiral; female reproductive system with offset spermatheca filled with refractive sperm and ovary with oocytes in multiple rows ..... *Boleodorus*
- Body more or less straight; sperm not refractive and oocytes not in multiple rows 17

17 - Tail hooked or bent near terminus which is pointed ..... *Basirienchus uncinatus* Geraert & Raski, 1986
- Tail more or less straight 18

18 - Stylet without knobs, anterior part with wide lumen ..... *Neopsilenchus*
- Stylet with or without knobs, anterior part conical with very fine lumen ..... *Basiria*

19 - Head with disc-like structure 20
- Head with smooth contour 22

20 - Head with small disc at the front end 21
- Head with large dome shaped structure ..... *Cucullitylenchus amazonensis* Huang & Raski, 1986

21 - Very slender (a = 62-67); caudal alae posteriorly concave ..... *Mitranema mitrum* Siddiqi, 1986
- Not so slender; caudal alae rounded ..... *Filenchus* (some *Filenchus* species, before considered as a separate genus *Discotylenchus*)

22 - Very slender (a = 60-180); bursa lobed 23
- Relative body width variable, from thick to slender; caudal alae, if present, rounded (five genera) 24

23 - Head quadrangular; amphidial pores on front; body constricted at vulva ..... *Ecphyadophora*
- Head flattened; long sinuous amphidial aperture; body not constricted at vulva ..... *Ecphyadophoroides*

24 - Cuticle deeply incised 25
- Cuticle not deeply incised 26

25 - Head quadrangular in front; body annulations zigzag in surface view, this distinct annulation continues on the head; lateral field a small ridge; male without caudal alae ..... *Miculenchus*
- Head flattened; lateral field a small ridge with 4, 6 or many lines (the many lines visible only using SEM); males with caudal alae ..... *Malenchus*

26 - Very slender species; annulation not so distinct; head very flattened with long sinuous amphidial aperture ..... *Lelenchus*
- Relatively thicker species; annulation usually distinct; head usually quadrangular; amphidial aperture when long, not sinuous 27

27 - Head high with longitudinal amphidial aperture on lateral side; clavate stylet knobs with ventrally situated opening of oesophageal lumen; dorsal oesophageal gland opening one half to one stylet length posterior to knobs ..... *Irantylenchus*
- Head quadrangular; annulation distinct; stylet with rounded knobs; lateral field with 2, 3 or 4 lines; dorsal gland opening close to knobs ... *Filenchus*

28 - Vulva provided with lateral flaps 29
- Vulva without flaps 30

29 - Lateral field 2 lines; vagina thin; post-vulval sac short ..... *Allotylenchus*
- Lateral field with 3 lines (central ridge can also appear as 2 lines close to each other); vagina thickened; post-vulval sac short ..... *Aglenchus*
- Lateral field with 4 or usually 6 lines; vagina not thickened; post-vulval sac well developed ..... *Cephalenchus*

30 - Lateral field and body annulation inconspicuous; caudal alae very small ..... *Polenchus*
- Lateral field and body annulation distinct; caudal alae distinct ..... *Tylenchus*

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