Article bibliographique

THE ANTERIOR SENSILLA OF NEMATODES

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The anterior sense organs of nematodes are commonly referred to as setae and/or papillae, according to the length of the projection above the surrounding cuticle. A common definition for "*papilla*" can e.g. be found in Webster's third new international dictionary : "a small projecting body part similar to a nipple in form". Henderson's dictionary of biological terms gives a short and very general definition for "*seta*" : "any bristle-like structure".

Setae are often present in aquatic species, rarely in terrestrial ones and not in zooparasitic stages. Recent electron-microscopic investigations have demonstrated that in quite a number of Secernentea, especially Tylenchida (De Grisse, Lippens & Coomans, 1974 ; Stone, 1974 ; Sher & Bell, 1975 ; De Grisse, 1977), but also some Spirurida and Strongylida (McLaren, 1970, 1972 & 1976), some Ascaridida (Wright, 1977), and in some of the zooparasitic Enoplia (Wright, 1974) and freeliving Chromadoria (Coomans & De Waele, 1979) so far studied, none or only a part of the so-called papillae do project from the head surface. Hence the terms "papilla" or "seta" are not generally applicable to the anterior sense organs of nematodes. Ward *et al.* (1975) use the term "sensilla" for the sense organs in the tip of the nematode's head and refer to a definition given by Bullock and Horridge (1965) for sensilla : "... simple types of sense organs involving only a few neurons". In Webster's dictionary a *sensillum* (plural *sensilla*) is defined as "a simple epithelial sense organ composed of one or a few cells with a nerve connection and usually taking the form of a spine, plate, rod, cone or peg". The term "sensillum" is in general use for sense organs in Arthropods, in nematodes however it has only been used in connection with the amphid (Chitwood & Chitwood, 1950, p. 163). In the latter case the term sensillum designated a receptor rather than the whole sense organ and hence was incorrectly used. In agreement with Ward *et al.* (1975) the term "sensillum" is adopted here to designate the nematode's anterior sense organs. In fact, it could also be used for other nematode sense organs, as long as their structure meets the definitions given above. The advantage of this general term is that it fits in all cases and it can be more specified by adding adjectives as papilliform-, setiform-, labial-, cephalic-, somatic-, caudal-, etc.

The basic arrangement of the anterior sensilla is represented in the now generally accepted and well documented scheme of De Coninck (1942 & 1965) (Fig. 1). According to this author, the primitive pattern consists of twelve labial sensilla, four cephalic ones and two amphids. The labial sensilla are situated in the medioradial plane of each lip and constitute an inner circlet of six *inner* (or internal) *labial sensilla* and an outer circlet of six *outer* (or external) *labial sensilla*. The position of these labial sensilla reflects the hexaradiate symmetry of the lips, hence they are subdorsally, laterally and sub-

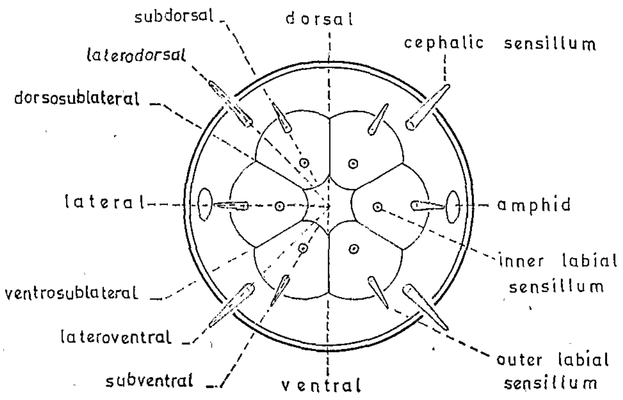


Fig. 1. Basic arrangement of the anterior sensilla in nematodes (modified after De Coninck, 1942).

ventrally situated. The four cephalic sensilla and the two amphids are postlabial and bilaterally symmetrical, with the cephalic sensilla occurring in the middle of each body quadrant, i.e. submedian and the amphids in lateral position close to the lip region. From this plesiomorphous condition several apomorphous ones have developed, such as a forward migration of the four cephalic sensilla so that they become labial in position ; a backward migration of the six outer labial sensilla, so that they become postlabial in position ; a forward migration of the amphids so that they open on the lateral lips ; a backward migration of the amphids till far behind the lip region ; an inward migration of the inner labial sensilla ; a reduction of some of the sensilla ; a pronounced differential development of the hexaradial and bilateral components ; a shift in position of the outer labial sensilla ; etc. The picture may be further complicated by the forward migration of some somatic sensilla or by duplications.

Apart from the above mentioned sensilla, there may be occasionnally a pair of lateral ocelli and recently discovered accessory sensilla.

Basic structure of nematode sensilla
(Fig. 2)

The basic structure of nematode sensilla comprises a neuronal and a non-neuronal part, with the latter surrounding the former. Originally the *non-neuronal part* may have consisted of unspecialized epidermal (hypodermal) tissue as has been reported for *Capillaria hepatica* (Wright, 1974) and *Trichinella spiralis* (McLaren, 1976) or somewhat more specialized "glial" tissue as in at least some sensilla in other Enoplia, e.g. *Tobrilus* (Storch & Riemann, 1973), *Aporcelaimellus* (Lippens *et al.*, 1974) and *Deontostoma* (Siddiqui & Viglierchio, 1977). Later on these non-neuronal elements differentiated into two distinct components, both specialized in a different way. These were first described by Goldschmidt in 1903 and named "Geleitzelle" and "Stützzelle". Very unfortunately these cells have been given many different names (Table 1) and sometimes the same name has been used for both cells by different authors. This confusion is partly due to the incorrect interpretation of Goldschmidt's terminology by some authors and to the fact that what he called "Geleitzelle" later on prooved to be a supporting cell, and what he called "Stützzelle" is apparently more a secretory cell.

Indeed, the anteriormost accessory cell in some nematodes has been shown to possess bundles of fibres (McLaren, 1972, 1974, 1976*a* & *b*) that apparently serve a supporting function. Its socket-like distal end that surrounds the sensillar channel below the head cuticle also indicates a supporting function. This part of the cell may surround the distal portion of the second non-neuronal cell (McLaren, 1972, 1974, 1976*a* & *b*) or may itself be partly surrounded by the latter (De Grisse, 1977). The so-called supporting cell may, however, serve other functions as well, such as the secretion of the cuticular lining of the sensillar channel (McLaren, 1971, cited in McLaren 1976*a* & *b* ; Ward *et al.*, 1975 ; De Grisse, 1977). In some instances this cell may be lacking as e.g. in the lateral outer labial sensilla of criconematids, where the reduced receptor ends free in the body cavity (De Grisse, 1977).

In conclusion, the anteriormost non-neuronal cell of the nematode sensillum seems to be a specialized epidermal cell that has a continuous supporting function and an intermittent secretory function (as other epidermal cells !) when it forms the cuticular lining of the sensillar channel. Since the formation of cuticle is a general

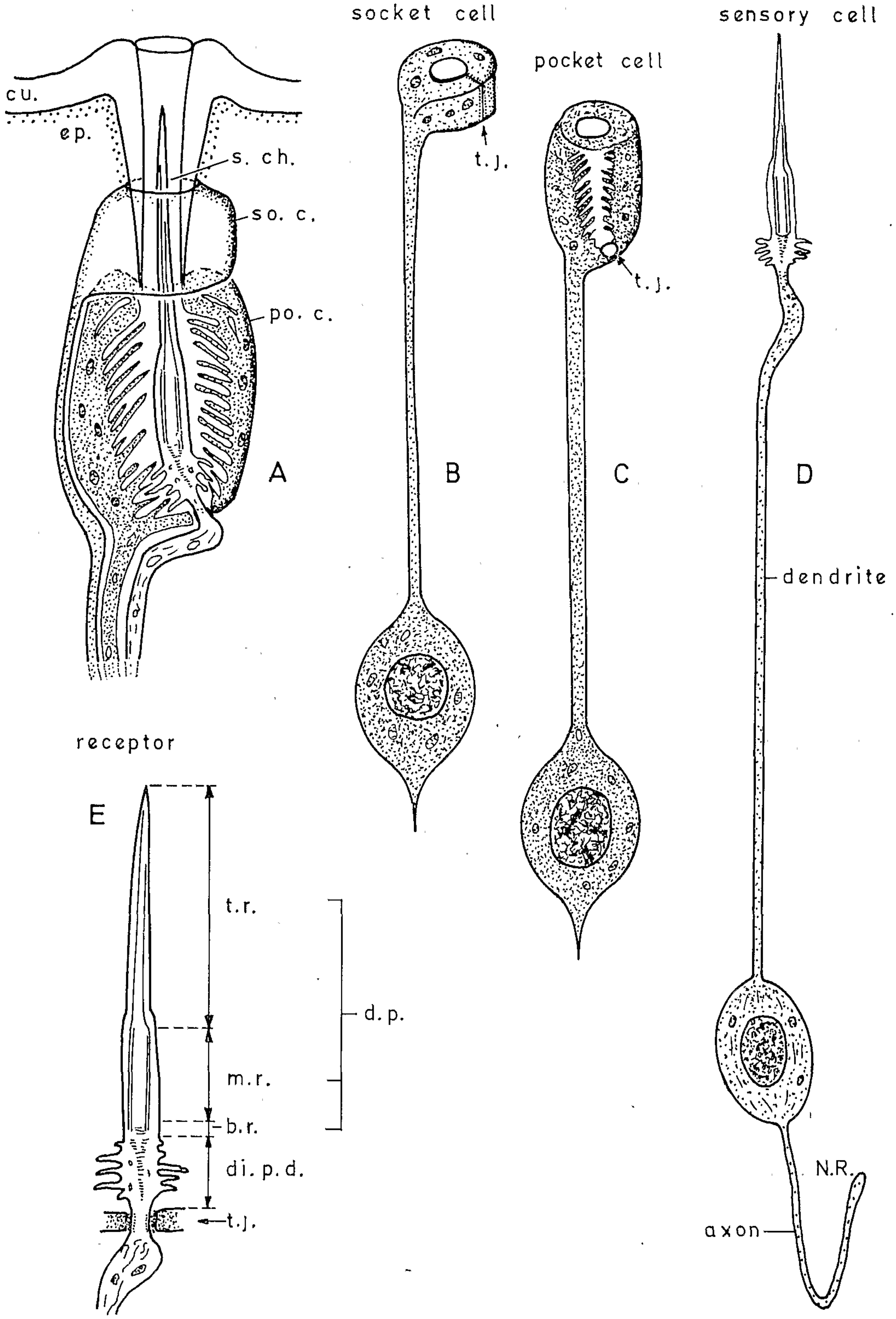


Fig. 2. Basic structure of nematode sensilla. A : Distal part with the three components. B : Supporting or socket cell. C : Gland or pocket cell. D : Sensory cell. E : Ciliary receptor. *b.r.* : basal region, *cu.* : cuticle, *d.p.* : dendritic process, *di.p.d.* : distal part of dendrite, *ep.* : epidermis, *m.r.* : median region, *n.r.* : nerve ring, *po.c.* : pocket cell, *s.ch.* : sensillar channel, *so.c.* : socket cell, *t.j.* : tight junction, *t.r.* : terminal region.

feature of epidermal cells in nematodes (as well as in many other invertebrates), the more special function here is the supporting one, hence the term "*supporting cell*" seems appropriate. When a purely descriptive term is preferred, it could be called a "*socket cell*", as proposed by Ward *et al.*, 1975.

Few studies so far have located exactly the position of the *perikaryons* of the sensillar cells. According to Ward *et al.* (1975) and Ware *et al.* (1975) the nuclei of the supporting cells are situated anterior to the nerve ring and mostly in the vicinity of the median bulb in *Caenorhabditis elegans*, with those of all the cephalic sensilla and some of the outer labial sensilla posterior to the median bulb and the others anterior to it. The nuclei of the glial cells in Enoplia are more anterior (cf. Lippens *et al.*, 1974 ; Siddiqui & Viglierchio, 1977).

Burr and Burr (1975) compare the supporting cell with the tormogen cell of insect sensilla, but it is difficult to compare these structures to this extent. Insect and nematode sensilla are similar but not homologous ; in insect sensilla there are normally *three* escort cells of which the tormogen cell is the outermost one, forming the cuticular basis of the hair (*tormos* = socket ; *genès* = producing) and producing secretions that "guide" the sensory stimuli (Altner, 1977). So, it seems better to avoid this term for nematode sensilla.

The second escort or accessory cell is situated behind the supporting cell with its anterior end surrounded by the latter (McLaren, 1972, 1974, 1976*a* & *b*) or itself slightly surrounding the supporting cell (De Grisse, 1977). The distal extension of this cell may be provided with microvilli or lamellae where it surrounds the terminal portions of the nerves. The internal structure of the cell, with usually well developed endoplasmic reticulum and secretory granules, indicates a secretory activity. However, the cell may vary considerably in structure and size according to species and even among different stages of the same species ; it also varies from one type of sensillum to another, being usually much better developed in the amphids. It was first discovered there and named "amphidial gland" (Chitwood & Chitwood, 1950, p. 153) ; later on (McLaren, 1976*a*) the term "papillary gland" was proposed for this cell in the other anterior sensilla. Papillary and amphidial gland cells have not been reported in some older studies, but it is not always clear whether they are really lacking or poorly developed and therefore overlooked. On the other hand, no glandular activity could be detected in tissues associated with the anterior sensilla in the recently studied *Heterakis gallinarum* (Wright, 1977).

The secretions of these glandular cells are supposed to be involved in receptor specificity and receptor sensitivity by regulating the ionic environment around the receptors, but more special functions have been proposed for the amphidial glands (see below).

Like the supporting cell, the second non-neuronal cell of a nematode sensillum seems to be a specialized epidermal cell with probably continuous though variable secretory activity, hence it could be called the "*sensillar gland cell*" or simply "*sensillar gland*" in general and *amphidial gland* when the gland cell of the amphid is specifically referred to. When a descriptive term is preferred, this cell could be called a "*pocket cell*", as proposed by Ware *et al.* (1975), or a "*goblet cell*" as proposed by De Grisse (1977). These terms refer to the ampulla-like distal part of the cell and have not been used ambiguously.

The cell bodies of the gland cells, except those of the amphidial glands, are anterior to the nerve ring.

Burr and Burr (1975) compare the sensillar gland cell with the trichogen cell of insect sensilla, but the latter cell forms the shaft of the hair (*thrix* = hair ; *genès* = producing) in insects and degenerates in the adult making a comparison even less sound than between tormogen cell and supporting cell.

It should be mentioned that the two non-neuronal components of nematode sensilla, the supporting and the gland cells are similar to nerve cells in having long, thin processes that run backward to their cell bodies. For this reason and also because in his micrographs some receptors seem to arise from gland cells, De Grisse (1977) believes both cell types are of neuronal origin. However, Ward *et al.* (1975) have pointed out that none of these cells gives synapses to any other cell and, therefore, can not be neuronal.

Finally, a number of nervous endings, travelling in the sensillar nerves, are not surrounded by escort or accessory cells and do not terminate

Table 1

Terminology used for the non-neuronal components of the nematode sensilla

Author	*Anteriormost cell*	*Posteriormost cell*
Goldschmidt, 1903 & 1908	Geleitzelle	Stützzelle
Bullock & Horridge, 1965	supporting cell	escort cell
De Coninck, 1965	cellule d'accompagnement	cellule de soutien
McLaren, 1972, 1974, 1976 *a* & *b*	supporting cell	multivesicular cell, gland cell, secretory cell (amphidial and papillary gland)
Baldwin & Hirschmann, 1973 & 1975	—	(amphidial) gland
Ward *et al.*, 1975	socket cell	sheath cell
Ware *et al.*, 1975	cap cell	pocket cell
Burr & Burr, 1975	sheath cell	secretory cell
Wergin & Endo, 1976	supporting cell	(amphidial) gland
De Grisse, 1977	supporting cell *	goblet cell, goblet shaped cell *
Endo & Wergin, 1977	supporting hypodermal cells (hypodermis)	

* Translated from the dutch terms "steuncel" and "bekercel" or "bekervormige cel" respectively.

at the cuticle ; this is so for the so called accessory sensilla.

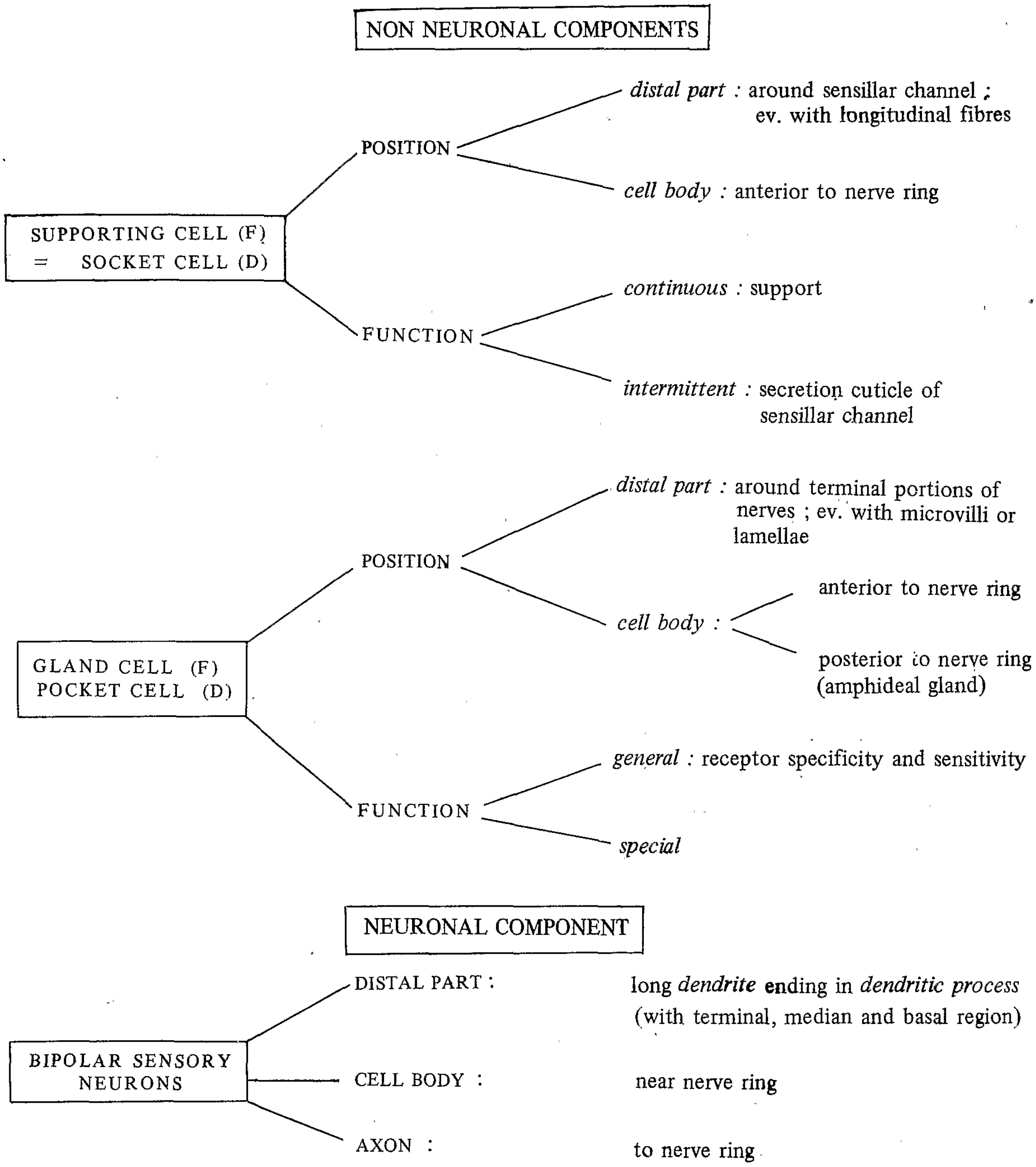
The *neuronal component* consists of the sensory neurons that have been shown to be of the bipolar type (Ward *et al.*, 1975 ; Ware *et al.*, 1975). The cell bodies are located near the nerve ring, with those of the amphidial neurons behind it and the others mostly anterior to it. The anterior extensions of the neurons have terminal processes specialized as receptive regions and should therefore be called *dendrites* ending in *dendritic processes.* The *axons*, except those of the amphidial neurons, bypass the nerve ring, then make a U-turn and enter the nerve ring from the rear. The axons of the amphidial neurons enter the ventral ganglia through commissures passing ventrally between the body muscles and the epidermis. All these neurons form synapses in the nerve ring (Ward *et al.*, 1975 ; Ware *et al.*, 1975).

The *dendritic process* usually is a modified cilium and therefore often called as such or also "ciliary receptor" or even "cilium", though its structure is very variable and different from that of a typical kinocilium. In those cases where patterned microtubules are present in the basal and middle portions of the process, their arrangement becomes irregular in the terminal portion. Although basal bodies have been reported in several studies, the typical pattern composed of nine triplets has never been found ; in some instances however a basal plate has been observed, hence a basal portion can be distinguished. The basal plate may even be composite and consist of three subsequent plates as in *Mononchus* (Grootaert & Wyss, 1979). Atypical basal bodies with peripheral doublets instead of triplets have been occasionally observed in other invertebrates, e.g. in *Littorina* (Mollusca-Gastropoda) (Buckland-Niks, 1973). The middle part usually shows more or less patterned microtubules with doublets and singlets in very variable arrangements according to species and sometimes to sensilla.

The tip of the dendrite may contain a rootlet and some vesicles ; it eventually bears a number

Table 2

Non-neuronal components



of extensions that have been called "peripheral processes" (McLaren, 1972), "nerve processes" (McLaren, 1974, 1976*a* & *b*), "microvilli of the nerve process" (Wergin & Endo, 1976) or "finger-like projections" (Ward *et al.*, 1975).

The inner labial sensilla

MORPHOLOGY

The six radially arranged inner labial sensilla usually protrude from the surrounding cuticle as papillae provided with terminal pores. In a number of plant- and animal parasitic nematodes, the inner labial sensilla do not protrude and may be simple pores as in e.g. *Meloidogyne* (Baldwin & Hirschmann, 1973 ; Wergin & Endo, 1974 ; Sher & Bell, 1975 ; Endo & Wergin, 1977) and many other Tylenchida (Sher & Bell, 1975 ; De Grisse, 1977) and as in *Capillaria* (Wright, 1974). In several Tylenchida the pores are covered by the head cuticle and open into an invaginated area, called the prestoma by De Grisse (1977). This inward migration is most pronounced for the lateral receptors. In *Hemicycliophora* (De Grisse, 1977) and several (many ?) animal parasitic Secernentea pores are lacking and the receptors are embedded in the head cuticle. This may also be the case for *Aphanolaimus* where external pores are lacking (Coomans & De Waele, 1979). Finally, the inner labial sensilla may be absent as in e.g. *Syphacia* (Dick & Wright, 1973 ; Tenora, Wiger & Barus, 1978 ; Mészaros *et al.*, 1978) and *Dipetalonema* (Mc Laren, 1970 & 1972).

From the scanty evidence so far available it nevertheless appears that there seems to be a tendency towards a reduction in the number of receptors in the more specialized forms. In the few Adenophoreans studied the number of receptors per sensillum varies from five in *Mononchus* (Grootaert & Wyss, 1979) and mermithids (Poinar & Hess, 1974), four in *Aporcelaimellus* (Lippens *et al.*, 1974) and *Labronema* (Grootaert, 1978) to three (lateral sensilla) or two in *Capillaria* (Wright, 1974). In Secernenteans the common number is two, but *Heterakis* (Wright, 1977) and Criconematoidea (De Grisse, 1977) have only one receptor.

In the lateral inner labial sensilla of *Capillaria* (Fig. 3 E) one of the three receptors has a dorso-ventrally expanded ellipsoidal bulb filled with electron dense material (Wright, 1974). One of the receptors in the inner labial sensilla of mononchs and dorylaims becomes much wider than the others and contains more microtubules (at least 15 peripheral doublets and 45 singlets in *Labronema*). In Secernentea with two receptors, these are different in shape and length. The shortest receptor in *Caenorhabditis* (Fig. 3 D) and *Aphelenchoides* has a plate-like terminal portion with electron dense matrix. According to De Grisse (1977) it is the longest receptor that contains an electron dense terminal plate in Tylenchina, instead of the shortest one as he believed in 1975 and as in the above mentioned forms.

The number of microtubules encountered in the basal region of these receptors varies usually from 5-9 doublets and 0-3 singlets. Rootlets may be present, rudimentary or lacking.

The cell bodies of the inner labial receptors lie in front of the nerve ring, as has been established unambiguously by Ward *et al.* (1975) and Ware *et al.* (1975).

FUNCTION

The function of the inner labial sensilla may be a combined chemoreceptive and mechanoreceptive one as in the lateral sensilla of *Capillaria* (with one mechanoreceptor and two chemoreceptors) or in all inner sensilla of Rhabditids and most Tylenchids. In other forms the function is unimodal, either chemoreceptive, as e.g. the subdorsal and subventral sensilla in *Capillaria* and all inner sensilla in Criconematoidea (except *Hemicycliophora* ?), or mechanoreceptive, as in *Heterakis* and probably also *Hemicycliophora.*

Chemoreception is deduced from the fact that the receptor(s) is(are) in contact with the exterior ; mechanoreception is deduced from the more protected position (covered or embedded by cuticle) and/or the terminal differenciation with dense material. The chemoreceptors are considered to be contact chemoreceptors.

The short mechanoreceptors in *Caenorhabditis*

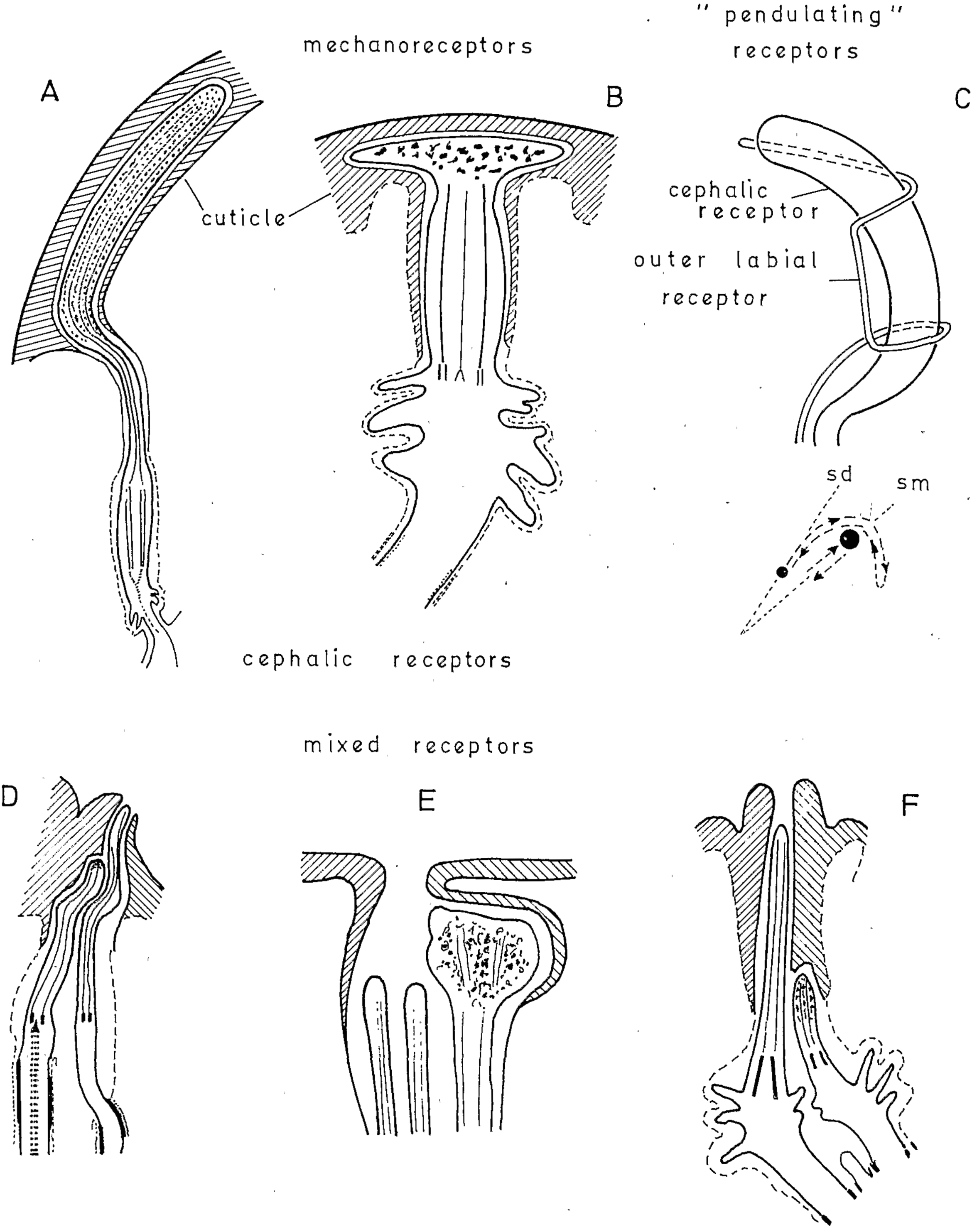
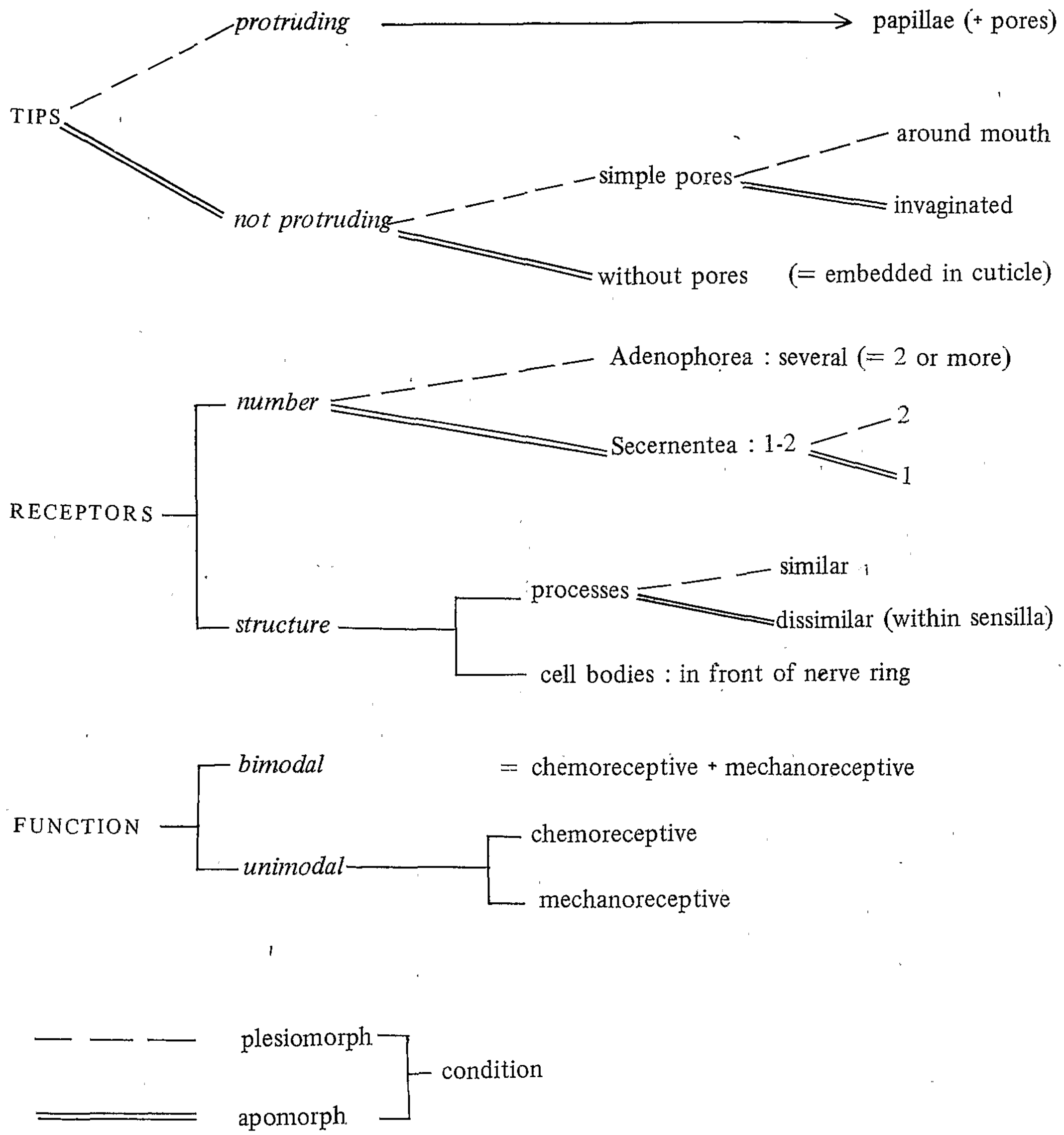


Fig. 3. Different types of receptors. A & B : Mechanoreceptors. A : Cephalic receptor of *Tylenchulus* (adapted from Natasasmita, 1979) ; B : Cephalic receptor of *Dipetalonema* (adapted from McLaren, 1976). C : Pendulating receptors of Hoplolaimidae (adapted from De Grisse, 1977). D-F : Mixed receptors. D : Receptors of inner-labial sensillum of *Caenorhabditis* (adapted from Ward *et al.*, 1975). E : Receptors of lateral inner labial sensillum of *Capillaria* (adapted from Wright, 1974). F : Receptors of lateral outer sensillum of *Heterakis* (adapted from Wright, 1977). *sd* = subdorsal, *sm* = submedian.

Table 3

INNER LABIAL SENSILLA (6)



are direct sensory-motor neurons. Indeed, the 32 anteriormost body muscles send processes to the nerve ring where neuromuscular synapses are formed, an unique feature among invertebrates (Ward *et al.*, 1975 ; Ware *et al.*, 1975).

The outer labial sensilla

MORPHOLOGY

The six outer labial sensilla are situated on the same radii as the inner ones. Their distal portions may protrude as papillae or setae, while in a number of apomorphous forms as many plant- and animal parasites they do not protrude and end as simple pores or are embedded in the cephalic cuticle. The latter situation is also present in *Caenorhabdilis*, but there the cuticle forms a bump above a small branch of the receptor (Ward *el al.*, 1975).

Some specialized forms as *Meloidogyne* (Baldwin & Hirschmann, 1973 ; Wergin & Endo, 1974), *Tylenchulus* (Natasasmita, 1979), *Syphacia* (Dick & Wright, 1973) and *Heterakis* (¹) (Wright, 1977) are devoid of outer labial sensilla ; while in some Filaroidea only the lateral ones are lacking. Also here, and as far as studied, Adenophorea have more receptors than Secernentea, e.g. four in *Mononchus* (Grootaert, 1978), *Aporcelaimellus* and *Labronema;* three in mermithids (Poinar & Hess, 1974) ; three or two in *Capillaria;* but only one in all Secernentea that possess outer labial sensilla. It should be mentioned that Baldwin and Hirschmann (1975) have reported the existence in *Heterodera* of paired dendrites leading to the outer labial and cephalic sensilla, but only one of them ending in a ciliary process. This is the only report of an eventual second nerve ending in these sensilla within the Secernentea. Since Baldwin and Hirschmann (1975) have mixed up the outer labial sensilla with the cephalic ones in their drawings 21-23, this result has to be verified.

All outer labial sensilla may possess equally well developed receptors, but in a number of cases the lateral ones differ from the subdorsal and subventral ones. This is the case with *Capillaria* where the subdorsal and subventral sensilla possess three, the lateral ones only two receptors (Wright, 1974). In Tylenchida the lateral sensilla are often reduced, this is especially so in Criconematoidea where the terminal part of the receptor is not surrounded by a supporting cell nor by a cuticular channel (De Grisse, Lippens & Coomans, 1974 ; De Grisse, 1977). The subdorsal and subventral sensilla each have a dendrite that "pendulates" around the cephalic one (De Grisse, Lippens & Coomans, 1974) (Fig. 3 C). This makes the course of these dendrites rather tricky unless serial sections are made. Apart from some exceptions, these receptors end in the cephalic cuticle.

The microtubules in the basal region of the receptors may consist of 5-9 peripheral doublets and 0-3 central singlets. Rootlets may be present or absent.

The cell bodies of the outer labial receptors lie also in front of the nerve ring.

FUNCTION

The outer labial sensilla may be bimodal—i.e. mechanoreceptive and chemoreceptive, as in (many ?) Adenophorea, or unimodal. In the latter case they are either mechanoreceptive (some Rhabditida, Spirurida and Tylenchida) or chemoreceptive as in *Capillaria.*

The cephalic sensilla

MORPHOLOGY

The four cephalic sensilla are submedian in position ; they usually protrude from the surrounding cuticle as setae or papillae with a terminal pore. In a number of parasitic nematodes

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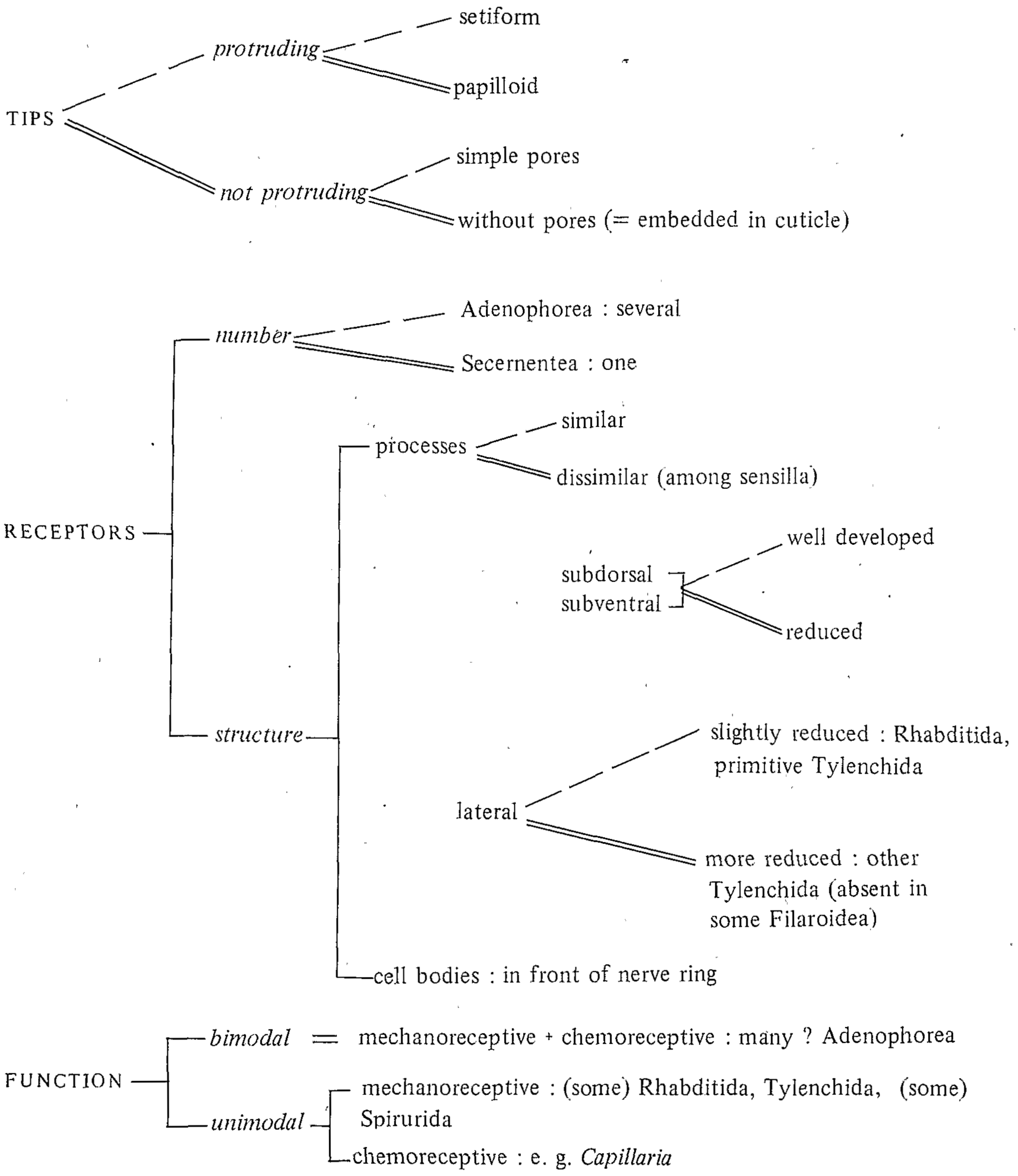
(¹) In *Heterakis* an outer papilla occurs in lateral position on each ventro-sublateral lip, but external to the amphid. It is doubtful whether this papilla is really a labial one in origin or the first one of a postlabial group that migrated on the lips. Not only is its position unusual, but its fine structure agrees completely with that of the postlabial papillae.

Table 4

OUTER LABIAL SENSILLA (6)



they do not protrude and in many of these the receptors are embedded within the head cuticle where they may end in flattened or bulbous differentiations filled with microtubules and electron dense material. In *Caenorhabditis* the receptors have a small electron dense branch which extends to a bump in the cuticle without penetrating through the cuticle (Ward *et al.*, 1975). Sometimes the cephalic sensilla are more developed in certain stages as e.g. in the infective third juvenile of *Neoplectana* (Poinar & Leutenegger, 1968) or in the male as e.g. in *Caenorhabditis* (Ward *et al.*, 1975), and a number of mainly aquatic nematodes.

Also here Adenophorea usually have more receptors in their cephalic sensilla than Secernentea. *Mononchus*, *Aporcelaimellus*, *Labronema* and *Capillaria* all have three receptors, but mermithids may have only two. Secernentea have two or only one receptor. When there are two receptors they may be different in structure (and function). Both may be well developed as in *Aphelenchoides* (De Grisse, 1977) and in males of *Caenorhabditis* (Ward *et al.*, 1975), consisting of a thick one embedded in the cuticle and a narrow one leading to a pore. In most Tylenchina, however, the narrow receptor is reduced, while it has disappeared in the hermaphrodite of *Caenorhabditis*, in several animal parasites, in *Meloidogyne* and in Criconematoidea.

The number of peripheral doublet microtubules in the basal region of the receptors varies from 6-9 ; in addition several central singlets may occur. Rootlets are usually absent.

The cell bodies of the subventral cephalic receptors lie in front of the nerve ring, those of the subdorsal ones just behind the nerve ring.

FUNCTION

The cephalic sensilla may have a bimodal function, i.e. mechanoreceptive and chemoreceptive. This is apparently so when differently structured receptors are present as in Secernentea with a thick probably mechanoreceptive receptor and a thin chemoreceptive one. In many nematodes the cephalic sensilla are supposed to be mechanoreceptive (Fig. 3 A, B). No doubt they have such a function in those Secernentea that possess only one receptor per sensillum or where the second receptor is reduced and no longer connected with the exterior. Little is known in this respect about Adenophorea, except that there the cephalic receptors communicate with the exterior through pores. At least in *Capillaria* the cephalic sensilla are considered to be purely chemoreceptive (Wright, 1974).

Special functions can be attributed to the cephalic sensilla when e.g. males have more developed sensilla than females, these may serve for the detection of sex attractants ; in some infective stages they may be important for detection of the host.

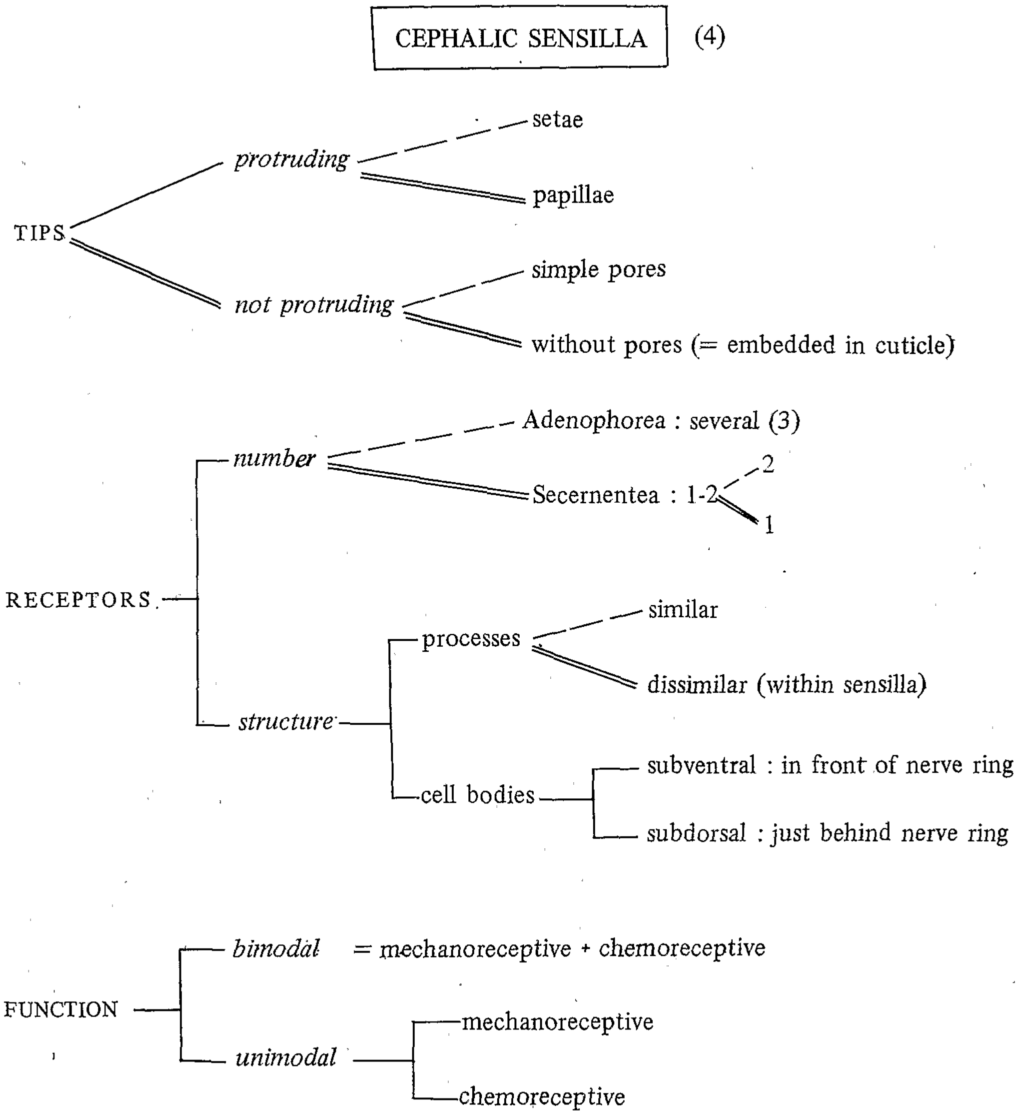
The amphids (Fig. 4)

MORPHOLOGY

Before discussing the details it is necessary to explain the terminology that will be used below. In several papers Riemann and colleagues proposed a useful terminology (Riemann, Rachor & Freudenhammer, 1970 ; Riemann, 1972 ; Storch & Riemann, 1973) that will be followed here. The distal part of the amphid is called the *fovea* and corresponds with what is usually called "amphid" or sometimes "amphideal pocket" in taxonomic descriptions. The fovea is either an external excavation of the head cuticle as in many Chromadoria or an invagination of the cuticle, thus forming a pocket connected with the exterior through an aperture, the *apertura amphidialis*. The fovea is completely or partially filled up with a gelatinous substance, the *corpus gelatum*, apparently secreted by the amphidial gland. The fovea is connected with the amphidial duct or *canalis amphidialis* through the duct pore or *porus canalis amphidialis*. The amphidial duct leads posteriorly into the *fusus amphidialis*, commonly called the sensilla pouch. It is here that the amphidial dendrites enter the sensillum. Fovea, amphidial duct and anterior part of the fusus are lined with cuticle (Storch & Riemann, 1973 (¹) ;

(¹) In this respect it is rather misleading that in the abstract of Storch and Riemann's paper it is said that "In the region of the fusus the cuticle is lacking", while they illustrate the presence of it in their figures 3 and 4 and refer to this cuticle on p. 166.

Table 5



De Grisse, 1977). The wall of the main and posterior part of the fusus is formed by the amphidial gland. When the fovea is small as in many Secernentea it may be difficult to delimit it from the canalis. It is even not excluded that the fovea itself has disappeared and that the duct pore has become the external opening.

Typically the amphidial aperture or the fovea are situated laterally, but in some Adenophorea and in many Secernentea they have slightly shifted dorsad. In Adenophorea and some Secernentea the aperture or the fovea are postlabial in position, but in most Secernentea and a few Adenophorea they have migrated onto the lateral lip region.

The most variable part of the amphid appears to be the fovea, especially when it is external as in the Chromadoria. This part may also differ

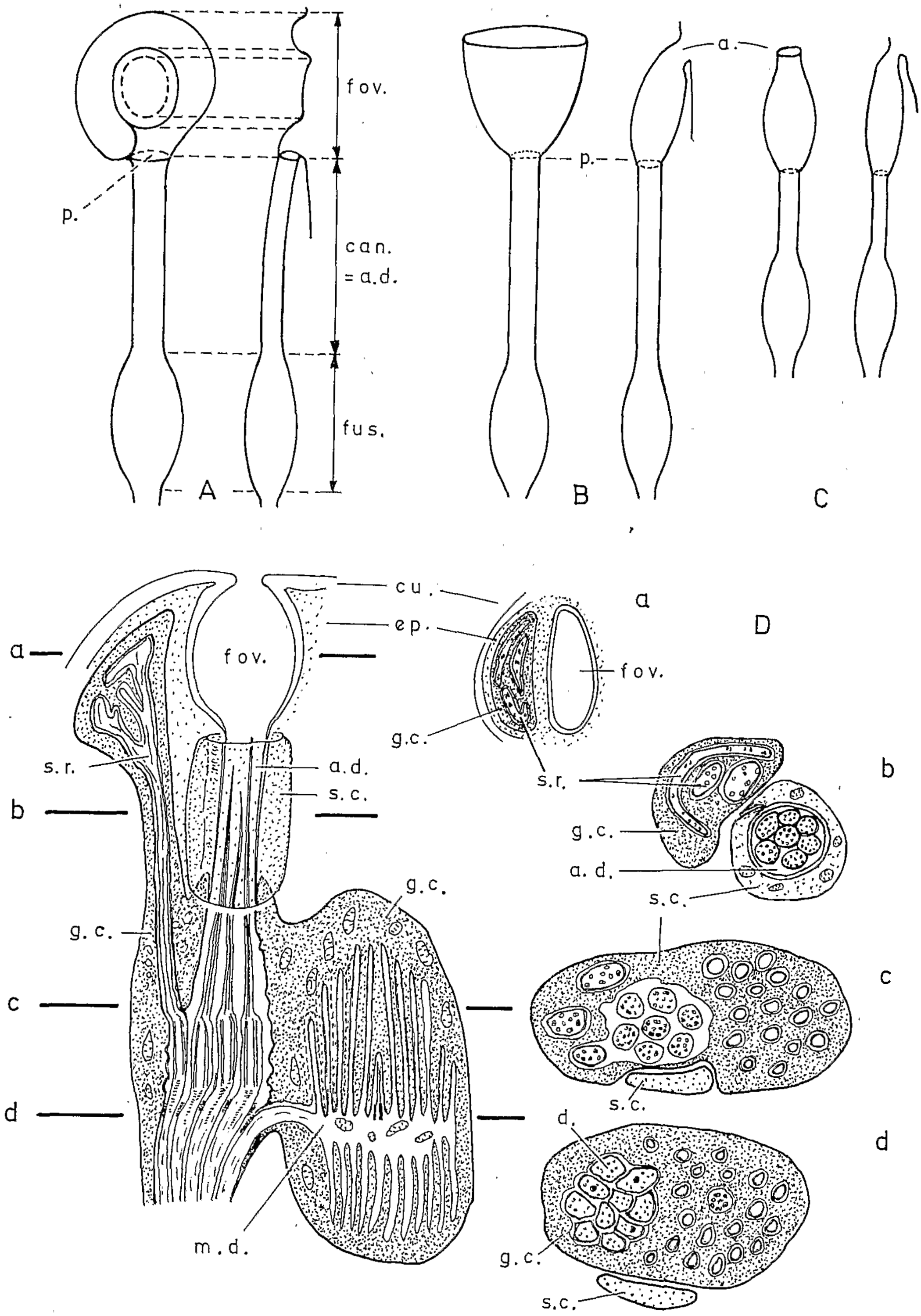


Fig. 4. Amphid structure. A : Amphid with external, spiral fovea ; seen from above and in profile. B & C : Amphids with internal fovea, seen from above and in profile. D : Amphidial structure of a secernentean (assembled from diagrams and micrographs of several authors) with four transverse sections a-d. *a.* : apertura, *a.d.* : amphidial duct, *can* : canalis amphidialis, *cu.* : cuticle, *d.* : dendrite, *ep.* : epidermis, *fov.* : fovea, *fus.* : fusus, *g.c.* : gland cell, *m.d.* : multivillous dendrite, *p.* : porus canalis or duct pore, *s.c.* : supporting cell, *s.r.* : sheath receptor.

among sexes, being sometimes considerably larger and more complex in males. The innermost part of the fovea leads to the porus canalis and the latter is exactly mediolateral in position or may have shifted dorsad. The duct and the fusus show some variation in length and width according to the group or even species.

The number of receptors is much higher in the amphid than in the other sensilla. The exact number is difficult to establish without serial sections, because some processes are forked and others do not enter the amphidial duct. Since the receptors that penetrate into the duct not only differ in structure but probably also in function from the others it is better to differrentiate them as *duct* or *canal receptors*, resp. *accessory* or *sheath receptors.* In order to avoid confusion with other accessory receptors the term "sheath receptors" is preferred. Again the number of receptors is usually higher in Adenophorea (only Enoplia have been studied !) than in Secernentea. The highest number of receptors reported so far is that for *Oncholaimus vesicarius* by Burr and Burr (1975) with 28-36 canal receptors and about ten sheath receptors. Strangely enough these receptors are connected with only four dendrites, three for the canal receptors and one for the sheath receptors. In *Paratrichodorus* 23 receptors have been reported (Hirumi & Chen, 1968 ; Hirumi, Raski & Jones, 1970). In *Mononchus* nineteen amphidial receptors were found in the male and seventeen in the second stage juvenile (Grootaert, 1978). Nineteen receptors were also found in *Labronema* (Grootaert, 1978) and inside the duct of *Xiphinema* (Roggen, Raski & Jones, 1967), while 22 receptors were reported for *Longidorus* (Hirumi, Raski & Jones, 1970 ; Taylor *et al.*, 1970). In mermithids the number varies from sixteen to nineteen (Poinar & Hess, 1974 ; Batson *in* Mc Laren 1976*a* & *b*). Storch & Riemann (1973) described sixteen receptors inside the amphidial duct of *Tobrilus.* The lowest number occurs in *Capillaria* (Wright, 1974), with only ten duct receptors.

In Secernentea the most detailed account is given for *Caenorhabditis* by Ward *et al.* (1975) and Ware *et al.* (1975). In the first paper the cavity of the amphid is called the duct and no distinction is made between duct and fusus, while in the second one the cavity is called a pouch. Apart from this and some other minor differences, there is an overall agreement between both studies. Twelve dendrites arrive in the fusus and eight of these give rise to ten duct receptors, since two of them possess two receptors each. The four other dendrites lead to five sheath receptors, all of them invading the gland cell. One of these dendrites is peculiar in that it has, besides a ciliary process, about 50 finger-like projections or microvilli that invade the gland cell dorsally from the fusal cavity or duct. This dendrite will be called here the "multivillous dendrite". Yuen (1968) mentioned thirteen receptors for *Panagrellus.*

In zooparasitic Secernentea the total number of amphidial receptors reported varies from three or four (*Litomosoides* cf. Mc Laren, 1971, cited in Mc Laren, 1976*b*) to nine (*Dirofilaria* cf. Kozek, 1968 ; *Dipetalonema* cf. Mc Laren, 1972*a*) in Spirurida, from thirteen to fifteen in Strongylida (Wright, 1975 ; Mc Laren, 1976*a*) and fifteen in the ascarid *Heterakis* (Wright, 1977). In *Nippostrongylus* as well as in *Heterakis* there are thirteen duct receptors and two sheath receptors.

Tylenchida commonly have seven canal receptors (Chen & Wen, 1972 ; Baldwin & Hirschmann, 1973 & 1975 ; De Grisse, Lippens & Coomans, 1974 ; Wergin & Endo, 1976 ; De Grisse, 1977), but in *Aphelenchoides* there are only six (De Grisse, 1977) and in one specimen of *Meloidogyne* eight receptors were found (Baldwin & Hirschmann, 1973). In addition three to five sheath receptors have been reported. One of the dendrites gives rise to numerous microvillous projections and one sometimes two ciliary receptors that invade the gland. This dendrite is clearly homologous with the multivillous dendrite of *Caenorhabditis*, but the number of microvilli is different e.g. 14-18 in males and 35 in females of *Tylenchulus* (Natasasmita, 1979), 75 in *Heterodera* (Baldwin & Hirschmann, 1975), 200 (Wergin & Endo, 1976) or up to 350 (Baldwin & Hirschmann, 1973) in *Meloidogyne.* Baldwin and Hirschmann (1973 & 1975) and De Grisse (1977) interpreted these projections as microvilli of the amphidial gland cell. Wergin and Endo (1976) erroneously described the "nerve process" (= multivillous dendrite) as lying dorsal to the other dendrites in *Meloidogyne*, similar to *Caenorhabditis.* Baldwin and

Hirschmann (1973, 1975) and Natasasmita (1979) have shown that the microvillous projections are ventral to the other dendrites in *Meloidogyne* and *Heterodera*, respectively *Tylenchulus*. Also some electron micrographs in Wergin and Endo's (1976) paper (their figures 11 & 12) show that the latter observation is correct. De Grisse (1977) considered the multivillous dendrite as part of the amphidial gland cell and its receptor(s) as amphidial gland receptor(s). In *Scutellonema* he has demonstrated the presence of two receptors (cf. nº 12 and 13 in his figures 349-355) implanted on the multivillous dendrite.

Other sheath receptors have been observed laterally to the amphidial duct ; they ascend toward the lateral cephalic sectors, become flattened into broad lamellar structures and terminate beneath the epidermis (Wergin & Endo, 1976 ; Natasasmita, 1979) ; they are called the lateral amphidial receptors by Natasasmita (1979). Here they will be called "external sheath receptors" ; the specification "external" may be more generally applicable than "lateral", since similar receptors described for *Caenorhabditis* may extend as far dorsad and ventrad that they approach their counterparts from the other lateral sector mediodorsally and -ventrally (Ware *et al.*, 1975).

Some of the above mentioned figures will have to be verified, since it is not always easy to find out where the receptors have been counted, inside the canal or inside the fusus.

The number of microtubules in the basal region of the receptors is extremely variable. From 5 to 39 doublets and 0-7 singlets have been reported.

The cell bodies of the amphidial receptors are enclosed within the lateral ganglia, behind the nerve ring.

FUNCTION

Several functions have been proposed for the amphids, but they are generally considered to be chemoreceptors. Especially since more is known about the ultrastructure of the amphids, it became evident that these sense organs are not only structurally complex, but must also have several functions.

Chemoreception was assumed because the amphids open to the outside so that a number of their receptors are in contact with the external environment. Although direct evidence for such a function is still lacking, the recent isolation of chemotaxis-defective mutants in *Caenorhabditis* (Lewis, in Ward *et al.*, 1975 & in Ward, 1976) provides strong indirect evidence. Indeed, these mutants show abnormalities in some of their amphidial receptors. The duct receptors are the most likely candidates for the perception of chemical substances. The external sheath receptors with their plate-like terminal portions resemble mechanoreceptors found in other invertebrates. The special sheath receptors in *Oncholaimus vesicarius* are supposed to be photoreceptors since they are located near and are shaded by a pigmented oesophageal cell (Burr & Burr, 1975). Furthermore a secretory activity has been postulated several times, although such an activity could not be demonstrated in a number of cases.

Chemoreception involves the response to many stimuli and is important for orientation, prey, host or mate detection (Croll, 1970 ; Bird, 1971 ; Green, 1971 ; Ward, 1976). Amphids are apparently distance chemoreceptors and the fact that they are often better developed in males (especially in rare aquatic species) may be related with the detection of sex attractants by the females. However, other distance chemoreceptors may exist as can be inferred from observations of live specimens, e.g. male rhabditids. Some caudal receptors allow the male to detect females nearby and provoke even backward movements of the males towards the females. This observation agrees with laser microbeam studies (Samoiloff, Balakanich & Petrovich, 1974) in which it was found that the copulatory spicules of *Panagrellus* function as posterior receptors for orientation to mating attraction. In view of their probable role in host finding, special attention should be given to the size and development of the amphids in the infective stages. At least in *Neoaplectana* is has been established that the amphids were more highly developed in the infective third stage juvenile (Poinar & Leutenegger, 1968).

The above mentioned presence of presumptive photoreceptors in the amphid of an *Oncholaimus*-species is the only substantial record of ciliary photoreceptors in nematodes. Since they are associated with pigment spots they probably have directional sensitivity.

Mechanoreception has been postulated several times. As already mentioned by Inglis (1964), it is difficult to believe that an elaborate fovea such as found in a number of freeliving Chromadoria could increase the efficiency of a chemoreceptive organ. This author supposed the amphids are a kind of stretch receptors that give information about the stress and strain to which the cuticle is being subjected during movement. Riemann (1966) thought they could detect pressure changes in the surrounding water. Riemann (1972), after giving a detailed account of the structure of the amphid in a number of aquatic nematodes where these organs are well developed and after reporting the presence of a corpus callosum, compares the amphids with sense organs of Chaetognatha and neuromasts of aquatic vertebrates. In all these sense organs the receptors are embedded in a viscous secretion. When looking at scanning electron micrographs of amphids with a spiral fovea (Coomans & De Waele, 1979) one has the impression that this structure is indeed suited to guide vibrations in the surrounding water toward the duct pore and further toward the receptors in a similar way as a mammals auricle guides vibrations toward the other parts of the ear. The supposition that at least aquatic nematodes possess some kind of vibration receptors is by no means farfetched since such receptors have been reported for a number of aquatic invertebrates (Horridge, 1966).

With respect to the secretory activity of the amphids, Mc Laren (1974, 1976*a* & *b*) has proposed the hypothesis that the receptor and its dendrite (called "axon" by her) form a sensory-motor unit. The receptor, after receiving an external stimulus would then stimulate its dendrite ("axon") and the latter would switch on the secretory activity of the gland. The same or perhaps other receptors may then monitor the output of secretion. Wergin and Endo (1976) have emended this hypothesis. According to these authors the accessory amphidial receptors (= sheath receptors) may function as tactoreceptors and also stimulate secretion by the amphidial gland. The secretory activity of the gland would be monitored by the nerve process (= multivillous dendrite). The amphid is regarded as a sensory organ capable of secreting closely monitored materials in response to chemical and tactile stimuli.

Although there is no direct evidence for a glandular activity of the sheath cell in a number of cases, a kind of secretory material seems to be invariably present in the amphidial lumen. Cytochemical studies have demonstrated the presence of cholinesterase in the amphids of a number of plantparasitic (Rohde, 1960 ; Bird, 1966) and animal parasitic nematodes (Mc Laren, 1972 ; Mc Laren, Burt & Ogilvie, 1974). In the latter paper it has been shown that *Necator* actively secretes the enzyme in the culture medium. At least in some parasitic nematodes as *Meloidogyne* and some Strongyles the secretory activity of the amphidial glands may be more important than in other nematodes. The mechanism by which this secretion is monitored remains unknown. Because of its close association with the sheath cell it seems likely however that the multivillous dendrite and its receptor(s) play an important role in this.

The accessory sensilla (Fig. 5)

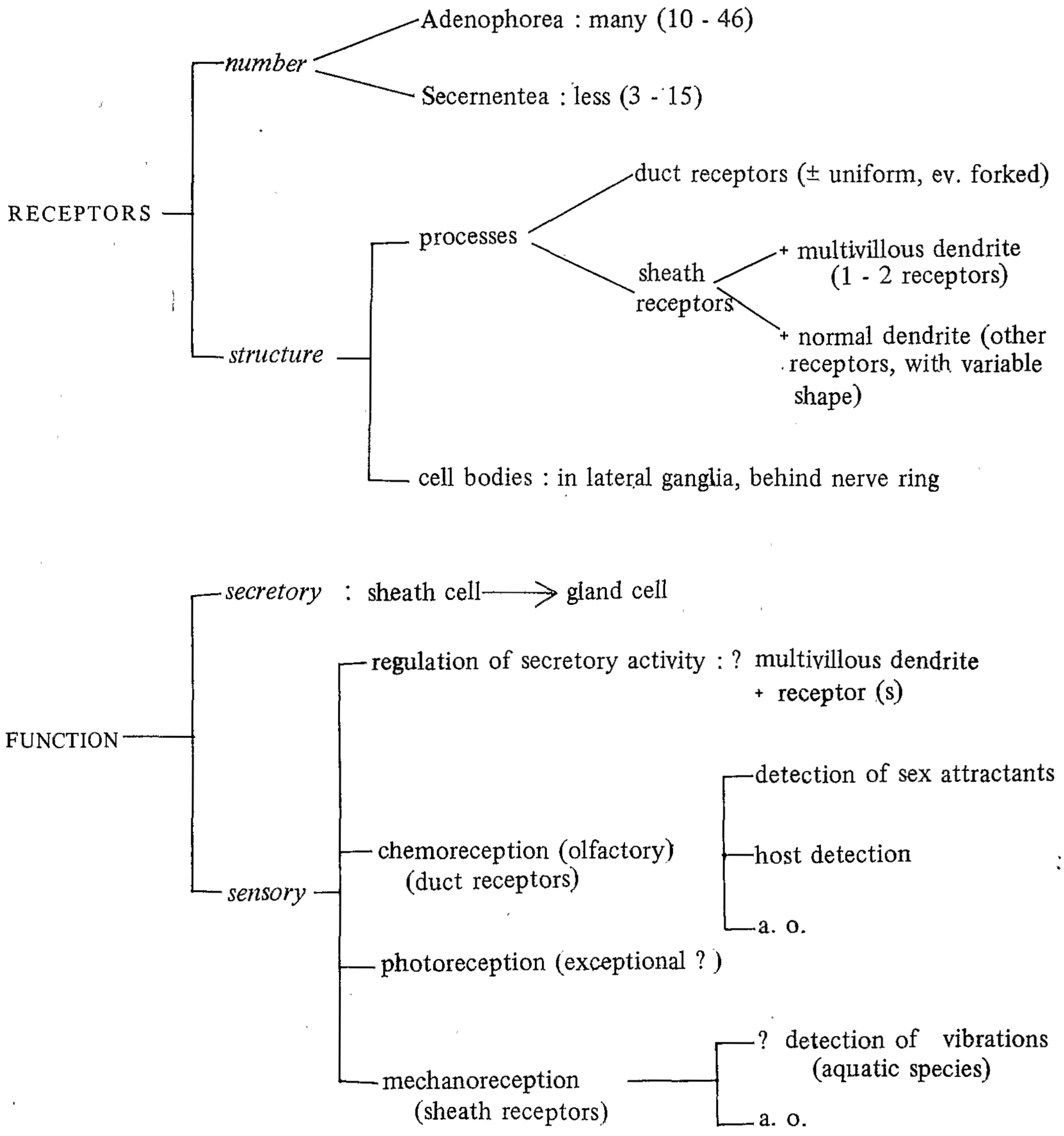
MORPHOLOGY

Accessory sensilla have been found so far only in Secernentea. They were first detected in *Pelodera* (De Grisse, Coomans & Demets, 1974) and subsequently described in more detail in *Caenorhabditis* (Ward *et al.*, 1975) *Meloidogyne* (Endo & Wergin, 1977), several Tylenchida (De Grisse, 1977) and *Tylenchulus* (Natasasmita, 1979).

These sensilla only consist of neuronal elements and a supporting cell as well as a sheath cell are lacking. The dendrites that lead to the sensilla originate from the lateral nerves. In each lateral region two dendrites branch off from the lateral nerve and run anteriad in the area between the dendrites of the lateral inner labial sensilla and the amphid. Then they lead to flattened receptors and diverge gradually toward the subdorsal or subventral head sectors where several convoluted lamellae are formed

Table 6

AMPHIDS (2)



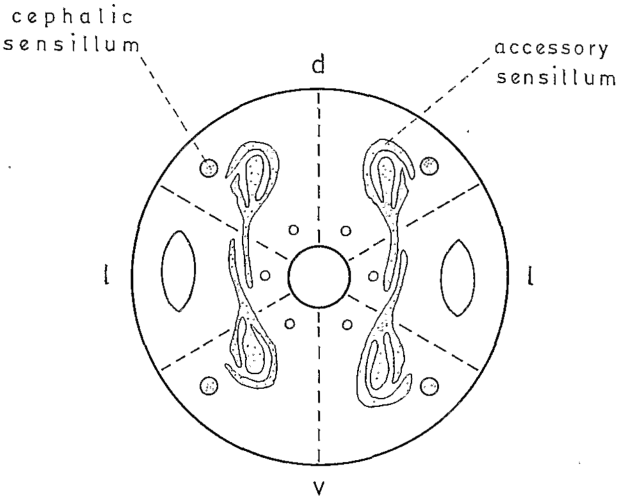


Fig. 5. Accessory receptors of *Tylenchulus* (modified after Natasasmita, 1979).

between the inner labial sensilla and the corresponding outer labial and cephalic ones (or between inner labial and cephalic sensilla when the outer labial ones are lacking as in *Meloidogyne* and *Tylenchulus*). The lamelliform receptor contains a modified cilium whose basal part consists of seven to nine peripheral doublets and is situated sublaterally, that is near the boundary of lateral and subdorsal sectors or that of lateral and subventral sectors, either in the lateral or in the subdorsal respectively subventral sector.

The accessory sensilla do not penetrate into the head cuticle, but invade the epidermis.

The most complete description of the accessory sensilla was given by Natasasmita (1979). Indeed, he was the only author that established the continuity between the lamellae in the subdorsal and subventral head sectors with those in the lateral sectors and so established the complete structure of the accessory sensilla. Such a connection between subdorsal and subventral lamellae with the lateral ones can also be inferred from the electron micrographs in Endo and Wergin's (1977) paper. The latter authors were the first to interprete the subdorsal and subventral lamellae as nervous structures but considered them as separate from the accessory sensilla and called them "accessory axons". Ward *et al.* (1975) described the accessory sensilla as "two additional ciliated accessory neurons... m and n" associated with each lateral inner labial sensillum. The cell bodies of the dorsosublateral m-neurons lie far behind the nerve ring, those of the ventrosublateral n-neurons occur in front of it.

FUNCTION

It is difficult to suggest a possible function for the accessory receptors. Endo and Wergin (1977) and Natasasmita (1979) compare them with mechanoreceptors, but the head is already provided with other mechanoreceptors and receptors for some other stimuli have not yet been detected. The elaborate lamellar extensions are suggestive for a photoreceptorial function. Indeed, similar structures are considered to be photoreceptors in other invertebrates. Soil nematodes in particular would benefit from a kind of light sense that would enable them to avoid the unfavourable conditions at the surface. Rhabditids with a phoretic behaviour on the other hand have to move to the surface in order to reach the carrying organism. Also here an anteriorly placed photoreceptor would be an advantage. Of course, this does not necessarily mean that the accessory sensilla are these photoreceptors. Other senses have been reported, such as a thermotaxis, without any precise information about possible receptors.

The ocelli and pigment spots

MORPHOLOGY

A number of aquatic Adenophoreans possess usually paired pigment spots or true ocelli, situated laterally or dorsolaterally along or partly inside the oesophagus, and commonly called "eye spots". The pigment associated with these structures may be granular or rarely diffuse ; it may be localized or dispersed over a certain area. Some eye spots are provided with a hyaline portion that has been referred to as a "lens" or comparable structure. According to

Table 7

ACCESSORY SENSILLA (4)

only neuronal component present

- *number*
  - Adenophorea : ?
  - Secernentea : 1

RECEPTORS

- *structure*
  - processes : lamelliform
  - cell bodies
    - dorsosublateral : behind nerve ring
    - ventrosublateral : in front of nerve ring

FUNCTION unknown (photoreceptors ? , thermoreceptors ?)

OCELLI & PIGMENT SPOTS (2)

NON NEURONAL COMPONENT

- SHADING PIGMENT
  - outside oesophagus
    - in pseudocoelom (O.)
    - in epidermis (P.S.)
  - inside oesophagus
    - in marginal cells (O.)
    - in radial cells (P.S.)

NEURONAL COMPONENT

- SENSORY CELL
  - with rhabdomeric receptor (O.)
  - with ciliary receptor (P.S.)

Schultz (1931), Croll (1970) and Bird (1971) only the latter eye spots can be regarded as true ocelli.

So far only a limited number of species have been studied at the ultrastructural level : the Enoplia *Deontostoma californicum* (Siddiqui & Viglierchio, 1970*a* & *b*), *Enoplus communis* (Croll, Evans & Smith, 1975) and *Oncholaimus vesicarius* (Burr & Webster, 1971 ; Burr & Burr, 1975) ; the Chromadoria *Chromadorina bioculata* (Croll, Riding & Smith, 1972), *Araeolaimus elegans* and *Chromadorina* sp. (Croll, Evans & Smith, 1975).

From these studies emerges that the pigment that characterizes the eye spot is in fact a shading pigment that occurs either in the body cavity, as in *Araeolaimus*, or in the oesophagus, as in *Deontostoma*, *Oncholaimus* and *Chromadorina*. When the pigment (mainly melanins) is confined to the oesophageal tissue, it may be stored especially in marginal muscle cells, as in *Deontostoma*, or in the most anterior radial muscle cells, as in *Oncholaimus*.

The sensory cell is located outside, but close to the oesophagus ; it either has a rhabdomeric receptor, as in *Deontostoma*, *Chromadorina* and *Araeolaimus*, or a ciliary one as in *Oncholaimus*. The latter structure forms a part of the amphid and has been described there. As the pigment spots in *Enoplus* are rather comparable with those of *Oncholaimus* and since no rhabdomere was found in that nematode (Croll, Evans & Smith, 1975) it is not excluded that *Enoplus* has a similar type of photoreceptor (McLaren, 1976*a*). In this respect the diffuse pigmentation, called the chromatrope, that occurs in the cephalic epidermis of gravid females of *Mermis subnigrescens* should also be mentioned. This pigment is probably a mixture of haemoglobin and oxyhaemoglobin (Ellenby, 1964 ; Ellenby & Smith, 1966 ; Croll, Evans & Smith, 1975) that may eventually shade a ciliary photoreceptor located in the amphid. Pending further research on both cases, this suggestion is purely speculative.

In *Deontostoma* the ocellus is of an inverted type, with the distal or rhabdomeric part of the sensory cell embedded in the anterior end of the pigment cell, the perikaryon located outside and anterior to it and with the proximal end of the sensory cell sending an axon to the lateral nerve (Siddiqui & Viglierchio, 1970*b*). The ocelli of the closely related genus *Leptosomatum* are similar to those of *Deontostoma* (Croll, Evans & Smith, 1975).

Apparently the so called lens of nematode ocelli is in fact the perikaryon of the sensory cell. The detailed structure of the rhabdomeric receptor so far found in nematodes resembles that of the rotifer *Asplanchna* (Eakin & Westfall, 1965).

FUNCTION

Although there is little physiological evidence for photosensitivity in nematodes, a number of behavioural photoresponses have been reported (Croll, 1970). Furthermore it is possible, on the basis of comparative morphology, to suggest a photoreceptive function for the nematode ocelli, which can now be defined as discrete photoreceptors composed of a lamellar rhabdomere, shaded directionally by a closely associated pigment cell (McLaren, 1976*a*). Pigment spots not associated with a rhabdomere may be merely aggregates of pigments whose origin and possible function is unknown and then cannot be considered to be involved in photoreception, but when situated near the amphid they may act as shading structures for a ciliary receptor, as was suggested for *Oncholaimus* and as may be true for some other nematodes as well.

Conclusions

Although the number of nematode species that have been examined until now with the electron miscroscope is very limited, the picture of the anterior sensilla that emerges from these studies allows some general statements.

The first of these is that the basic arrangement of the anterior sensilla as proposed by De Coninck (1942 & 1965) is valid throughout the group. Departures from this basic arrangement may occur when some of the sensilla are no longer present as in several parasitic forms, or when additional sensilla are present as in certain marine nematodes (Hendelberg, 1978 & 1979).

Further complications are the occasional occurrence of sexual dimorphism and the presence of accessory sensilla. In view of the general applicability of De Coninck's scheme, his (emended) terminology is used here.

The second general conclusion is that the basic structural unit of the anterior sensilla (but this is also true for most of the other nematode sensilla) consists of two parts : (1) a neuronal component comprising one or more bipolar sensory neurons that lead to modified cilia with variable microtubular arrangements and (2) a non-neuronal part that may be rather unspecialized epidermal or glial tissue or that may be differentiated into an anterior supporting (or socket-) cell and a pocket (or gland-) cell behind it.

The number of receptors per sensillum varies according to taxa, but there seems to be a tendency towards a reduction in number in the more specialized forms ; Secernentea generally have less receptors than Adenophorea. The terminal processes may be similar in structure or dissimilar. In the latter case the dissimilarity exists either within a certain type of sensillum (inner labial-, cephalic sensilla and amphids) or among the different sensilla of one type (outer labial sensilla). The dissimilarity apparently reflects a difference in function too. The labial and cephalic sensilla may have a bimodal or unimodal function. When different types of receptors are present in such a sensillum some may be chemoreceptive and others mechanoreceptive. The chemoreceptors of labial and cephalic sensilla are likely to be contact or short distance receptors and therefore comparable in function with gustatory organs. The mechanoreceptors are connected with well developed papillae or setae in aquatic forms, but are embedded in the head cuticle in many soil and parasitic forms. In the latter case their terminal portion is often expanded, either plate-like or bulboid, and provided with dense material. Whether the bimodality is the plesiomorphous condition or not remains an open question till more information becomes available about primitive species. The general picture so far seems to indicate that the inner labial sensilla are rarely purely mechanoreceptive or chemoreceptive. Clearly chemoreception here is important for detecting and testing the food. On the other hand, it should be stressed that the mechanoreceptors of the inner labial sensilla of *Caenorhabditis* have been identified as direct sensory-motor neurons connected with the anterior body muscles. These receptors may be involved in controlling the feeding movements of the head end. The outer labial and cephalic sensilla are apparently less important for chemoreception than for mechanoreception and many Secernentea have lost their chemoreceptors especially in the outer labial sensilla.

The amphids are the nematode's most complex sense organs, as well in their morphology as in their function. They can be considered as essentially multifunctional, with chemoreception as one of their most important functions. In contrast with the other anterior sensilla, the amphids are considered to be distance chemoreceptors involved in many behavioural functions and hence comparable to olfactory organs. No evidence is available for a mechanoreceptive function of the amphids, yet the structure of this organ is a number of aquatic nematodes is suggestive for such a function. Photoreception seems likely in some aquatic forms. Finally, the amphids are also secretory organs that probably regulate their own secretory activity.

The function of the recently discovered accessory sensilla remains enigmatic, but receptors for a kind of dermal light sense and for the reception of thermal stimuli have yet to be determined.

Discrete photoreceptors apparently evolved several times and along several lines. They are most frequent in marine forms living on littoral algae and on the sediment. Although the presense of ocelli is usually considered to be a primitive condition, these structures are the most complex photoreceptors that nematodes possess. The pigments spots and their associated amphidial photoreceptors are less elaborate and may represent a stage that originated later in the evolution and so did not yet reach such a high complexity. Nevertheless, the occurrence in nematodes of both types of photoreceptors—rhabdomeric and ciliary—gives further weight to the conclusion of Vanfleteren and Coomans (1976) that the photoreceptor type is not conservative enough to ascertain the phyla along the main lines of evolution.

To summarize, it can be said that the story of the anterior sense organs is far more complex than could be inferred from light microscope studies and that, despite the recent information gained from electron microscopic investigations, still many problems exist. Future research should further consider the detailed morphology especially of more plesiomorphous forms, but also further develop studies with mutants and surgical ablations with laser microbeams in order to see how far deviations in or destruction of some of the receptors are reflected in changes in behaviour. Although the nematode nervous system is considered to be a conservative system with a rather small number of cells, different behavioural patterns exist according to the different environments and ecological niche occupied by the species. This no doubt is correlated with a different degree of development and functional differences of the various sense organs.

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Note added in proof :

Dr. K. Wright kindly informs me that the "type II sense organs" of *Nippostrongylus* (Wright, 1975) and the "doublet papillae" of *Heterakis* (Wright, 1977) are in fact composed of a cephalic and outer labial receptor each. Therefore the statement made above that outer labial sensilla are lacking in *Heterakis* is not correct.