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# Fine structure of receptor organs in oribatid mites (Acari)

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**Abstract:** Receptor organs of oribatid mites represent important characters in taxonomy. However, knowledge about their detailed morphology and function in the living animal is only scarce. A putative sensory role of several integumental structures has been discussed over years but was only recently clarified. In the following the present state of knowledge on sensory structures of oribatid mites is reviewed.

Setiform sensilla are the most obvious sensory structures in Oribatida. According to a classification developed mainly by GRANDJEAN the following types are known: simple setae, trichobothria, eupathidia, famuli and solenidia. In *Eupelops* sp. the simple notogastral setae are innervated by two dendrites terminating with tubular bodies indicative of mechanoreceptive cells. A similar innervation was seen in trichobothria of *Acrogalumna longipluma.* The trichobothria are provided with a setal basis of a very high complexity not known from other arthropods. The setal shafts of these two types of sensilla are solid and without pores. They thus represent so called no pore sensilla (np-sensilla). In contrast the shafts of the eupathidium and the solenidion forming the double horn of the palp tarsus in *Acrogalumna longipluma* are "hollow" and contain dendritic processes. The simple cuticular wall of the solenidion bears pores. The solenidion hence represents a wall pore sensillum (wp-sensillum) most likely functioning in olfaction. According to SEM figures eupathidia and famuli may have terminal pores, but this needs to be proven by TEM. Terminal pore sensilla (tp-sensilla) frequently represent contact chemoreceptors (gustatory sensilla). Nothing is known about the functional implications of the various different shapes of these setal types.

Some preliminary results on slit sense organs (lyrifissures) are given. In *Scutovertex minutus* a notogastral slit sense organ is represented by a cleft in the "normal" procuticle containing a modified, presumable more flexible cuticle. This cuticle bears a small process apparently connected with a dendrite containing a tubular body. Hence these structures likely represent mechanoreceptors similar to slit sense organs in other arachnid groups, which are stimulated by alterations of cuticular strains. The fine structure of the slit sense organ of *Scutovertex*, though only fragmentarily known, differs in some respect from that of, e.g. spiders or ticks.

The chelicerae of Oribatida contain nerve fibres which terminate within the teeth of the chelae. It has been suggested that these terminations may serve as gustatory receptors.

Many Oribatida possess photosensitive areas or organs. These are present in the form of small ocelli in a few early derivative taxa (e.g. *Heterochthonius gibbus*) and are located on the prodorsum. On the contrary many Brachypylina have "clear spots" or lenticuli located at the anterior border of the notogaster, hence in an opisthosomal position according to present interpretation. These structures indicate the presence of very peculiar light recep-

 

tors, which are regarded as being secondarily evolved organs. The receptor cells are evidently derived from photosensitive neurons with perikarya located in the synganglion. The receptor poles of these cells are lamellated and are in some species surrounded by pigment containing cells likely derived from the fat body (e.g. *Hydrozetes lemnae*, *Scutovertex sculptus*, *Scapheremaeus argentina*). In others the lamellated bodies are surrounded by extensions of the ventriculus corresponding to the preventricular glands (*Parapirnodus* sp.).

Genital papillae and Claparède organs have never been seen to be innervated. Hence a sensory function as sometimes suggested is unlikely. From the fine structure, which is almost identical with that of genital papillae of other actinotrichid mites and ionocytes of other arthropods, it seems most likely that these organs are involved in water-, ion- and osmoregulation.

Porose organs which are present in many oribatid taxa do not serve as sensory structures. Some are innervated, but only by efferent neurons. Some porose organs of certain taxa have a close spatial connection with simple setae in juveniles and/or adults. This may indicate a functional but also an evolutionary or ontogenetical link between these structures.

## Introduction

Similar to other arthropods and to other Acari in particular, oribatid mites possess a complex sensory system which includes setiform sensilla (sensory hairs or setae), non-setal sensilla, photosensitive areas and/or photoreceptor organs. All these represent exteroreceptors; interoreceptors such as mechanoreceptive neurons associated with muscles, present in other arthropod groups, have not been observed in Acari (ALBERTI & COONS in press). Thus sense organs of Acari are always in some way connected with integumental peculiarites and thus are usually of a high taxonomic value. Hence there is a vast amount of information about, e.g. types, location and appearance in ontogeny. A specific nomenclature was first developed to designate these structures, in particular setiform organs, with respect to Oribatida (e.g. GRANDJEAN 1935a, 1946a, 1947, NORTON 1977). This nomenclature was subsequently introduced into other acarine and arachnid taxa (e.g. VAN DER HAMMEN 1989) and has largely replaced the traditional descriptive classification of arthropod sensilla according to external shape (e.g. sensilla basiconica, sensilla chaetica, sensilla trichodea), at least in Actinotrichida (i.e. Actinedida, Oribatida, Acaridida). There is no doubt that these studies gave much progress to the development of acarine and oribatid systematics. Despite this importance, few publications have focussed more closely on these organs to elucidate their detailed structure and specific function.

Fine structural and electrophysiological studies on a variety of arthropods during the last decades brought a profound knowledge of arthropod sensory systems that resulted in a function-related classification of setal organs (e.g.

ALTNER 1977). However, Acari (except ticks) and Oribatida in particular have largely been neglected. With the high structural variation in acarine sensory organs compared to that in web spiders, which is probably the best investigated arachnid group, a considerable lack of knowledge is evident. The present paper reviews some recent results on oribatid sensory systems and adds some new information.

## Setiform Sensilla

Under this heading are considered those sensory organs which possess a cuticular shaft protruding externally over the surface of the integument. Such structures are frequently referred to as hairs, bristles or setae.

### Main categories of arthropod sensilla based on ultrastructural features

As background information, the classification elaborated for setiform sensilla of other arthropods, which is based primarily on fine structure (see ALTNER 1977; ALTNER & PRILLINGER 1980; STEINBRECHT 1984; BARTH & BLICKHAN 1984; ALTNER & LOFTUS 1985; FOELIX 1985; REISSLAND & GÖRNER 1985; HESS & VLIMANT 1986; STEINBRECHT 1997) and distinguishes the following main types, is briefly reviewed:

'No pore sensilla' (np-sensilla) do not have pores or slits in the cuticular setal shaft. The shaft frequently is solid. These sensilla are mainly mechanoreceptive and usually have a movable base (socket). The dendritic processes of the receptor cells terminate at the base of the setal shaft and each contains a bundle of densely arranged microtubules embedded in electron dense material. These tubular bodies are characteristic of arthropod mechanoreceptors and are considered to represent the site of stimulus transduction (THURM 1982). There are also np-sensilla with a shaft containing dendrites. Such sensilla may represent thermo- or hygroreceptive organs. They may also be innervated by mechanoreceptive cells at their basis. Hence these sensilla may be mono-, bi- or multimodal.

'*Terminal pore sensilla*' (tp-sensilla) have a terminal or subterminal pore. The shaft is hollow and contains dendrites. These sensilla usually represent contact chemoreceptive (gustatory) sensilla. They usually have an additional mechanoreceptive termination contacting the base of the seta, which is movable. They are thus bimodal sensilla. Tp-sensilla may also be hygroreceptive and/or thermoreceptive.

'*Wall pore sensilla*' (wp-sensilla) have numerous pores or slits in the setal shaft, which is also hollow and contains dendrites that may or may not

 

branch. These sensilla generally represent olfactory receptor organs and may be monomodal in function or may also be involved in hygro- and/or thermoreception. They may or may not be provided with a movable socket.

The pores or slits presumably allow or mediate the entrance of molecules into the shaft where they eventually reach the membrane receptors in the dendritic membranes, thereby provoking stimulus transduction (STEINBRECHT 1997).

There may be many subtypes based mainly on the fine structure of the walls of the sensilla (see, e.g. IVANOV & LEONOVICH 1983; FOELIX 1985; HESS & VLIMANT 1986; COONS & ALBERTI in press with further ref.).

A movable socket does not necessarily imply that the setal base is innervated and that the sensillum acts as a mechanoreceptive organ.

This classification, which implies a functional component and requires an electron microscope (TEM = transmission electron microscope, SEM = scanning electron microscope) for analysis, needs to be brought into correspondence with the classification of sensilla used broadly in systematics of Acari, at least of Actinotrichida (see above). The latter classification is in part based on a peculiarity of the cuticle of most of the setiform sensilla in Actinotrichida, i.e. the presence of birefringence under polarized light (Fig. 1A, B; for details see GRANDJEAN 1935a, 1946a, 1947; COINEAU 1974; NORTON 1977, 1990; KETHLEY 1990; PHILIPS 1990; EVANS 1992).

Types of actinotrichid setiform sensilla

Based primarily on light microscope (LM) investigations two main types of setiform sensilla may be distinguished in Actinotrichida, each of which encompass several subtypes:

I) Setae without a cytoplasmic core (the hair shaft is comprised of cuticular material only). Setae of this type are indicated by Latin letters.

a) *Simple setae*: These are thought to present mechanoreceptors since they are set into movable sockets (but see above). They may be arranged in distinct patterns on the body as well as on the appendages. In many taxa the number of setae has increased considerably (neotrichy) and sometimes may cover the whole body densely (e.g. velvet mites). Perhaps this type of seta shows the most diverse shapes (Fig. 1A, C, D). It is usually composed of a birefringent axis and an external non-birefringent layer. The latter is often referred to as chitinous but includes also epicuticular material. The axis may be hollow (see below) (GRANDJEAN 1947; COINEAU 1974; KRANTZ 1978; WOOLLEY 1988; EVANS 1992).

The setation of mites is modified during ontogeny. The order of appearance of a seta may be indicated by Arabic numerals (1, 2, 3) added to the notation of the seta. N1 (protonymph), N2 (deutonymph) or N3 (tritonymph) indicate the stage of ontogenetic appearance. These specifications may also be added to the other types of setae.

b) *Trichobothria*: In Actinotrichida these specialised setae occur in restricted numbers on the body as well as on the legs (Fig. 1B, 11) (GRANDJEAN 1943a; KETHLEY 1990). Anactinotrichida only exceptionally possess trichobothria (EVANS 1992; ALBERTI & COONS in press). In general, bothridial setae insert in deep, cup-like sockets (bothria, bothridia) (VAN DER HAMMEN 1980; REISSLAND & GÖRNER 1985). At most there are two pairs of trichobothria on the dorsal prosoma (prodorsum), a number found only in actinedid mites (e.g. the endeostigmatid Bimichaeliidae, Nanorchestidae; Bdelloidea; Erythraeoidea). However, most often the number is reduced to only one pair (many Actinedida) or trichobothria are completely lacking (e.g. Cheyletoidea; Erythraeoidea; Eriophyoidea; Hydrachnidia; Halacaroidea, etc.). Oribatida are well known for their well-developed pair of trichobothria on the prodorsum (Fig. 1B, 2, 11), which is the only pair they possess. An additional pair of trichobothria on the body is exceptionally found in the actinedid family Ereynetidae and is located dorsolaterally on the posterior of the opisthosoma. In a similar position a pair of trichobothria is found in the eupodid genus *Benoinyssus*, e.g. in *Benoinyssus ereynetoides* (Eupodidae, Eupodoidea) (BAKER 1990). Acaridida always lack trichobothria.

Trichobothria represent mechanoreceptors and are specifically differentiated in many oribatid mites (some, however, lack them; see below). In older literature the bothridia were often termed pseudostigmata in Oribatida (since they were originally regarded as stigmata) and the trichobothria were hence termed pseudostigmatic organs (in the descriptive literature and determination keys terms such as organon, sensillum or sensillus are also in use). The bothridial setae also are said to have an axis of birefringent material (Fig. 1B; see, however, HAUPT & COINEAU 1975; ALBERTI et al. 1994; see below). The axis may be hollow (GRANDJEAN 1935a, 1947; VITZTHUM 1940/43) but does not have a cytoplasmic core (EVANS et al. 1961; ALBERTI et al. 1994). The shape may differ considerably. In its most simple form it is a long, thin hair, often provided with spicules. This type is most common in actinedid mites (cf. Fig. 1B, 2B); however, even in this group various forms may occur (e.g. Bimichaeliidae; Tarsonemina; KRANTZ 1978; KETHLEY 1990). In *Bimichaelia* (Bimichaeliidae) the posterior pair is globose whereas the anterior pair is setiform. Further, in, e.g. some endeostigmatid mites (Actinedida), the trichobothria are unusually arranged. In *Lordalycus peraltus* (Lordalycidae) the an-

 

terior pair of trichobothria is located in a distinctive depression (GRANDJEAN 1939a) and in species of Nanorchestidae the minute bothridial setae of the anterior pair connect to an adjacent pair of normal setae (GRANDJEAN 1942). Remarkably, a similar arrangement evolved with the posterior pair of trichobothria in some Bdellidae (Bdelloidea) (ATYEO 1960) and with the trichobothria on tarsus I of certain Smarisidae (Erythraeoidea) (GRANDJEAN 1947).

Oribatida exhibit the greatest variation in shapes of bothridial setae. They also have the most complex bothridia of all arthropods (GRANDJEAN 1961; TARMAN 1961; ALBERTI et al. 1994) (Fig. 2). It is evident that these receptor organs are correlated with the life habits of the mites. They are reduced or even lacking in aquatic mites (including Oribatida; see NORTON et al. 1995) and are said to have predominantly clavate or capitate forms in arboreal oribatid mites (AOKI 1973). The exact functional significance of these differences in shapes is not known. For example, it has been suggested that the clavate shape is more related to gravity perception (AOKI 1973; see also COLLOFF & NIEDBAŁA 1996). However, NORTON & PALACIOS-VARGAS (1982) thought that this shape might be related to another phenomenon, i.e. the need to reduce sensitivity. The clavate bothridial seta could prevent overstimulation of the receptors in an environment (leaves, bark) that is continually exposed to moving air.

Similar to other setae, the structural characteristics of trichobothria may change among the various instars of a given species (CALUGAR & VASILIU 1979). Since the cuticular structures and peculiar arrangements provide the specific window through which the animal contacts its environment (BARTH & BLICKHAN 1984), the functional significance of all these variations is a broad field for study.

II) Seta-like sensilla with a cytoplasmic core. (Sensilla of this type are indicated with Greek notations).

These sensilla possess a protoplasmic core meaning that there may be extensions of the receptor cell(s) reaching into it. In LM observations, in particular of macerated specimens, they therefore appear to have a hollow axis. These setae exist in three types: eupathidia, famuli and solenidia (Fig. 3, 4, 5, 6A). Eupathidia and famuli, together with bothridial setae and simple setae are sometimes referred to as true setae, whereas solenidia are considered to have not developed from normal setae (EVANS et al. 1961; KRANTZ 1978; WOOLLEY 1988; KETHLEY 1990; EVANS 1992).

a) *Eupathidia* (acanthoides, pseudoacanthoides of GRANDJEAN 1946a) are spine-like setae with a sheath of birefringent material around the hollow axis. They are located on palps and legs and sometimes are branched (e.g. in the

oribatid genus *Hypochthonius*, Hypochthoniidae; Fig. 3, 4). Eupathidia, which may be simply indicated with ak, may replace simple setae and are thus homologous. They are given the same notations as normal setae would have in the same position, when a designation of this homology is desired. To indicate the eupathidial condition, the Greek letter zeta (ζ) is added. Eupathidial setae are also located on the distal lobes of genital structures (ovipositors, spermatopositors). These setae bear different Greek letters (GRANDJEAN 1956a, 1956b, 1960).

b) *Famuli* are setae that resemble the eupathidia and are mainly defined by their location on tarsus I (rarely tarsus II) and their usually smaller size. A famulus may be umbellate, stellate or peglike and may be hidden in a small pit. It is designated by an eta (ε; also e is used) (Fig. 3, 5).

c) *Solenidia* completely lack a birefringent material and often insert into the cuticle with a broad, immovable basis (Fig. 3, 4). Solenidia may occur on the genua, tibiae and tarsi, but rarely on the femora. In Oribatida they are always lacking on the femora. Notations for solenidia are both segmental and developmental: femorals are "theta" (θ), genuals are "sigma" (σ), tibials are "phi" (φ) and tarsals are "omega" (ω) and the order or stase of appearance is added (see above). These sensilla often have transversely striated walls (they are thus usually represented in line drawings with transverse striations) and may again differ considerably in shape. In some taxa they may represent long, erect, bacilliform seta-like organs (Actinedida: Anystidae, Labidostommatidae; Acaridida: Acaridae) or whip-like forms (many Acaridida, Oribatida). In others they are peg-like (Actinedida: many Tarsonemina). In several taxa solenidia on tarsus I are recumbent (Actinedida: Eupodoidea), lying in a specialised membranous depression. This peculiarity is most developed within the Rhagidiidae (Eupodoidea) in which these solenidia are T-shaped sensilla, composing the rhagidial organs (VITZTHUM 1940/43; ZACHARDA 1980).

A unified nomenclature for the shape of setiform organs of oribatid mites has been proposed by MAHUNKA & ZOMBORI (1985). To obtain an impression of the diversity of setal shapes the reader is referred to the illustrations of genera of oribatid mites of the world in BALOGH & BALOGH (1992).

Different types of setiform sensilla may be arranged together to form coupled setae. In Nanorchestidae and some Bdellidae as well as Smarisidae a minute trichobothrium is associated with a normal companion seta (as already mentioned). A very peculiar setal complex has recently been described in *Grandjeanicus gabonensis* (Endeostigmata, Grandjeanicidae) which perhaps provides a basis for acoustic communication (COINEAU et al. 1997). Various coupled setae are also known from other Actinedida as well as Acaridida.

 

Furthermore, in many oribatid mites, the genu and the tibia of the legs commonly have a solenidion and a companion seta originating from the same or immediately adjacent alveolus, with the solenidion almost always distal to the seta (GRANDJEAN 1935a; NORTON 1977) (Fig. 3B, 5A, B). A very intimate combination of an eupathid with a solenidion composing a "double horn" occurs on the palp tarsus of many Brachypylina (Oribatida) (GRANDJEAN 1935a, 1946b) (Fig. 3C, 5D). The eupathid is always below (distal to) the solenidion. The functional significance of these arrangements is not known.

This short overview demonstrates the already very detailed knowledge about an extensive diversity of setal structures. Nevertheless, the scarcity of recent ultrastructural observations highlights the urgent necessity of redefining these types. In particular, it seems that the lumen of the hollow axis of some of the setae (simple setae, trichobothria) may only be an artifact, a misinterpretation based on the different optical properties of the cuticular material involved. E.g. in the trichobothria of an actinedid and several oribatid species an extensive lumen was never seen (HAUPT & COINEAU 1975; ALBERTI et al. 1994; see below).

## Fine structure of setiform sensilla of Oribatida

In the following a more detailed report on some selected oribatid setal organs is given.

### 1) *Simple setae*

These setae have not yet been studied in detail. Each notogastral seta of *Eupelops* sp. is located over a portion of the procuticle which is considerably thinner than the surrounding cuticle (Fig. 7). The seta is movable, set into a socket (alveolus) provided with a thin articulating membrane which contains radiating fibres. This membrane is contacted by two dendrites which terminate with conspicuous tubular bodies. These terminations are surrounded by a common thick-walled tube of dense material corresponding to the so-called helmet of other Arachnidsarachnids. The helmet shows semicircular protrusions on the inner side directed towards the dendrites. Tubular bodies are indicative of mechanoreceptive cells. The peculiar shape of the wall of the helmet was also found in other mechanoreceptors, e.g. in the actinedid mite, *Microcaeculus steineri* (HAUPT & COINEAU, 1975). Further details on, e.g. enveloping cells and exact shape of the setal basis are still unknown in oribatid mites.

In a number of Oribatida, simple setae are close to secretory porose organs, which suggests that these organs are in some way coupled (see below).

A curiosity occurs in the oribatid family Hermanniellidae. Most of the notogastral setae of adult mites are minute, in particular those positioned underneath the portion of tritonymphal exuvial cuticle (scalp) that the adult carries. The minute adult setae are positioned directly underneath the large tritonymphal setae and appear to be stimulated when the nymphal setae are moved (Fig. 6B) (GRANDJEAN 1962a).

2) *Trichobothria*

Despite their high degree of differentiation, trichobothria of oribatids have only recently been studied by TEM (ALBERTI et al. 1994, 1995). In *Acrogalumna longipluma* (Galumnaidae) the setal base is curved in a S-shape that follows the tortuous arrangement of the bothridium, which is divided by thin lamellae into several chambers (Fig. 8-12). The setal base is an elongate oval in transverse section and attaches to a thin articulating membrane provided with radiating fibres. Two dendrites terminate with tubular bodies at the base of the bothridial seta, but only one really contacts the seta. The tubular bodies are surrounded by distinctively structured dense tubes (regarded as derivatives of the dendritic sheath) that contact the setal base and the socket via very thin cuticular (?) fibres. These latter fibres are probably homologous to the helmet seen in the notogastral setae of, e.g. *Eupelops* sp. and in mechanoreceptive sensilla of actinedid mites or other arachnids (see above and REISSLAND & GÖRNER 1985). A complete dendritic sheath does not seem to be present. The external chambers of the bothridial wall are covered by the specific cerotegument, whereas fine ribs of the cuticle proper are present in the internal chambers. Distally, the bothridial seta exhibits fine spicules and a rounded shape in transverse section. The hair shaft is solid over most of its length. Four layers surround a thin and dense inner core: an inner layer of electron-lucent material, a thin dense layer, an external layer of electron-lucent material and a dense epicuticular layer. Proximally, within the bothridium, setal shape becomes angular (transverse section) and its surface shows ring-shaped irregularities. The dense core enlarges and opens to contain a lumen that is continuous with the receptor lymph cavity at the setal base. This lumen, as well as the thin, dense core, was not observed in the trichobothria of *Microcaeculus steineri* (HAUPT & COINEAU 1975).

Oribatid trichobothria thus present the following major peculiarities: high variety of shapes of bothridial setae, very complex bothridia provided with cerotegumental material and cuticular ribs, setal base and bothridium most often curved (reaching an S-shape in the extreme), seta with elongate oval base provided with a lumen continuous with the receptor lymph cavity, a reduced helmet, a very elaborate dendritic sheath (dense tubes) that only sur-

 

rounds the prominent tubular bodies, the tubular bodies of different shape – one being elongate (correlating with the oval shape of the setal base) and only this one contacting the setal base (Fig. 8-11). ALBERTI et al. (1994) suggested that several features improve the sensitivity of the sense organ: 1) hanging insertion of the bothridial seta instead of sitting upright in the socket. The latter, plesiomorphic condition is seen in the early derivative oribatid mite taxon Palaeosomata, in non-oribatid mite groups and in other arachnids (TARMAN 1961; GRANDJEAN 1961); 2) oval shape of the setal base causing directionality (Fig. 10B, 11B,C) (HAUPT & COINEAU 1975; BARTH & BLICKHAN 1984); 3) peculiar shape and properties of dense tubes (ALBERTI et al. 1994, 1995). The increase in sensitivity during evolution probably went along with increased strengthening of the cuticle and required, on the other hand, improvement of protective properties of the bothridium (REISSLAND & GÖRNER 1985). These requirements likely were achieved by the progressive internalisation of the hair base, the participation of the hydrophobic (fungicidal, bacteriocidal?) cerotegument in forming the walls of the external chambers, thus preventing entrance of water (and microorganisms) and development of the lamellae and ribs on the walls of the internal chambers and the hair base, which prevent blockage of the setal base by solid particles.

The air chamber (bothridium) surrounding the setal base is the starting point for a distinctive development in certain Oribatida. For instance, in Crotonioidea and Phthiracaroidea sac- or trachea-like structures arise from the bothridium, thus probably enhancing gas exchange in the prosoma (Fig. 12; GRANDJEAN 1934a, 1939b). It could also be speculated that ventilation of these organs may be important in keeping the bothridium clean (ALBERTI et al. 1995, 1997; NORTON & ALBERTI 1997; NORTON et al. 1997).

Certainly, oribatid trichobothria are the most intricate setal sense organs perceiving substrate or airborne vibrations as stimuli (PAULY 1956; REISSLAND & GÖRNER 1985).

3) *Eupathidia, Famuli, Solenidia*

Only preliminary results are available about oribatid sensilla of type II (Fig. 3-6A). Based on SEM-observations, solenidia seem to represent wp-sensilla, whereas eupathidia and famuli have a smooth surface and probably a terminal pore. Sections of the peculiar paired setae (double horn) located on the palp tarsi of many Brachypylina (Oribatida) and composed of one solenidium and one eupathidium have substantiated this view (ALBERTI, personal observations) (Fig. 6A). Thus, solenidia most often may represent olfactory receptor organs whereas eupathidia may serve as gustatory receptor organs, though in the latter a terminal pore has not yet been demonstrated by TEM. The role of

the famuli is even more enigmatic. Because of their usually small size a function as contact chemoreceptor seems less likely.

Certainly much additional work is needed before a sound generalised interpretation on all these sensilla is possible.

## Non-setal Sensilla

Non-setal sensilla have no seta-like shaft extending above the surface of the cuticle. They may also be termed intracuticular receptors (HESS & VLIMANT 1986).

### 1) Slit sense organs and cupules

Slit sense organs are comparable to similar organs found in other arachnids. Such organs are frequently arranged in small groups with parallel slits in spiders. These groups appear lyre-shaped, hence the term lyriform organs for these groups and lyrifissures for the single slit sense organ. No such grouping occurs in Acari. Hence the term slit sense organ is preferred. Cupules are also sensory structures that are not setiform and are discussed here. They are regarded as homologes of slit sense organs since they occur in the corresponding places on the body. The term is derived from their appearance as a cup-like depression in the cuticle, rather than being slit-like. It seems as if this difference is related to the grade of sclerotisation: softer cuticles tend to have cupules, stronger cuticles show typical slit sense organs. Cupules can be replaced in the course of postembryonic development by slits, e.g. in oribatid mites having weakly sclerotised juveniles, the cupules are replaced by slit sense organs in the sclerotised body regions of the adults (GRANDJEAN 1933). However, this correlation between cuticular properties and the two forms of receptor organs does not seem to be strict (VITZTHUM 1940/43).

These organs (and very likely cupules as well) are cuticular receptors that perceive stimuli arising from strains in the cuticle that arise from various forces. The latter include stress generated by movements of the mite itself or by changes in internal pressures (proprioreception). Or, they may mediate sensitivity to external forces such as gravity, substrate vibrations, or perhaps even sound (exteroreception) (BARTH 1982; BARTH & BLICKHAN 1984; HESS & VLIMANT 1986).

In mites, slit sense organs (or cupules) tend to be reduced in number during evolution (GRANDJEAN 1935b). Their numbers in anactinotrichids are generally greater than in actinotrichids (GRANDJEAN 1936). This reduction probably was already prevalent in the prosomal region of the body at the beginning of

 

acarine evolution. Thus in Opilioacarida, Holothyrida and Gamasida at most only three sternal and three prodorsal pairs may be present (LINDQUIST 1984). On the body of Actinotrichida maximally seven pairs of slit sense organs or cupules are found, all on the opisthosoma (LINDQUIST 1984). They are restricted to the dorsolateral regions and appear during ontogeny in a distinct developmental pattern. A slit sense organ is present near the base of the palpal tarsus in almost all early derivative actinotrichids, and is retained by quite a few of the derivative oribatid lineages and quite a few of the actinedid groups that do not exhibit major modifications of the palpal segments (GRANDJEAN 1935a, 1939a, 1940, 1943b). With respect to the legs, at most a single slit sense organ occurs on each leg tarsus in Oribatida. They may be completely lacking in some Actinedida (GRANDJEAN 1936). On the contrary, slit sense organs are quite frequent on the legs of anactinotrichid mites (EVANS & TILL 1979; EVANS 1992).

The slit sense organs and cupules do not represent real openings in the cuticle. Their lucent appearance in the LM is a result of reduction of the procuticle in these organs. The epicuticle remains always intact.

Slit sense organs are best known from spiders (BARTH 1982; BARTH & BLICKHAN 1984) and regarding Acari have only been studied to some detail in ticks (HESS & VLIMANT 1986; see also ALBERTI & COONS in press; COONS & ALBERTI in press). In spiders there are two dendritic terminations under a single slit; one almost reaches the slit membrane, the other terminates deeper in the procuticular cleft. Both are provided with tubular bodies. The location of the terminations are often indicated by a small spot within the slit. A similar arrangement is found in tick slit sense organs though details are different. In contrast the cheliceral slit sense organ of a gamasid mite, *Varroa jacobsoni*, is innervated by only one mechanosensitive neuron (NUZZACI et al. 1992)

The slit sense organs and cupules of actinotrichid mites have not yet been studied adequately. It is merely known that they are innervated (PENMAN & CONE 1974; ALBERTI & CROOKER 1985). In Oribatida the opisthosoma of deutonymphs, tritonymphs and adult mites bears seven pairs of slit sense organs at most which are designated from anterior to posterior as follows: ia, im, ip, ih, ips, iad and ian (GRANDJEAN 1933; EVANS 1992).

In *Scutovertex minutus*, (ia) and (im) were studied (see also SCHUSTER 1958). They are hardly detectable in SEM when viewed from the exterior. However, in macerated specimens they are easily recognized when viewed from the interior (Fig. 13). The slits are oriented almost at right angle with regard to the longitudinal axis of the body. The procuticle of the slits is slightly thinner, but does not form a simple cleft as in, e.g. spiders (BARTH 1982; BARTH & BLICKHAN 1984). Instead of a cleft, there is a narrow portion of

modified cuticle to which a small cuticular process attaches. Remarkably both slit sense organs slightly differ in their cuticular components. In contrast to the anterior organ, the small process of the posterior structure points into a depression of the adjacent normal procuticle. The organs are almost in line with the series of insertion sites of the circumgastric muscle band.

Based on the TEM of the posterior slit sense organ, the normal procuticle of the slit organ is traversed by a portion of modified cuticle that appears less sclerotised. This would allow flexion and hence stimulation of the receptor cell, which attaches to this region with a dendritic process containing a tubular body. It may be that this attachment site is included in the thin cuticular process just mentioned which thus would be tubular and would resemble the coupling cylinder found in spider slit sense organs (BARTH 1982; BARTH & BLICKHAN 1984). The exact number of receptor cells is not known.

### 2) Putative sensory structures within the chelicerae

Actinotrichid mites are known to possess innervated chelicerae from fine structural investigations of several Actinedida, e.g. spider mites (Tetranychidae; MOTHES & SEITZ 1981; ANDRÉ & REMACLE 1984; ALBERTI & CROOKER 1985; NUZZACI & DE LILLO 1991a), false spider mites (Tenuipalpidae; NUZZACI & DE LILLO 1991b), Penthaleidae (Eupodoidea; NUZZACI & DE LILLO 1991c), Eriophyoidea (NUZZACI 1976; NUZZACI & ALBERTI 1996) and Oribatida (WALZL 1987).

WALZL (1987) found that the chelicerae of the oribatid *Hermannia gibba* are innervated by dendrites of sensory cells that terminate under small pits on the teeth of both digits, suggesting a gustatory sensitivity. Similar structures were found in *Acrogalumna longipluma* (Fig. 14), but details are still lacking.

## Porose organs: sense organs?

In many oribatid taxa "porose areas" and related invaginated structures (saccules, vesicles) are striking features of taxonomic importance (Fig. 11A; see ALBERTI & NORTON 1997). Whereas some authors considered these organs to represent glandular structures (OUDEMANS 1913, 1916; WILLMANN 1931; VITZTHUM 1940/43; JONES 1954; HOEBEL-MÄVERS 1967), GRANDJEAN (1934a) and most authors following him ascribed respiratory functions to them. WOODRING & COOK (1962) recognised two fundamental types of porose organs, respiratory and secretory. The secretory type was first investigated ultrastructurally by ALBERTI et al. (1981). Secretory porose organs of oribatid mites represent more or less distinct fields of small pores within the procuticle that are found in various body regions. Within higher Oribatida,

 

there are frequently four pairs of notogastral porose organs (octotaxic system), that are used to define the taxon Poronota (GRANDJEAN 1954b; Fig. 11A).

In some poronotic oribatid mites porose organs reflect sexual dimorphism, e.g. species of Galumnidae (BERNINI 1984), Mycobatidae (BEHAN-PELLETIER 1988), Oripodidae (AOKI 1966) or Mochlozetidae (MAHUNKA 1978b; NORTON 1983). The male shows the more complex structure with enlarged or fused porose organs, organs in a different position than in the female, or organs set on tubercles (some Mochlozetidae) (NORTON & ALBERTI 1997; NORTON et al. 1997). For example, in *Acrogalumna longipluma* (Galumnidae), the male alone bears a large medial notogastral field of about 60 small porose organs. Though largely having an ultrastructure similar to that of normal porose organs, these organs are innervated by two axons (ALBERTI et al. 1996, 1997).

Even more enigmatic are porose organs found in many Lohmanniidae (GRANDJEAN 1934b, 1950; JUDSON 1993). In these early derivative oribatid mites numerous secretory porose organs are distributed over the body. The cellular components of these areas differ strikingly from all secretory porose organs described so far. A structurally complex large cell surrounds a conspicuous extracellular space into which extends a pair of branching axons.

Hence at least some of the organs are evidently innervated. However, these nerve endings represent efferent nerves, therefore are not indicative of a sensory function. Remarkably, there is in certain taxa (e.g. Oripodoidea, Phenopelopoidea) a tendency of porose organs (at least on the body) to be close to setae (see Fig. 7). Hence, it seems plausible to assume that porose organs and setae are sometimes functionally and probably also ontogenetically or evolutionary coupled (NORTON et al. 1997; NORTON & ALBERTI 1997).

## Genital papillae and claparède organs: sense organs?

Genital papillae (= acetabula, genital discs) are characteristic features of many actinotrichid mites. They virtually are constitutive characters of the taxon (GRANDJEAN 1969; VAN DER HAMMEN 1969, 1989; KETHLEY 1982; LINDQUIST 1984; EVANS 1992) and are typically present in three pairs in the adults and tritonymphs, in two pairs in the deutonymphs and in one pair in the protonymphs (Fig. 15C). In general, papillae of the first pair appear first during ontogeny and are usually larger than the middle and posterior pairs (GRANDJEAN 1938). However, there may be exceptions with the direction of development from posterior to anterior, e.g. in the brachypyline oribatid *Oppia nitens* (Oppioidea, Oppiidae) (BEHAN-PELLETIER 1991). In this and other

brachypyline oribatids the genital papillae of given species may differ structurally.

Larvae and prelarvae lack genital papillae (the genital opening is not yet developed). Instead, these instars have Claparède organs (=Urporen, Urstigmata, Epimeralporen, Bruststiele, Larvalorgane, Prälarvalorgane, etc.; VERCAMMEN-GRANDJEAN 1975) (Fig. 15A, B). Whereas genital papillae are located within the progenital chamber of both sexes, the Claparède organs are located between the bases of the first and second pairs of legs. Usually only one pair of Claparède organs is present, often covered by a cuticular, scale-like lid derived from the most lateral epimeral (coxisternal) seta (1c) (see NORTON et al. 1995). It is not known whether this lid is innervated. Claparède organs of prelarvae are usually more simple. Genital papillae may be protruded by everting the genital region through increased hemolymph pressure. In some taxa, e.g. Oribatida and Acaridida, they may fold out like a finger of a glove and reach a considerable length. They may be retracted by small muscles. The Claparède organs probably are only slightly moved by internal pressure variations. For *Damaeus onustus*, GRANDJEAN (1955) described muscles for this organ that are similar to those of genital papillae.

GRANDJEAN (1938, 1946a) observed that with few exceptions species that possess genital papillae also possess Claparède organs and vice versa (OUDEMANS-GRANDJEAN rule; JOHNSTON & WACKER 1967), and he regarded these structures as homeotypic (homonomous) organs (VAN DER HAMMEN 1980; see also KRANTZ 1977; BAKER & KRANTZ 1985; see also ALBERTI & COONS in press for more details).

Genital papillae of nymphs and adults and Claparède organs of prelarvae and larvae of Actinotrichida variously have been reported to function as sense organs, or glands, or adhesive suckers, or even respiratory organs (see VERCAMMEN-GRANDJEAN 1975; ALBERTI 1979; VAN DER HAMMEN 1980 with references). VIETS (1939, 1940) suggested a correlation between the occurrence of epimeral pores (Claparède organs) in larvae of some halacarids and the presence of these mites in brackish waters. Ultrastructural and histochemical studies (BARTSCH 1973, 1974; ALBERTI 1977, 1979; FASHING 1988; ALBERTI & BADER 1990; ALBERTI & LÖWENFELD 1990; WITALINSKI et al. 1990; ALBERTI et al. 1992) as well as ecophysiological evidence (OLOMSKI 1986, 1991) have established the close similarity of genital papillae/Claparède organs to chloride cells/ionocytes of other taxa such as freshwater insects (KOMNICK 1977) or soil arthropods (e.g. Machilidae: BITSCH 1974; Collembola, Diplura: EISENBEIS 1974, 1976) which are mainly composed of transporting cells (Fig. 15D). This suggests the possibility of a similar function in waterbalance, osmoregulation or in regulating ions. ALBERTI (1979) corre-

 

lated this possible function with complexity, position, and number of genital papillae and with different environments in which the taxa of actinotrichid mites may live, an aspect which was further developed for freshwater mites by BARR (1982). NORTON et al. (1983) recognised that atrophy or disappearance of genital papillae in several sarcoptiform taxa (e.g. Oribatida: *Aphelacarus*, Aphelacaridae; Haplochthoniidae; Cosmochthoniidae; Pediculochelidae; Acaridida: Hypoderatoidea, Psoroptidia) correlates well with preference, or at least tolerance, of environments low in available moisture.

Genital papillae and Claparède organs have not yet been found to be innervated (ALBERTI 1977, 1979; BAKER & KRANTZ 1985; ALBERTI & LÖWENFELD 1990; LÖWENFELD & ALBERTI personal observations; WITALINSKI et al. 1990). Hence the interpretation of these organs as sensory structures has to be discarded.

The functional significance of a sexual dimorphism represented by differences in the shape and position of genital papillae in the two sexes which is found in some oribatid mites (see e.g. BEHAN-PELLETIER 1996) remains to be discovered.

## Photosensitive areas and photoreceptor organs (eyes)

### Prodorsal eyes

Eyes are found only in some taxa of Acari, e.g. Opilioacarida, some Ixodida, many Actinedida. Oribatida and Acaridida are usually regarded as being blind (but see below). According to GRANDJEAN (1958) the primitive number of eyes in Acari is probably six (three pairs). This number is present in some actinedid mites (GRANDJEAN 1958; COINEAU 1970; WACHMANN et al. 1974) and consists of two pairs of lateral eyes and one pair of median eyes (anterior eyes). The latter are often located on the ventral side of a frontal protuberance, the naso, and may be fused to form one unpaired eye (GRANDJEAN 1958; COINEAU 1970; ALBERTI 1975). Naso and corresponding eyes have not been found in anactinotrichid mites, hence the 6 eyes found in some opilioacarid mites may not be exactly homologous with those of Actinotrichida.

Thus, the assumption of GRANDJEAN (1958) regarding the original complement of eyes in Acari should be reconsidered and is probably only relevant for actinotrichid mites.

A prominent naso is also present in some of the lower Oribatida (e.g. Palaeacaroidea, Archeonothroidea, Brachychthonioidea) (WOOLLEY 1988) (Fig. 16B-D). Three eyes, one frontal and a pair of lateral eyes, are present in some species of the family Heterochthoniidae (GRANDJEAN 1928; BALOGH & MA-

HUNKA 1983) (Fig. 16A). A similar complement of (unpigmented) eyes was found in the oribatid mite *Eobrachychthonius* sp. (Brachychthoniidae) by TRAVÉ (1968) (Fig. 16D). The fine structure of these eyes, which are probably plesiomorphic, still needs to be investigated.

**Secondarily developed eyes of Oribatida (clear spot, lenticulus)**

Some Oribatida possess an area in the anterior region of the notogaster which is less dark than the surrounding integument (Fig. 17).This peculiarity, well-known to many acarologists and regarded by some of them as photosensitive areas (e.g. OUDEMANS 1913, 1916; VITZTHUM 1940/43), have been found only in higher oribatids (GRANDJEAN 1961). They are represented as an unpaired clear spot at the anterior margin of the notogaster (dorsal opisthosoma). In some species this region may be elevated in a lens-like manner, hence the term lenticulus (Fig. 17B, C). These structures are in a different position from eyes in other Arachnida or Acari including those of the mentioned early derivative Oribatida, which are always located in the prosoma. Hence, GRANDJEAN (1961) considered these structures, clear spots and lenticuli, to be secondary characters.

A lenticulus was already described by OUDEMANS (1916), reporting on the very detailed observations of PIERSIG on a *Hydrozetes* sp. (taxonomy according to GRANDJEAN 1961). In this species the lenticulus was said to exhibit paired red pigment areas and a fine longitudinal line. Hence, it was assumed that this organ was primarily a paired structure. EM studies by ALBERTI & FERNANDEZ (1988, 1990) clarified the status of this character (Fig. 18, 19).

The lenticulus of *Hydrozetes lemnae* (Hydrozetidae) is comprised of a convex-concave corneal lens, two lamellated bodies, two pigment cells and two cells of the fat body. Furthermore, there are glial cells surrounding the lamellated bodies and a thin layer of epidermal cells between the lens and the lamellated bodies (Fig. 18, 19). The lamellated bodies are the receptor poles of photoneurons that belong to the central nervous system, since their very large perikarya are located within the synganglion (Fig. 18). From Fig. 18A one receives an impression of the astonishing magnitude of these receptor poles in comparison to the synganglion or even to the whole animal. Lamellated bodies and perikarya are connected by dendritic extensions surrounded by a glial sheath. The lamellae of the bodies are arranged as vertical sheets parallel to the longitudinal axis of the body. They contain numerous small cup-like vesicles, microtubules and few mitochondria (Fig. 18B, 19B). Concentrations of dense particles (glycogen?) are also present, usually at the base of the lamellated body. The pigment cells, presumed to be derived from fat body cells,

 

contain many small lipid-like inclusions, which are likely responsible for the red colour seen in life (Fig. 18, 19A).

The dendritic connection of the lamellated body with the perikarya consists of a bundle of four or five dendritic processes which fuse shortly before entering the perikaryon (Fig. 18). Each perikaryon contains, in addition to the large electron-lucent nucleus, profiles of rough ER, Golgi bodies, a few mitochondria, some lysosomes and numerous microtubules. The latter occur predominantly in the region of the axon hillock. The axon which emerges is similarly relatively large. It traverses through the synganglion to the opposite side and terminates near the corresponding perikaryon in a small dense optic neuropil. Both axons run parallel to each other over some distance and, in this region, are not separated by glial cells. The axons establish a very simple chiasma opticum, containing only two axons (Fig. 18).

In *Hydrozetes* and in some other oribatid mites (e.g. *Scutovertex sculptus* ⟨Scutoverticidae⟩, *Scapheremaeus argentina* ⟨Cymbaeremaeidae⟩; ALBERTI & FERNANDEZ 1990, personal observations; ALBERTI et al. 1991) provided with lenticuli, the receptor poles are rather close to the cuticle and are distant from the synganglion. Except for the shape of the lens, which is convex-concave in *Hydrozetes* and *Scutovertex* but biconvex in *Scapheremaeus* (Fig. 18, 20C), other components are rather similar. In contrast, in other oribatid mites having a simple clear spot rather than a lenticulus, the receptor poles are attached to the synganglion and are not "elevated" by dendritic bundles. The receptor poles are similarly represented as lamellated bodies. Such an arrangement was found, e.g. in *Chamobates voigtsi* (Chamobatidae), *Euzetes globulus* (Euzetidae), *Oribatella quadricornuta* (Oribatellidae), *Achipteria coleoptrata* (Achipteriidae) and *Acrogalumna longipluma.* In these species pigment cells are nearly always (*Achipteria* probably presents an exception) lacking (ALBERTI & FERNANDEZ 1990, personal observation; ALBERTI et al. 1991) (Fig. 20A-C). It is not known whether inclusions in the proventricular glands (MICHAEL 1883, 1884, WOODRING & COOK 1962; organons racémiformes, GRANDJEAN 1962b, see also BERNINI 1984; LUDWIG et al. 1992) compensate for this lack in specific pigment cells. Such an interpretation is favored by recent unpublished observations of ALBERTI & FERNANDEZ according to which lamellated bodies may occur rather ventrally in position (i.e. at a level with the esophagus, passing through the synganglion) and in intimate contact with a modified anterior portion of the proventricular glands. This was found in *Parapirnodus* sp. (Oripodidae) (Fig. 20B) and in a species of unknown systematic position (ALBERTI & FERNANDEZ personal observation).

According to our present knowledge of photoreceptor organs in Acari (cf. KAISER & ALBERTI 1991; ALBERTI & COONS in press; COONS & ALBERTI in

press) the lamellated bodies are restricted to certain oribatid mites. Lamellated receptor poles are also exceptional with regard to the whole animal kingdom (EAKIN 1972; WESTFALL 1982; ALI 1984). Interestingly, they have been found in the reduced stemmata of some (predominantly substrate inhabiting) brachyceran larvae (Diptera) (MELZER & PAULUS 1989).

The fine structure of these peculiar structures (lenticulus, clear spot) thus substantiates the view that they are secondarily evolved light receptor organs (GRANDJEAN 1961). The receptor cells with their perikarya located in the synganglion obviously represent modified neurons of the central nervous system. Evidently Oribatida have reduced their primary eyes with few exceptions (e.g. Heterochthoniidae) but in many of the higher oribatids new light receptor organs have been developed combining prosomal (photoneurons) with opisthosomal (cornea) components.

The selective pressure which brought about these enigmatic organs is still a matter of speculation (ALBERTI & FERNANDEZ 1990).

Altogether one can distinguish three or four basic types of photoreceptor organs (eyes) within the Acari: the rather complex, inverted rhabdomeric eyes of opilioacarids, the less complex, more or less everted rhabdomeric eyes of ticks and actinedid mites (lateral as well as median eyes) and the secondarily developed organs of various oribatid mites (ALBERTI et al. 1991). In addition less complex and rather indistinct photosensitive areas may be present (e.g. in certain ticks, Gamasida and Acaridida; see ALBERTI & COONS in press; COONS & ALBERTI in press). Among these, the secondarily evolved eyes of some Oribatida range among the most simple, but – relative to body size – largest photoreceptor organs in the animal kingdom. For instance, the lenticulus of *Hydrozetes* contains only two receptor cells. The size ratio of body/eye is approximately eight (500µm:64µm=7.8) and hence reaches the magnitude of cephalopods (e.g. *Sepia officinalis*: 40cm:3.5cm=11.4), which are known to include the Metazoa having the relatively and absolutely largest eyes (cf. man: e.g. 180cm:2.4cm=75).

## Conclusion

The present paper constitutes but a small glance of biodiversity reflected in a restricted area of study and by no means covers even this small selected area. Many efforts are necessary to discover the many peculiarities and, more important, to understand their functional, selective importance. Unfortunately, the small size of these creatures hinders an experimental approach. However, understanding the detailed structure is at least a first, and certainly an essential step toward such a goal. By comparison with results obtained from more

 

convenient taxa it may be possible to reach a profound interpretation. Studying animal morphological diversity cannot end with a "simple" description of characters, though such a description is indispensable, of course, and is by no means underestimated. These characters need to be *understood* to make diversity and its evolution "alive"! Such a deeper understanding of characters will certainly help to improve systematical concepts.

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## References

ALBERTI, G., 1975: Prälarven und Phylogenie der Schnabelmilben (Bdellidae, Trombidiformes). – Z. zool. Syst. Evolut.-forsch. **13**: 44-62.

ALBERTI, G., 1977: Zur Feinstruktur und Funktion der Genitalnäpfe bei *Hydrodroma despiciens* (Hydrachnellae, Acari). – Zoomorphologie **87**: 155-164.

ALBERTI, G., 1979: Fine structure and probable function of genital papillae and Claparède organs of Actinotrichida. – In RODRIGUEZ, J. (Ed.): Recent Advances in Acarology, Vol. II, pp. 501-507. – New York: Academic Press.

ALBERTI, G., STORCH, V., RENNER, H., 1981: Über den feinstrukturellen Aufbau der Milbencuticula (Acari, Arachnida). – Zool. Jb. Anat. **105**: 183-236.

ALBERTI, G., CROOKER, A. R., 1985: Internal anatomy. – In HELLE, W., SABELIS, M. W. (Eds.): Spider Mites, Their Biology, Natural Enemies and Control. World Crop Pests. Vol. 1A, pp. 29-62. – Amsterdam: Elsevier.

ALBERTI, G., FERNANDEZ, N. A., 1988: Fine structure of a secondarily developed eye in the freshwater moss-mite, *Hydrozetes lemnae* (COGGI, 1899) (Acari: Oribatida). – Protoplasma **146**: 106-117.

ALBERTI, G., BADER, C., 1990: Fine structure of external "genital papillae" in the fresh water mite *Hydrovolzia placophora* (Hydrovolziidae, Actinedida, Actinotrichida, Acari). Experim. & Appl. Acarology **8**: 115-124.

ALBERTI, G., FERNANDEZ; N. A., 1990: Aspects concerning the structure and function of the lenticulus and clear spot of certain oribatids (Acari, Oribatida). – Acarologia **31**: 65-72.

ALBERTI, G., LÖWENFELD, I. K., 1990: Feinstruktur der Genitalpapillen actinotricher Milben (Acari). – Mitt. Dtsch. Ges. allgem. angew. Ent. **7**: 463-466.

ALBERTI, G., KAISER, T. H., FERNANDEZ, N. A., 1991: Fine structure of photoreceptor organs in Acari. – In DUSBABEK, F., V. BUKVA, V. (Eds): Modern Acarology. Vol. **2**, pp. 343-857. – Prague and The Hague: Academia and SPB Academic Publ. bv.

ALBERTI, G., KAISER, T. H., LÖWENFELD, I. K., 1992: Zur Feinstruktur der Ventralsäckchen und vergleichbarer Organe bei Spinnentieren (Arachnida). – Verh. Dtsch. Zool. Ges. (1992). Short Communications. 85. Jahresvers. Kiel: 197.

ALBERTI, G., MORENO, A. I., KRATZMANN, M., 1994: Fine structure of trichobothria in oribatid mites with special emphasis on *Acrogalumna longipluma* (BERLESE, 1904) (Oribatida, Acari, Arachnida). – Acta Zoologica (Stockholm) **75**: 57-74.

ALBERTI, G., MORENO, A. I., KRATZMANN, M., 1995: Fine structure of trichobothria in moss mites (Oribatida). – In KROPCZYNSKA, D., BOCZEK, J., TOMCZYK, A. (Eds.): The Acari – Physiological and Ecological Aspects of Acari-Host Relationships; pp. 23-30. – Warszawa: Dabor.

ALBERTI, G., NORTON, R. A. (Eds.), 1997: Porose Integumental Organs of Oribatid Mites (Acari, Oribatida). – Stuttgart: Zoologica **48/146**.

ALBERTI, G., NORTON, R. A., ADIS, J. A., FERNANDEZ, N. A., FRANKLIN, E., KRATZMANN, M., MORENO, A. I., WEIGMANN, G., WOAS, ST., 1996: Areae porosae and related organs in oribatid mites (Oribatida). – In MITCHELL, R. D., HORN, D. J., NEEDHAM, G. R., WELBOURN, W. C. (Eds.): Acarology IX – Proceedings, pp. 277-283. – Columbus: Ohio Biology Survey.

ALBERTI, G., NORTON, R. A., ADIS, J. A., FERNANDEZ, N. A., FRANKLIN, E., KRATZMANN, M., MORENO, A. I., WEIGMANN, G., WOAS, ST., 1997: Porose integumental structures of oribatid mites (Acari, Oribatida): 2. Fine structure. – Zoologica. **48/146**: 33-114.

ALBERTI, G., COONS, L. B., (in press) Acari – Mites. In HARRISON, F. W. (Ed.): Microscopic Anatomy of Invertebrates. Vol. 8C. – New York, John Wiley & Sons, Inc.

ALI, M. A. (Ed.), 1984: Photoreception and Vision in Invertebrates. – New York and London: Plenum Press.

ALTNER, H., 1977: Insektensensillen; Bau und Funktionsprinzipien. – Verh. Dtsch. Zool. Ges. **1977**: 139-153.

ALTNER, H., PRILLINGER, L., 1980: Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. – Intern. Rev. Cytol. **67**: 69-139.

ALTNER, H., LOFTUS, R., 1985: Ultrastructure and function of insect thermo- and hygroreceptors. – Ann. Rev. Entomol. **30**: 273-295.

ANDRÉ, H. M., REMACLE, C., 1984: Comparative and functional morphology of the gnathosoma of *Tetranychus urticae* (Acari: Tetranychidae). – Acarologia **25**: 179-190.

AOKI, J. I., 1966: Epizoic symbiosis: an oribatid mite, *Symbioribates papuensis*, representing a new family, from cryptogamic plants growing on backs of papuan weevils (Acari: Cryptostigmata). – Pacific Insects **8**: 281-289.

AOKI, J., 1973: Oribatid mites from Iriomote-jima, the Southernmost island of Japan. – Mem. Nat. Sci. Mus. **6**: 85-101.

ATYEO, W. T., 1960: A revision of the family Bdellidae in North and Central America (Acarina: Prostigmata). – Univers. Kansas Sci. Bull. **40**: 345-499.

BAKER, A. S., 1990: A survey of external morphology of mites of the superfamily Eupodoidea BANKS, 1894 (Acari, Acariformes). – J. Nat. Hist. **24**: 1227-1261

BAKER, A. S., 1985: A note on Claparède organs in larvae of the superfamily Eupodoidea (Acari: Acariformes). – J. nat. Hist. **19**: 739-744.

BAKER, G. T., KRANTZ, G. W., 1985: Structure of the male and female reproductive and digestive systems of *Rhizoglyphus robini* Claparède (Acari, Acaridae). – Acarologia **26**: 55-65.

BALOGH, J., BALOGH, P., 1992: The Oribatid Mites Genera of the World. Vol. 1. – Budapest: Hungarian Nat. Hist. Mus.

BALOGH, J., MAHUNKA, S., 1983: The Soil Mites of the World. 1. Primitive Oribatids of the Palaearctic Region. – Budapest: Academia Kiadó.

BARR, D., 1982: Comparative morphology of the genital acetabula of aquatic mites (Acari, Prostigmata): Hydrachnoidea, Eylaoidea, Hydryphantoidea, and Lebertioidea. – J. Nat. Hist. **16**: 147-160.

BARTH, F. G., 1982: Spiders and vibratory signals: Sensory reception and behavioral significance. – In WITT, P. N., ROVNER, J. S. (Eds.): Spider Communication. Mechanisms and Ecological Significance, pp. 67-122. – Princeton, New Jersey: Princeton University Press.

BARTH, F. G., BLICKHAN, R., 1984: Mechanoreception. – In BEREITER-HAHN, J., MATOLTSY, A. G., RICHARDS, K. S. (Eds): Biology of the Integument. I. Invertebrates, pp. 554-582. – Berlin, Heidelberg, New York, Tokyo: Springer-Verlag.

BARTSCH, I., 1973: *Porohalacerellus alpinus* (THOR) (Halacaridae, Acari), ein morphologischer Vergleich mit marinen Halacariden nebst Bemerkungen zur Biologie dieser Art. – Entomol. Tidskr. **94**: 116-123.

BARTSCH, I., 1974: Über das Auftreten von Epimeralporen besonders bei den Rhombognathinae (Halacaridae, Acari). – Zool. Anz. **193**: 266-268.

BEHAN-PELLETIER, V. M., 1988: Redefinion of *Zachvatkinibates* (Acari: Mycobatidae), with description of a new species and immatures of *Z. maritimus* SHALDYBINA 1973. – Can. Entomol. **120**: 797-813.

BEHAN-PELLETIER, V., 1991: Observations on genital papillae of pycnonotic Brachypylina (Acari: Oribatida). – Acarologia **32**: 71-78.

BEHAN-PELLETIER, V. M., 1996: *Naiazetes reevesi* n. g., n. sp. (Acari: Oribatida: Zetomimidae) from semi-aquatic habitats of Eastern North America. – Acarologia **37**: 345-355.

BERNINI, F. 1984: Notulae oribatologicae XXXII. Some new galumnid mites (Acaridida, Oribatida) from North Africa exhibiting sexual dimorphism with some observations on racemiform organs. – Animalia **11**: 103-126.

BITSCH, J., 1974: Fonction et ultrastructure des vésicules exortiles de l'abdomen des Machilides. – Pedobiologia **14**: 142-143.

CALUGAR, M., VASILIU, N., 1979: Modifications morphologiques de l'organe trichobothrial durant l'ontogénie des Oribates (Acari, Oribatei). – Rev. Roum. Biol.-Biol. Animale **24**: 107-112.

COINEAU, Y., 1970: A propos de l'oeil antérieur du naso de Caeculidae. - Acarologia **12**: 109-118.

COINEAU, Y., 1974: Eléments pour une monographie morphologique, écologique et biologique des Caeculidae (Acariens). – Mém. Mus. Nat. Hist. Nat. (n.s.), Sér. A, Zool. **81**, 299pp. + pl. 1-24.

 

COINEAU, Y., THÉRON, P. D., VALETTE, C., 1997: Une association de phanères, constituant probablement un système de communication sonore original chez les Acariens. – Acarologia **38**: 111-116.

COLLOFF, M. J., NIEDBAŁA, W., 1996: Arboreal and terrestrial habitats of phthiracaroid mites (Oribatida) in Tasmanian rainforests. – In MITCHELL, R., HORN, D. J., NEEDHAM, G. R., WELBOURN, W. C. (Eds.) Acarology IX – Proceedings; pp. 607-611. – Columbus, Ohio Biological Survey.

COONS, L. B., ALBERTI, G., (in press) Acari – Ticks. – In HARRISON, F. W. (Ed.): Microscopic Anatomy of Invertebrates. Vol. 8B. New York, John Wiley & Sons, Inc.

EAKIN, R. M., 1972: Structure of invertebrate photoreceptors. – In AUTRUM, H., JUNG, R., LOWENSTEIN, W. R., MCKAY, D. M., TEUBER, L. H. (Eds): Handbook of Sensory Physiology. Vol. VII/1, pp. 624-684. – Berlin, Heidelberg, New York: Springer.

EISENBEIS, G., 1974: Licht- und elektronenmikroskopische Untersuchungen am Ventraltubus arthropleoner Collembolen (Insecta). – Cytobiol. **9**: 180-202.

EISENBEIS, G., 1976: Zur Feinstruktur und Histochemie des Transportepitheles abdominaler Coxalblasen der Doppelschwanzart *Campodea staphylinus* (Diplura, Campodeidea). – Ent. Germ. **3**: 185-201.

EVANS, G. O., 1992: Principles of Acarology. – Wallingford: C.A.B International.

EVANS, G. O., SHEALS, J. G., MACFARLANE, D., 1961: The terrestrial Acari of the British Isles. Vol. 1. – London: British Museum (Nat. Hist.).

EVANS, G. O., TILL, W. M., 1979: Mesostigmatic mites of Britain and Ireland (Chelicerata: Acari: Parasitiformes). An introduction to their external morphology and classification. – Trans. Zool. Soc. Lond. **35**: 139-270.

FASHING, N. J., 1988: Fine structure of the Claparède organs and genital papillae of *Naiadacarus arboricola* (Astigmata: Acaridae), an inhabitant of waterfilled treeholes. – In CHANNABASAVANNA, G. P., VIRAKTAMATH, C. A. (Eds.): Progress in Acarology, Vol. I, pp. 219-228. – New Delhi: Oxford & IBH Publ. Co.

FOELIX, R. F., 1985: Mechano- and chemoreceptive sensilla. – In BARTH, F. G. (Ed.): Neurobiology of Arachnids, pp. 118-137. – New York: SpringerVerlag.

GRANDJEAN, F., 1928: Sur un oribatide pourvu d'yeux. – Bull. Soc. Zool. France **53**: 235-242.

GRANDJEAN, F., 1933: Etude sur le développement des Oribates. – Bull. Soc. zool. France **58**: 30-61.

GRANDJEAN, F., 1934a: Les organes respiratoires secondaires des Oribates (Acariens). – Ann. Soc. ent. France **103**: 109-146.

GRANDJEAN, F., 1934b: La notation des poils gastronotiques et des poils dorsaux du propodosoma chez les Oribates (Acariens). – Bull. Soc. Zool. France **59**: 12-44.

GRANDJEAN, F., 1935a: Les poils et les organes sensitifs portés par les pattes et le palpe chez les oribates. Première partie. – Bull. Soc. Zool. France **60**: 6-39.

GRANDJEAN, F., 1935b: Observations sur les Acariens (2e série). – Bull. Mus. Hist. Nat., Paris **7**: 201-208.

GRANDJEAN, F., 1936: Observations sur les Acariens (3e série). – Bull. Mus. Nat. Hist. Nat., Paris **8**: 84-91.

GRANDJEAN, F., 1938: Observations sur les Bdelles (Acariens). – Ann. Soc. ent. France **107**: 1-24

GRANDJEAN, F., 1939a: Quelques genres d'Acariens appartenant au groupe des Endeostigmata. – Ann. Sci. Nat. Zool. sér. **11** (2): 1-122.

GRANDJEAN, F., 1939b: Observations sur les Oribates (11e série). – Bull. Mus. Nat. Hist. Nat., Paris **11**: 110-117.

GRANDJEAN, F., 1940: Les poils et les organes sensitifs portés par les pattes et le palpe chez les Oribates II. – Bull. Soc. Zool. France **65**: 32-44.

GRANDJEAN, F., 1942: Observations sur les Acariens (7e série). – Bull. Mus. nat. Hist. natur. **14** (2): 264-267.

GRANDJEAN, F., 1943a: Les trichobothries pédieuses des Acariens et leur priorité chez les Bdelles. – C. R. Séanc. Soc. Phys. Hist. natur. Genève **60**: 241-246.

GRANDJEAN, F., 1943b: Le développement postlarvaire d'Anystis (Acarien). – Mém. Mus. Nat. Hist. Nat., n.s. **18**: 33-77.

GRANDJEAN, F., 1946a: Au sujet de l'organe de Claparède, des eupathidies multiples et des taenidies mandibulaires chez les Acariens actinochitineux. – Archives **28**: 63-87.

GRANDJEAN, F., 1946b: Les poils et les organes sensitifs portés par les pattes et le palpe chez les oribates. Troisième partie. – Bull. Soc. zool. France **71**: 10-29.

GRANDJEAN, F., 1947: L'origine de la pince mandibulaire chez les Acariens actinochitineux. – Arch. Sci. Phys. Nat., Genève **29**: 305-355.

GRANDJEAN, F., 1950: Etude sur les Lohmanniidae (Oribates, Acariens). – Arch. Zool. exp. gén. **87**: 96-162.

GRANDJEAN, F., 1954: Essai de classification des Oribates (Acariens). – Bull. Soc. zool. France **78**: 422-446.

GRANDJEAN, F., 1955: L'organe de Claparède et son ecaille chez *Damaeus onustus* KOCH. – Bull. Mus. nat. Hist. natur. **27**: 285-292.

 

GRANDJEAN, F., 1956a: Caractères chitineux de l'ovipositeur, en structure normale chez les Oribates (Acariens). – Arch. Zool. exp. gén. **93**: 96-106.

GRANDJEAN, F., 1956b: Observations sur les Oribates (34. sér.). – Bull. du Mus., 2 sér., **28**: 205-212.

GRANDJEAN, F., 1958: Au sujet du naso et de son oeil infère chez les oribates et les Endeostigmata (Acariens). – Bull. Mus. 2e Sér. **30**: 427-435.

GRANDJEAN, F. 1960: *Damaeus arvernensis* n. sp. (Oribatei). Acarologia **2**: 250-275.

GRANDJEAN, F., 1961: Nouvelles observations sur les oribates. (1re sér.). – Acarologia **3**: 206-231.

GRANDJEAN, F., 1962a: Au sujet des Hermanniellidae (Oribates). Premiére partie. – Acarologia **4**: 237-273.

GRANDJEAN, F., 1962b: Nouvelles observations sur les Oribates (2e série). – Acarologia **4**: 396-422.

GRANDJEAN, F., 1969: Stases. Actinopiline. Rappel de ma classification des Acariens en 3 groupes majeurs. Terminologie ens soma. – Acarologia **11**: 796-827.

HAUPT. J., COINEAU,Y., 1975: Trichobothrien und Tastborsten der Milbe *Microcaeculus* (Acari, Prostigmata, Caeculidae). – Z. Morph. Tiere **81**: 305-322.

HESS, E.,VLIMANT, M., 1986: Leg sense organs of ticks. – In SAUER, J. R., HAIR, J. A. (Eds): Morphology, Physiology, and Behavioural Biology of Ticks, pp. 361-390. – Chichester: Ellis Horwood.

HOEBEL-MÄVERS, M., 1967: Untersuchungen über die Funktionsanatomie des Oribatidendarmes. Diss. TH. Braunschweig, 45pp.

IVANOV, V. P., LEONOVICH, S. A., 1983: Sensory organs. – In BALASHOV, Y. S. (Ed.): An Atlas of Ixodid Tick Ultrastructure, pp. 191-220. – Spec. Publ. Entomol. Soc. Am.

JOHNSTON, D. E., WACKER, R. R., 1967: Observations on postembryonic development in *Eutrombicula splendens* (Acari-Acariformes). – J. Med. Entomol. 4: 306-310.

JONES, B. M., 1954: On the role of the integument in acarine development and its bearing in pupa-formation. – Quart. J. Microscop. Sci. **95**: 169-181.

JUDSON, M., 1993: Description of the first African representative of the genus *Javacarus* (Acari: Lohmanniidae) from Cameroon. – J. Afr. Zool. **105**: 347-354.

KAISER, T. H., ALBERTI, G., 1991: The fine structure of the lateral eyes of *Neocarus texanus* CHAMBERLIN and MULAIK, 1942 (Opilioacarida, Acari, Arachnida, Chelicerata). – Protoplasma **163**: 19-33.

KETHLEY, J., 1982: Acariformes. – In PARKER, S. P. (Ed.): Synopsis and Classification of Living Organisms.Vol. 2, pp. 117-145. – New York: McGraw Hill.

KETHLEY, J., 1990: Acarina: Prostigmata (Actinedida). – In DINDAL, D. L. (Ed.): Soil Biology Guide, pp. 667-756. – New York: John Wiley & Sons.

KOMNICK, H., 1977: Chloride cells and chloride epithelia of aquatic insects. – Int. Rev. Cytol. **49**: 285-329.

KRANTZ, G. W., 1977: On the occurrence of Claparède organs in the Halacaridae (Acari: Actinedida). – Acarologia **19**: 62-66.

KRANTZ, G. W., 1978: A Manual of Acarology. 2nd ed. – Corvallis: Oregon State Univer. Book Stores.

LINDQUIST, E. E., 1984: Current theories on the evolution of major groups of Acari and on their relationships with other groups of Arachnida, with consequent implications for their classification. – In GRIFFITHS, D. A., BOWMAN, C. E. (Eds.): Acarology VI. Vol., pp. 28-621. – Chichester: Ellis Horwood.

LÖWENFELD, I. K., 1987: Vergleichende Untersuchungen zur Ultrastruktur der Genitalnäpfe bei Actinotrichida (Acari, Arachnida). – Unpubl. Master thesis, Univers. Heidelberg, 168pp. + 43pl.

LUDWIG, M., KRATZMANN, M., ALBERTI, G., 1992: Observations on the proventricular glands ("organes racemiformes") of the oribatid mite *Chamobates borealis* (Acari, Oribatida): an organ of interest for studies on adaptation of animals to acid soils. – Exp. Appl. Acar. **15**: 49-57.

MAHUNKA, S., 1978: Neue und interessante Milben aus dem Genfer Museum XXIV. First contribution to the oribatid fauna of the Dominican Republic (Acari: Oribatida). – Redia **61**: 551-564.

MAHUNKA, S., ZOMBORI, L., 1985: The variability of some morphological features in oribatid mites. – Fol. Entomol. Hung. **46**: 115-128.

MELZER, R. R., PAULUS, H. F., 1989: Evolutionswege zum Larvalauge der Insekten. Die Stemmata der höheren Dipteren und ihre Abwandlung zum Bolwig-Organ. – Z. zool. Syst. Evolut.-forsch. **27**: 200-245.

MICHAEL, A. D., 1883: Observations on the anatomy of the Oribatidae. – J. Royal Microsc. Soc. 1883: 1-25, 2 pl.

MICHAEL, A. D., 1884: British Oribatidae. Vol. 1. – London: Ray Society.

MOTHES, U., SEITZ, K. A. 1981: Functional microscopic anatomy of the digestive system of *Tetranychus urticae* (Acari, Tetranychidae). – Acarologia **22**: 257-270.

 

NORTON, R. A., 1977: A review of F. GRANDJEAN'S system of leg chaetotaxy in the Oribatei and its application to the Damaeidae. – In DINDAL, D. L. (Ed.): Biology of Oribatid Mites, pp. 33-62. – State University of New York.

NORTON, R. A., 1983: Redefinition of *Mochloribatula* (Acari: Mochlozetidae), with new species, recombinations and notes on plant associations. – Acarologia **24**: 449-464.

NORTON, R. A., 1990: Acarina: Oribatida. – In DINDAL, D. L. (Ed.): Soil Biology Guide, pp. 779-803. – New York: John Wiley & Sons.

NORTON, R. A., PALACIOS-VARGAS, J. G., 1982: Nueva Belba (Oribatei: Damaeidae) de muscos epifitos de Mexico. – Folia Entomol. Mex. **52**: 61-73.

NORTON, R. A., OCONNOR, B. M., JOHNSTON, D. E., 1983: Systematic relationships of the Pediculochelidae (Acari: Acariformes). – Proc. Entomol. Soc. Wash. **85**: 493-512.

NORTON, R. A., BEHAN-PELLETIER, V. M., WANG, H.-F., 1995: The aquatic oribatid mite genus *Mucronothrus* in Canada and the Western U.S.A. (Acari: Trhypochthoniidae). – Can. J. Zool. **74**: 926-949.

NORTON, R. A., ALBERTI, G., 1997: Porose integumental structures of oribatid mites (Acari, Oribatida): 3. Functional and evolutionary aspects. – Zoologica **48/146**: 1-31.

NORTON, R. A., ALBERTI, G., WEIGMANN, G., WOAS, ST., 1997: Porose integumental structures of oribatid mites (Acari, Oribatida): 1. Overview of types and distribution. – Zoologica **48/146**: 115-143.

NUZZACI, G., 1976: Contributo alla conoscenza dell'anatomia degli Acari Eriofidi. – Entomologica, Bari, **12**: 21-55.

NUZZACI, G., DE LILLO, E., 1991a: Fine structure and functions of the mouthparts involved in the feeding mechanisms in *Tetranychus urticae* KOCH (Tetranychoidea: Tetranychidae). – In DUSBABEK, F., BUKVA, V. (Eds.): Modern Acarology. Vol. 2, pp. 301-306. – Prague: Academia and The Hague: SPB Academic Publ. bv.

NUZZACI, G., DE LILLO, E., 1991b: Fine structure and functions of the mouthparts involved in the feeding mechanisms in *Cenopalpus pulcher* (CANESTRINI and FANZAGO) (Tetranychoidea: Tenuipalpidae). – In SCHUSTER, R., MURPHY, P. W. (Eds.): The Acari. Reproduction, Development and Life-History Strategies, pp. 367-376. – London: Chapman & Hall.

NUZZACI, G., DE LILLO, E., 1991c: Contributo alla conoscenza delle parti boccali di *Penthaleus major* (DUGÈS) (Acari: Eupodoidea Penthaleidae). – Atti 16. Congr. naz. ital. Entomol. Bari-Martina Franca: 265-277.

NUZZACI, G., DE LILLO, E., F. PORCELLI, F., 1992: Functional morphology of mouthpart sensilla in females of *Varroa jacobsoni* OUDEMANS (Acari: Varroidae). – Entomologica, Bari, **27**: 41-67.

NUZZACI, G., ALBERTI, G., 1996: Internal anatomy and physiology. – In LINDQUIST, E. E., SABELIS, M. W., BRUIN, J., (Eds.): Eriophyoid Mites – Their Biology, Natural Enemies and Control. World Crop Pests. Vol. **6**, pp. 101-150. – Amsterdam: Elsevier Sci. Publ.

OLOMSKI, R., 1986: Die Osmo- und Volumenregulation der Süßwassermilbe *Limnesia maculata* (O. F. MÜLLER, 1776) (Acari: Hydrachnidia). – Verh. Dtsch. Zool. Ges. **79**: 315-316.

OLOMSKI, R., 1991: Effects on the habitat salinity on the osmotic and ionic regulation of the freshwater mites *Eylais tantilla* KOEN. and *E. planipons novata* VIETS (Acari: Hydrachnidia). – In DUSBABEK, F., BUKVA, V. (Eds.): Modern Acarology. Vol. 2, pp. 357-364. – Prague: Academia and and The Hague: SPB Academic Publ. bv.

OUDEMANS, A. C., 1913: Acarologisches aus Maulwurfsnestern. – Arch. f. Naturgesch. **79**, A: 1-69, pl. XV-XVIII.

OUDEMANS, A. C., 1916: Notizen über Acari, 25. Reihe. (Trombidiidae, Oribatidae, Phthiracaridae.). – Arch. f. Naturgesch. **82**, A: 1-84.

PAULY, F., 1956: Zur Biologie einiger Belbiden (Oribatei, Moosmilben) und zur Funktion ihrer pseudostigmatischen Organe. – Zool. Jahrb. **84**: 275-328.

PENMAN, D. R., CONE, W. W., 1974: Structure of cuticular lyrifissures in *Tetranychus urticae*. – Ann. Entomol. Soc. Amer. **67**: 1-4.

PHILIPS, J. R., 1990: Acarina: Astigmata (Acaridida). – In DINDAL, D. L. (Ed.): Soil Biology Guide, pp. 757-778. – New York: John Wiley & Sons.

REISSLAND, A., GÖRNER, P., 1985: Trichobothria. In BARTH, F. G. (Ed.): Neurobiology of Arachnids, pp. 138-161. – Berlin, Heildelberg, New York, Tokyo: Springer-Verlag.

SCHUSTER, R., 1958: Beitrag zur Kenntnis der Milbenfauna (Oribatei) in pannonischen Trockenböden. Sitz. ber. Österr. Akad. Wiss., Mathem.-naturwiss. Kl., Abt. I, Wien **167**: 221-235.

STEINBRECHT, R.A., 1984: Chemo-, Hygro-, and Thermoreceptors. – In BEREITER-HAHN, J., MATOLTSY, A. G., RICHARDS, K. S. (Eds): Biology of the Integument. I. Invertebrates, pp. 523-553. – Berlin, Heidelberg, New York, Tokyo: Springer-Verlag.

STEINBRECHT, R.A., 1997: Pore structures in insect olfactory sensilla: a review of data and concepts. – Int. J. Insect Morphol. & Embryol. **26**: 229-245.

 

TARMAN, K., 1961: Über Trichobothrien und Augen bei Oribatei. – Zool. Anz. **167**: 51-58.

THURM, U., 1982: Mechanoelektrische Kommunikation. – In HOPPE, W., LOHMANN, W., MARKL, H., ZIEGLER, H. (Eds.): Biophysik, pp. 691-696. – Berlin, Heidelberg, New York: Springer-Verlag.

TRAVÉ, J., 1968: Sur l'existence d'yeux lateraux depigmentes chez *Eobrachychthonius* JACOT (Oribatei). – Acarologia **10**: 151-158.

VAN DER HAMMEN, L., 1969: Notes on the morphology of *Alycus roseus* C. L. KOCH. – Zool. Meded. Leiden **43**: 177-202.

VAN DER HAMMEN, L., 1980: Glossary of Acarological Terminology. Vol. I. General Terminology. – The Hague: Dr. W. Junk Publ.

VAN DER HAMMEN, L., 1989: An Introduction to Comparative Arachnology. – The Hague: SPB Publishing bv.

VERCAMMEN-GRANDJEAN, P. H., 1975: Les organes de Claparède et les papilles genitales de certains Acariens – sont-ils des organes respiratoires? – Acarologia **17**: 624-630.

VIETS, K., 1939: Meeresmilben aus der Adria (Halacaridae und Hydrachnellae, Acari). – Arch. Naturgesch. **8**: 518-550.

VIETS, K., 1940: Meeresmilben aus der Adria (Halacaridae und Hydrachnellae, Acari). – Arch. Naturgesch. **9**: 1-135.

VITZTHUM, H. GRAF, 1940/43: Acarina. Bronns Klassen u. Ordnungen des Tierreichs. 5. Bd. IV. Abtlg. 5. Buch. – Leipzig: Akadem. Verl. ges. Becker & Erler.

WALZL, M. G., 1987: The cheliceral sense organs of the adult oribatid mite *Hermannia gibba* (C. L. KOCH) (Actinotrichida: Acari). – European Cell Biology Suppl. **18**, 43: Abstr. 98.

WESTFALL, J. A., (Ed.) 1982: Visual Cells in Evolution. – New York: Raven Press.

WILLMANN, C., 1931: Moosmilben oder Oribatiden (Cryptostigmata). Die Tierwelt Deutschl. Jena: G. Fischer, 79-200.

WITALINSKI, W., SZENDLAK, E., BOCZEK, J., 1990: Anatomy and ultrastructure of the reproductive system of *Acarus siro* (Acari: Acaridae). – Experim. & Appl. Acarol. **10**: 1-31.

WOODRING, J. P., COOK, E. F., 1962: The internal anatomy, reproductive physiology, and molting process of *Ceratozetes cisalpinus* (Acarina: Oribatei). – Ann. Entom. Soc. Amer. **55**: 164-181.

WOOLLEY, T. A., 1988: Acarology. Mites and Human Welfare. – New York: John Wiley & Sons.

ZACHARDA, M., 1980: Soil mites of the family Rhagidiidae (Actinedida: Eupodoidea). Morphology, Systematics, Ecology. – Acta Univers. Carol. Biol. **5-6**: 489-785.

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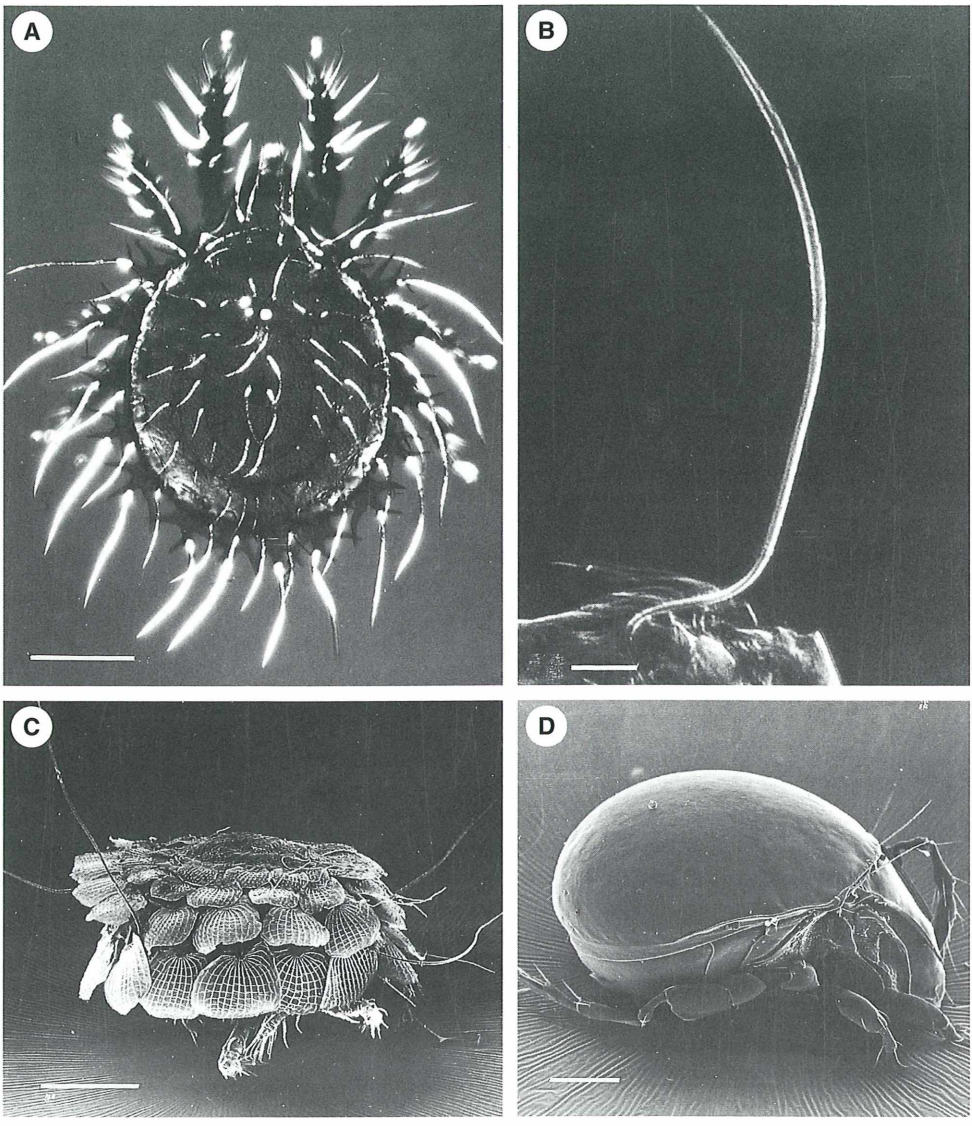


Fig. 1: Some characteristics of setiform sensilla. A: Tritonymph of the oribatid *Cepheus dentatus* (Cepheidae) bearing the scalps of larva, protonymph and deutonymph. Polarised light. Setae show birefringence typical for actinotrichid mites. Scale bar 200µm. B: Trichobothrium of the oribatid mite *Acrogalumna longipluma* (Galumnidae) in polarised light. Note axis of setae is not birefringent and thus appears hollow (cf. Figs 9-12). Scale bar 20µm. C and D: Shapes of setae may differ considerably between juveniles and adults in some Oribatida. C: Tritonymph of *Conoppia palmicincta* (Cepheidae) with fan-shaped setae at the margins of its scalps. Note four very long body setae. Scale bar 400µm. D: The adult mite has only very minute notogastral setae which are not visible in this low magnification. Scale bar 200µm.

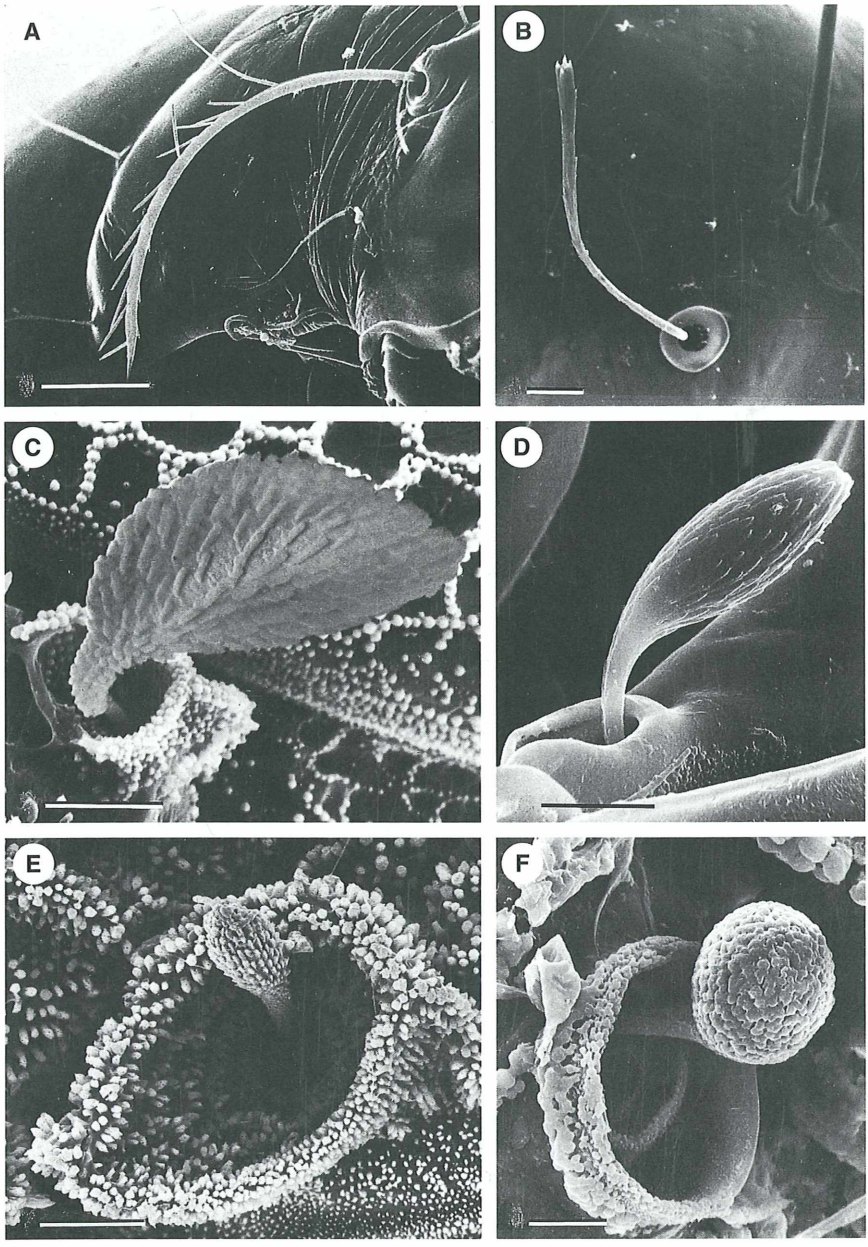


Fig. 2: Trichobothria of Oribatida. Note different shapes and proportions of bothridial setae and bothridia. A: *Eniochthonius minutissimus* (Eniochthoniidae). Scale bar 20µm. B: *Collohmannia gigantea* (Collohmanniidae). Scale bar 20µm. C: *Licnodamaeus pulcherrimus* (Licnodamaeidae). Scale bar 10µm. D: *Adoristes ovatus* (Liacaridae). Scale bar 10µm. E: *Niphocepheus nivalis* (Niphocepheidae). Scale bar 20µm. F: *Cymbaeremeus cymba* (Cymbaeremeidae). Scale bar 10µm.

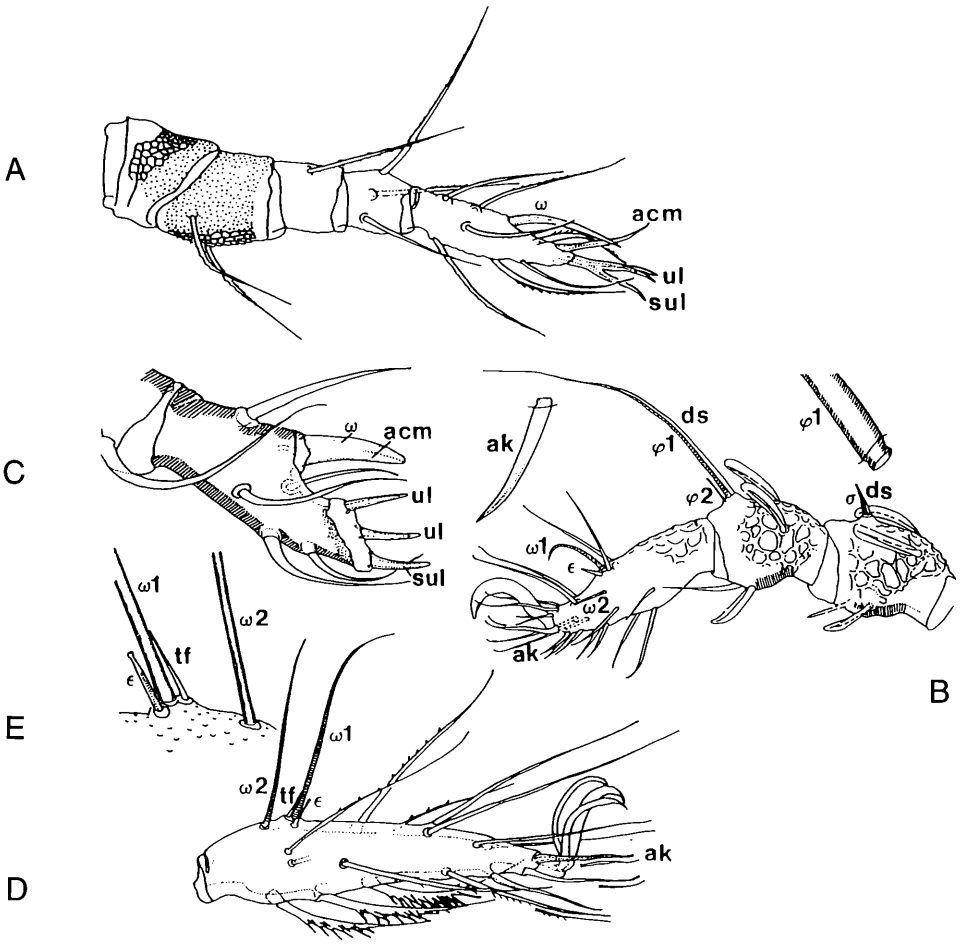


Fig. 3: Various leg and palpal setae of Oribatida: Simple setae, eupathidia, famuli, solenidia. A: *Hypochthonius rufulus* (Hypochthoniidae). Right palp. Note solenidion (ω) and eupathidia (acm, ul, sul). Eupathidia ul and sul are fused, forming a furcate eupathidium. (After GRANDJEAN 1946b.) B: *Hermannia reticulata* (Hermanniidae). Genu, tibia and tarsus of left leg I. Solenidia of tarsus (ω1, ω2), tibia (φ1, φ2), and genu (σ ), famulus (ε), and eupathidia (ak) are indicated. Note solenidia (ω1) on tibia and (σ) on genu forming coupled setae with corresponding companion setae (ds). (After GRANDJEAN 1935a.) C: *Acrogalumna longipluma.* Tarsus of right palp. Solenidion (ω) and eupathidium (acm) are coupled setae forming a "double horn". Eupathidia ul and sul are also indicated. (After GRANDJEAN 1935a.) D: *Acrogalumna longipluma.* Right tarsus I with solenidia (ω1, ω2), famulus (ε) and eupathidia (ak) indicated. ω1 associated with a reduced simple companion seta (tf) (From GRANDJEAN, 1935a.) E: *Acrogalumna longipluma.* Solenidion (ω1) and associated sensilla of left tarsus I enlarged. (After GRANDJEAN 1935a).

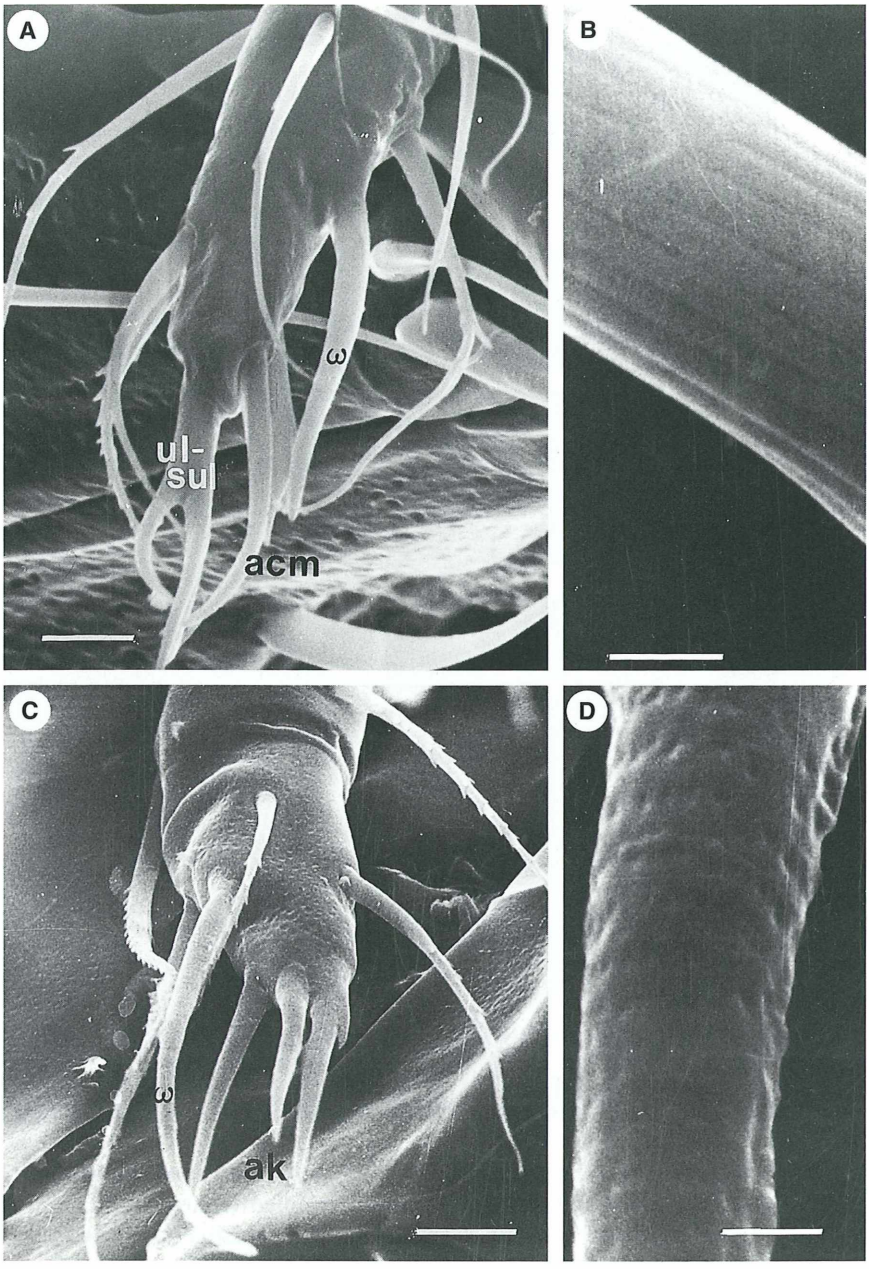


Fig. 4: Type II sensilla of Oribatida (cf. Fig. 3). A: *Hypochthonius rufulus*. Tarsus of palp with solenidion (ω) and eupathidia (ul-sul, acm) indicated. Scale bar 5µm. B: *Hypochthonius rufulus*. Solenidion in higher magnification. Note striation. Scale bar 0.5µm. C: *Phthiracarus* sp. (Phthiracaridae). Tarsus of palp. Solenidion (ω) and eupathidia (ak) are indicated. Scale bar 5µm. D: *Phthiracarus* sp. Enlarged view of solenidion (ω) demonstrating wall pores. Scale bar 0.5µm.

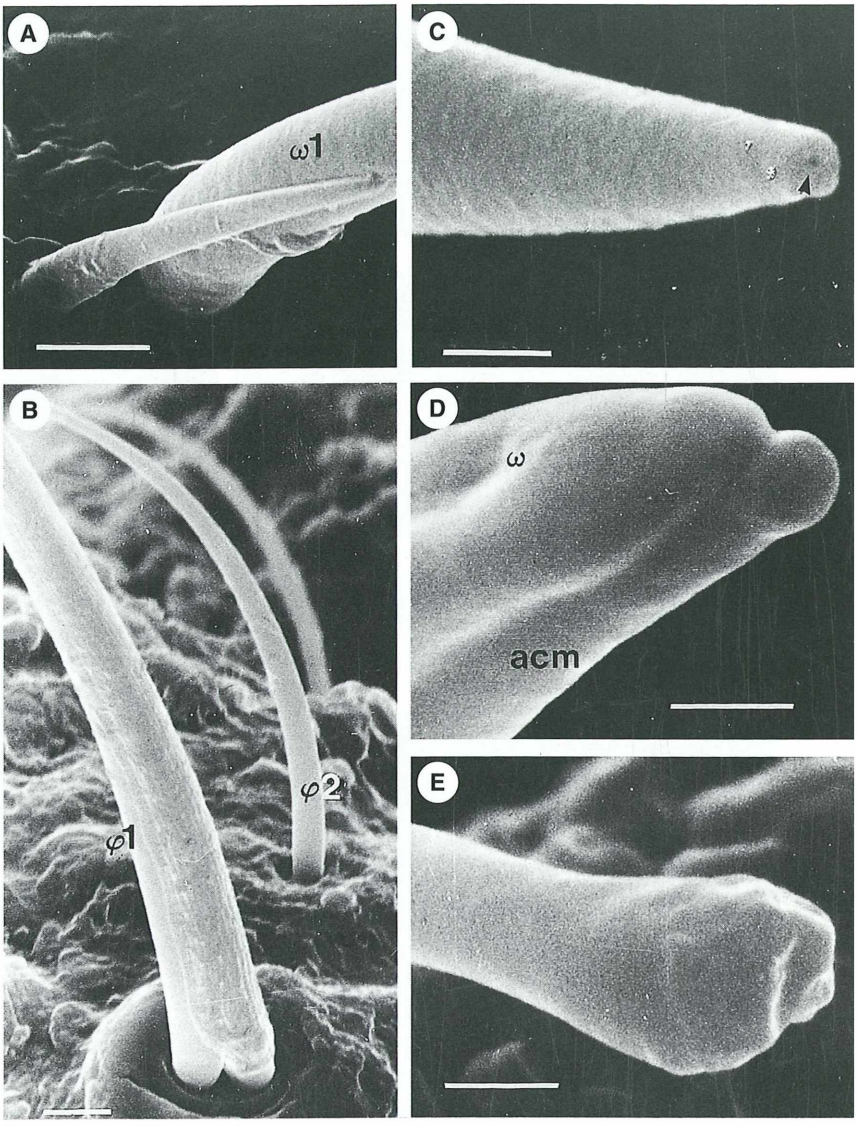


Fig. 5: Type II sensilla of Oribatida (cf. Fig. 3). A: *Acrogalumna longipluma.* Detail
tarsus of leg I with large solenidion ω1 coupled with reduced simple compa
ion seta. Scale bar 2μm. B: *Hermannia gibba.* Sensilla on tibia of leg I showi
coupled setae composed of solenidion ω1 and simple companion seta as well
separate solenidion ω2. Scale bar 4μm. C: *Phthiracarus* sp. Enlarged view
the tip of the middle eupathidium (cf. Fig. 4C) showing terminal pore (arro
head). Scale bar 0.5μm. D: *Acrogalumna longipluma.* "Double horn" of palp
tarsus composed of eupathidium (acm) and solenidion (ω). Note very intima
arrangement of both sensilla. Scale bar 0.5μm. E: *Acrogalumna longiplum*
Tip of famulus ε of tarsus of leg I. Scale bar 0.5μm.

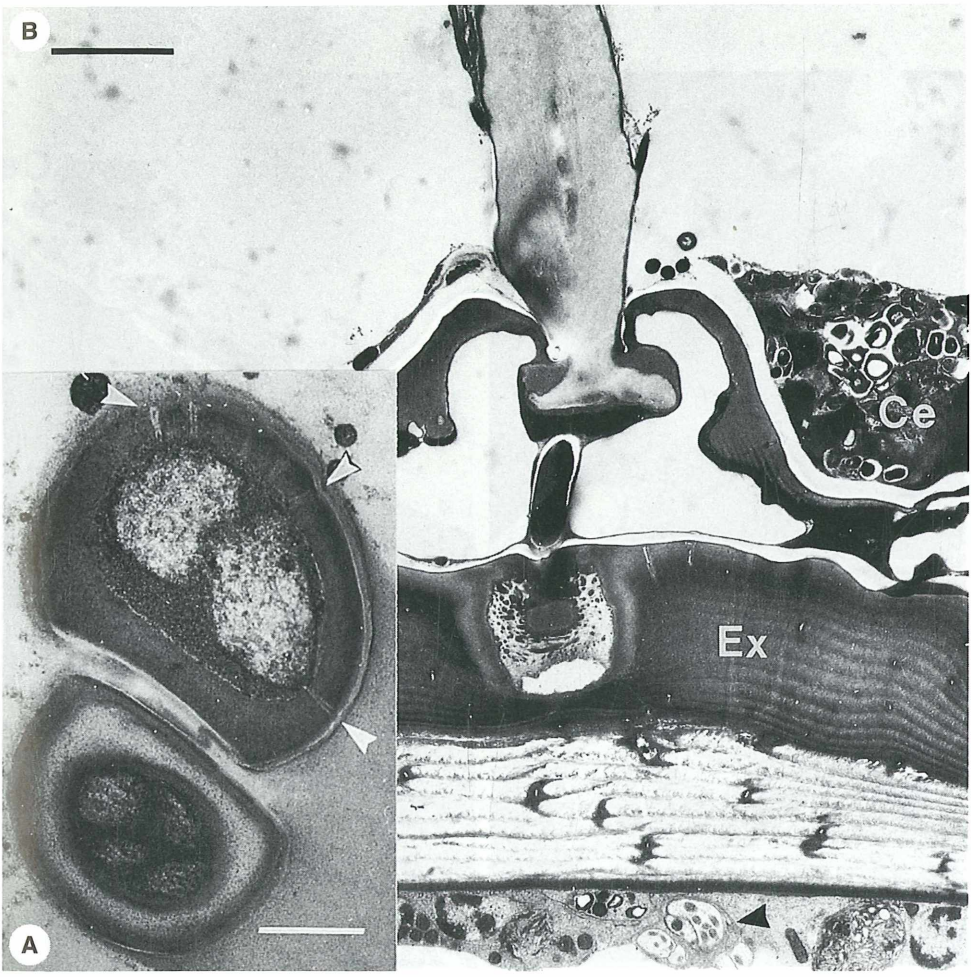


Fig. 6: A: Transverse section through "double horn" on palp tarsus of *Acrogalumna longipluma*. Note simple wall pores (arrowheads) in the solenidion which contains two dendrites. The eupathidium has no wall pores (at least in this section) and contains four dendrites. Furthermore, note distinctly different aspects of the cuticle of both setae. Scale bar 0.25µm. B: Notogastral simple seta of adult oribatid *Hermanniella* sp. (Hermanniellidae). Note that the tritonymphal exuvium together with its setae is retained and covers the adult integument. The tritonymphal seta is placed over the minute adult seta, which thus is moved indirectly by the tritonymphal seta. Arrowhead points to small nerve. Scale bar 2.5µm. Ce, cerotegument; Ex, exocuticle of adult mite.

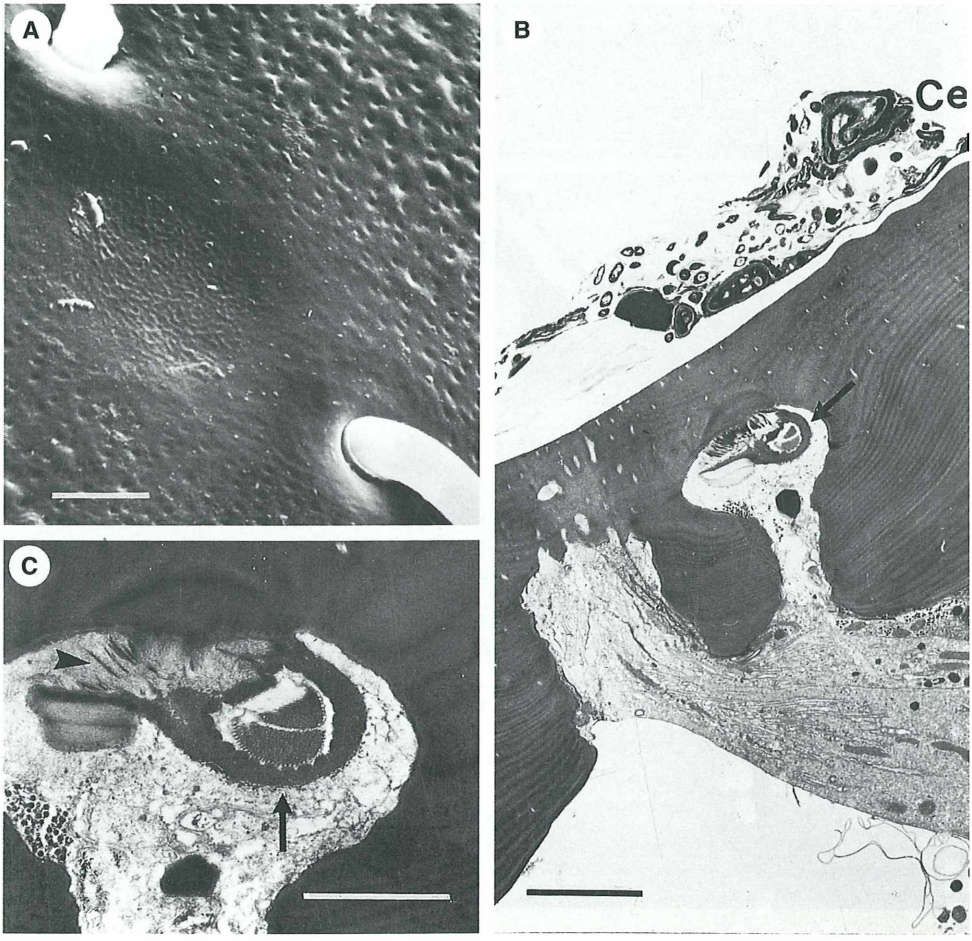


Fig. 7: Simple Setae. A: SEM of porose area A1 of *Eupelops torulosus* (Phenopelopidae) between setae lp and h3 (cleaned specimen). Scale bar 5µm. B. Section trough a porose area (left) and alveolus of adjacent seta (right) of *Eupelops* sp. Arrow points to two tubular bodies of receptor cells ensheathed in the helmet. Scale bar 5µm. C: Enlarged detail of B demonstrating two tubular bodies (arrow) and peculiar structure of helmet wall. Arrowhead points to radial fibres within articulating membrane of setal basis. Scale bar 2µm. Ce, cerotegument. (After ALBERTI et al. 1997).

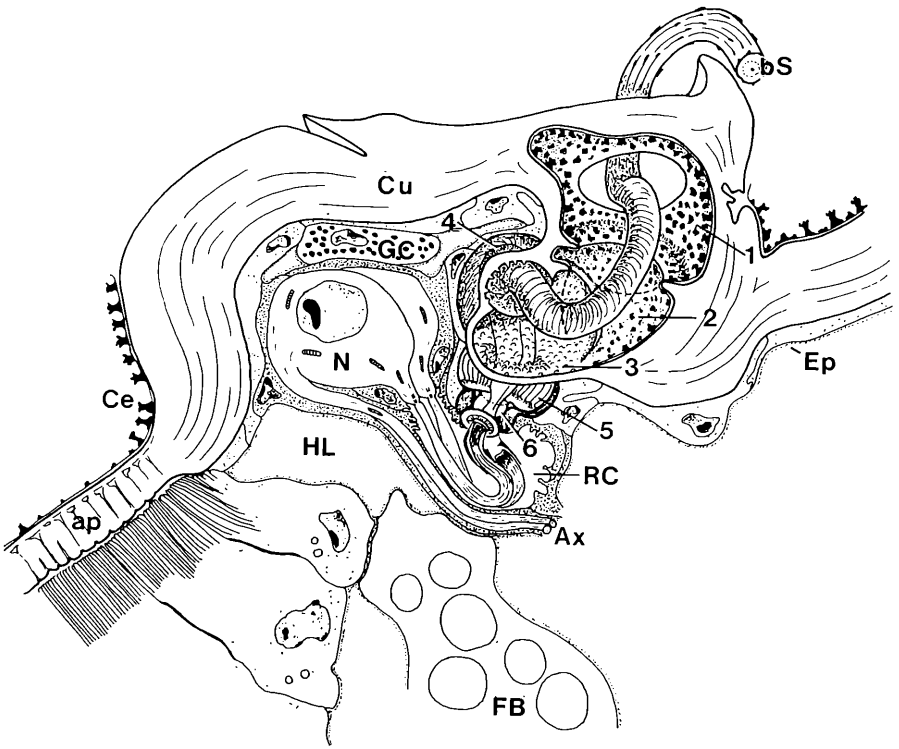


Fig. 8: Diagram reconstructed from horizontal sections showing trichobothrial base of *Acrogalumna longipluma*. ap, area porosa; Ax, axons; bS, bothridial seta; Ce, cerotegument; Cu, cuticle; Ep, epidermis; FB, fat body; GC, granulocyte; HL, haemolymph; N, nucleus of receptor cell; RC, receptorlymph cavity. Numbers indicate chambers of bothridium. Note that peripheral chambers are provided with a cerotegumental layer. (After ALBERTI et al. 1994).

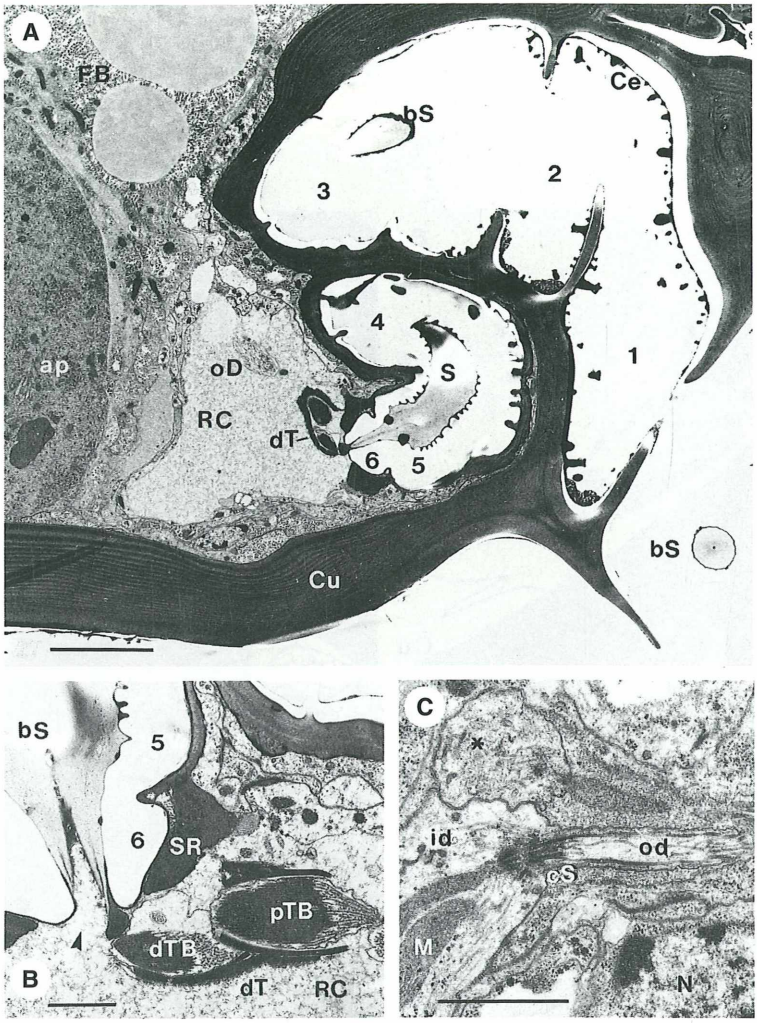


Fig. 9: Trichobothrium of *Acrogalumna longipluma*. A: Overall aspect of trichobothrial base of *Acrogalumna longipluma* in transverse section (relative to the mite's body). Scale bar 5µm. B: Tubular bodies surrounded by dense tubes and setal base. Note that only one tubular body has direct contact to setal base. Arrowhead points to open connection between receptor lymph cavity and lumen of bothridial seta. Scale bar 1µm. C: Ciliary segment of one receptor cell. Asterisk indicates the other receptor cell. Scale bar 1µm. ap, cell belonging to porose area; Ce, cerotegument; CS, ciliary segment; Cu, cuticle; bS, bothridial seta; dT, dense tubes (modified dendritic sheath); dTB, distal tubular body; FB, fat body; id, inner dendritic segment; M, mitochondrion in receptor cell; N, nucleus of enveloping or epidermal cell; od, outer dendritic segment; pTB, proximal tubular body; RC, receptor lymph cavity; SR, socket ring. Numbers indicate bothridial chambers. (After ALBERTI et al. 1994).

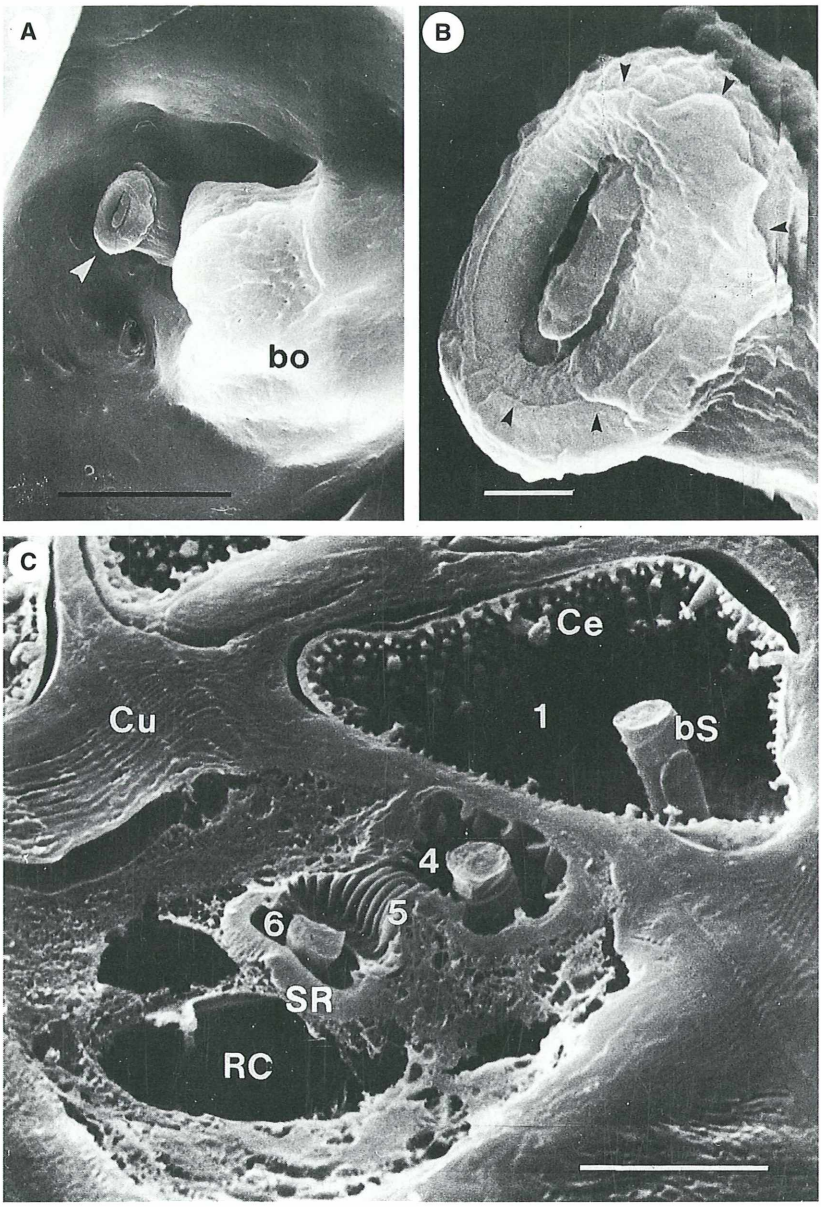


Fig. 10: SEM views of trichobothrial base of *Acrogalumna longipluma*. A: Inner aspect of bothridium from a macerated specimen (arrowhead points to setal base). Scale bar 10µm. B: Enlarged detail. Note oval shape of setal base. Arrowheads indicate remnants of fibrillar helmet, which connects the dense tubes with the setal base and socket. Scale bar 2µm. C: Oblique view over sectioned trichobothrial base. Scale bar 0.5µm. bo, bothridium; bS, bothridial seta (met three times in the section); Ce, cerotegument; Cu, cuticle; SR, socket ring; RC, receptor lymph cavity. Numbers indicate bothridial chambers. (After ALBERTI et al. 1994, 1995).

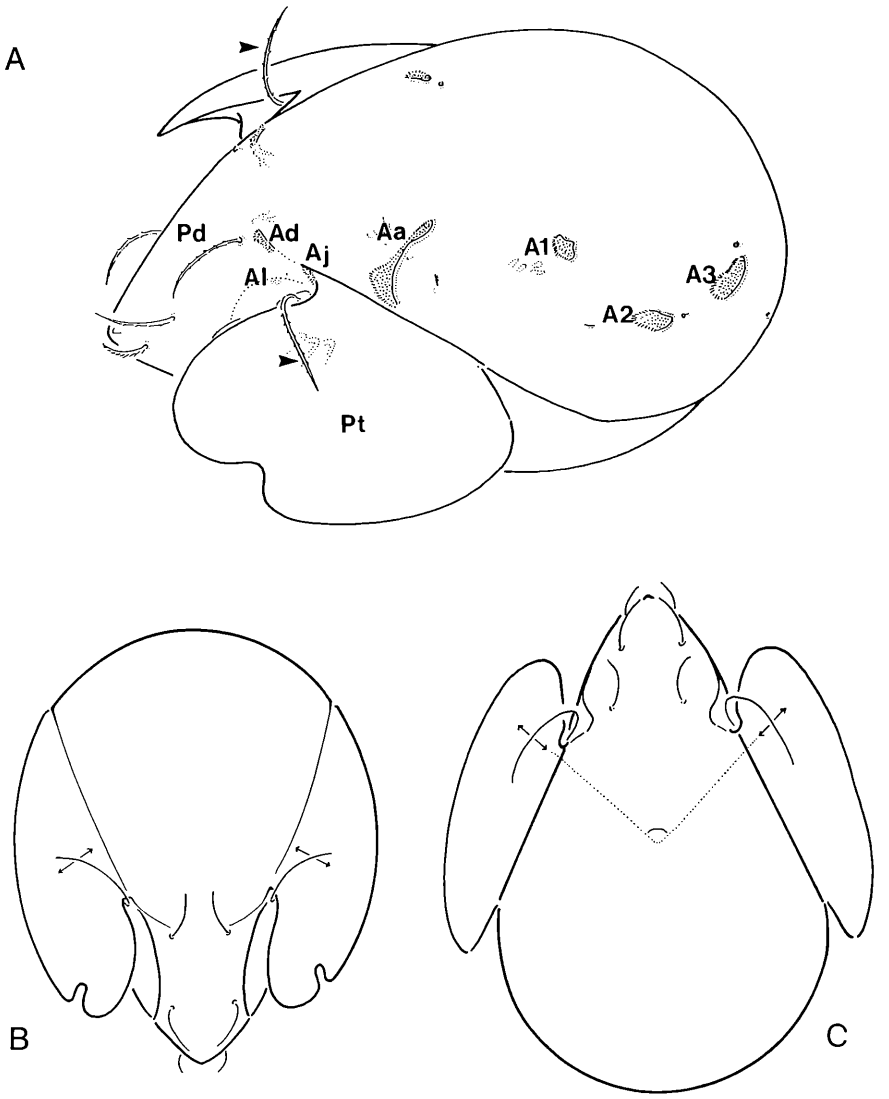


Fig. 11: Sketches of *Acrogalumna longipluma* demonstrating positions of the trichobothria and their movements. A: Line drawing based on a macerated specimen. Arrowheads point to bothridial setae. Note also porose areas of notogastral series: Aa, A1, A2, A3 (octotaxic system) and humeral series: Ad, Aj, Al). B: frontal and C: dorsal views drawn from living specimens of *Acrogalumna longipluma* indicating how the trichobothria are borne in life (appendages and details omitted). The movements of the trichobothria when reacting to a current of air are shown (double arrows). In the dorsal view, the directions of movement have been prolonged posteriorly by dotted lines, which meet with a right angle approximately above the brain of the animal (cf. PAULY 1956). Pd, prodorsum; Pt, pteromorph. (After ALBERTI et al. 1994).

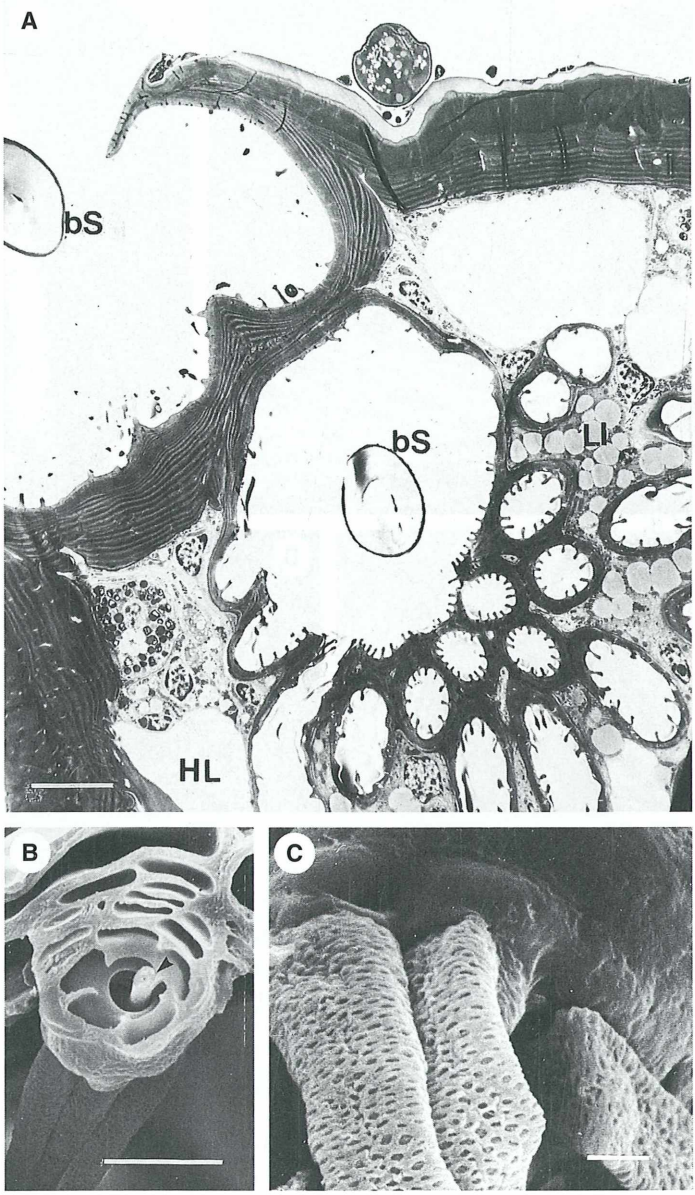


Fig. 12: In some Oribatida the bothridium is a region from which additional structures such as brachytracheae start. A: TEM of bothridium of *Nothrus silvestris* (Nothridae) with cluster of brachytracheae. Scale bar 5µm. B: SEM of brachytracheae of *Steganacarus magnus* (Phthiracaridae) (internal view, macerated specimen). The very complex bothridium (sectioned) surrounds the bothridial seta (arrowhead). Proximally three brachtracheae run into the depth of the prodorsum. Scale bar 20µm. C: Detail of brachytracheae of same specimen. Scale bar 5µm. bS, bothridial seta; HL, haemolymph; LI, lipid droplets. (After ALBERTI et al. 1997).

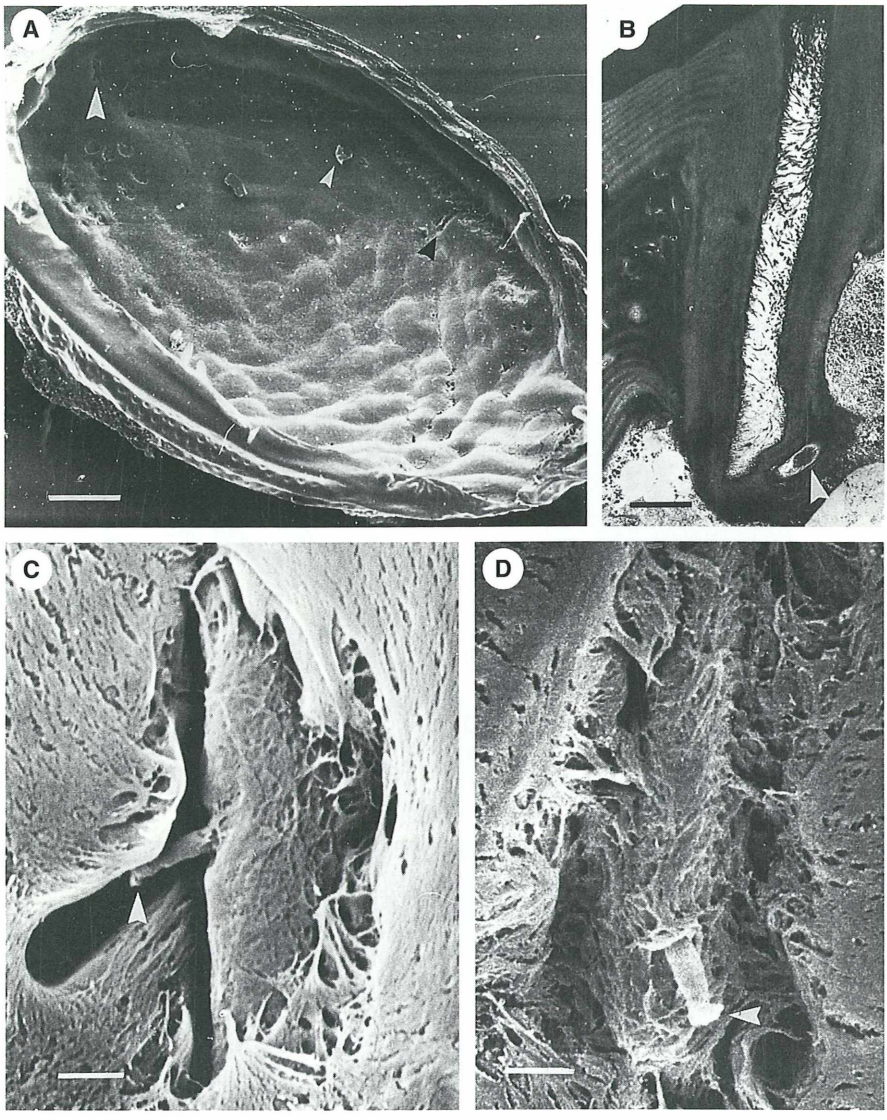


Fig. 13: Details of two notogastral slit sense organs of *Scutovertex minutus* (Scutoverticidae). A: Internal SEM view of notogaster after dissolving tissues with lactic acid. Black arrowhead shows the slit sense organ (im), large white arrowhead indicates the posterior organ (ip) (cf. SCHUSTER 1958). Small white arrowhead points to lateral opisthosomatic gland. Scale bar 50μm. B: TEM of posterior slit sense organ with dendritic process containing a tubular body (arrowhead) within internally projecting portion of the cuticle. Note modified cuticle above this region. Scale bar 1μm. C. The same organ in SEM, seen from the anterior (cf. Fig. 13A). Arrowhead points to cuticular process located in a depression of the procuticle. Scale bar 1μm. C: Slit sense organ (im). Arrowhead indicates cuticular process. Scale bar 2μm.

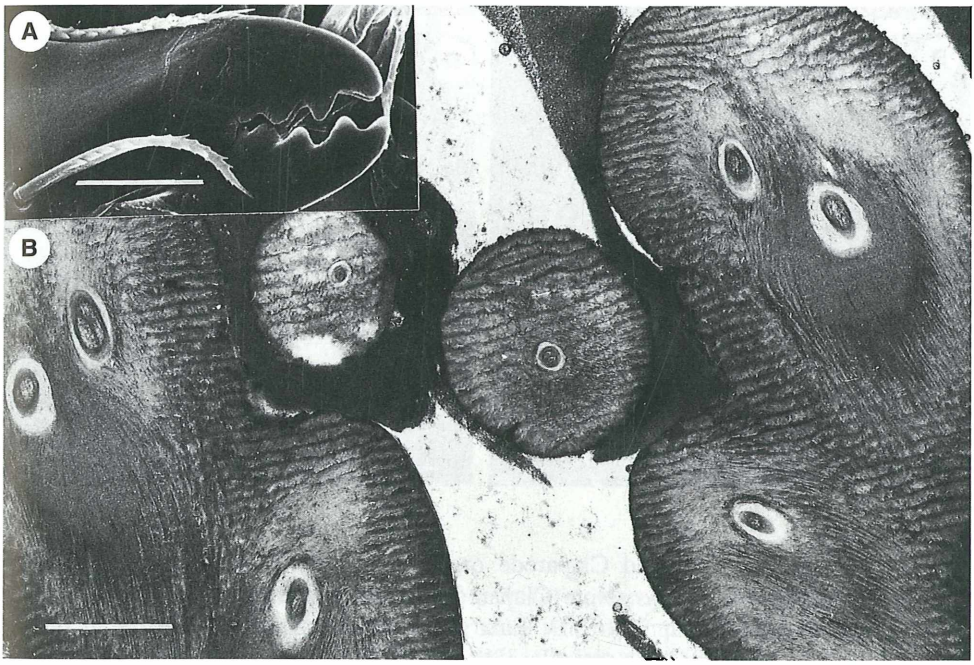


Fig. 14: Chelicera of *Acrogalumna longipluma*. A: SEM view of right chelicera. Note distinct teeth. Scale bar 10µm. B: Horizontal section of teeth. Note dendritic processes penetrating into the teeth. Scale bar 2µm.

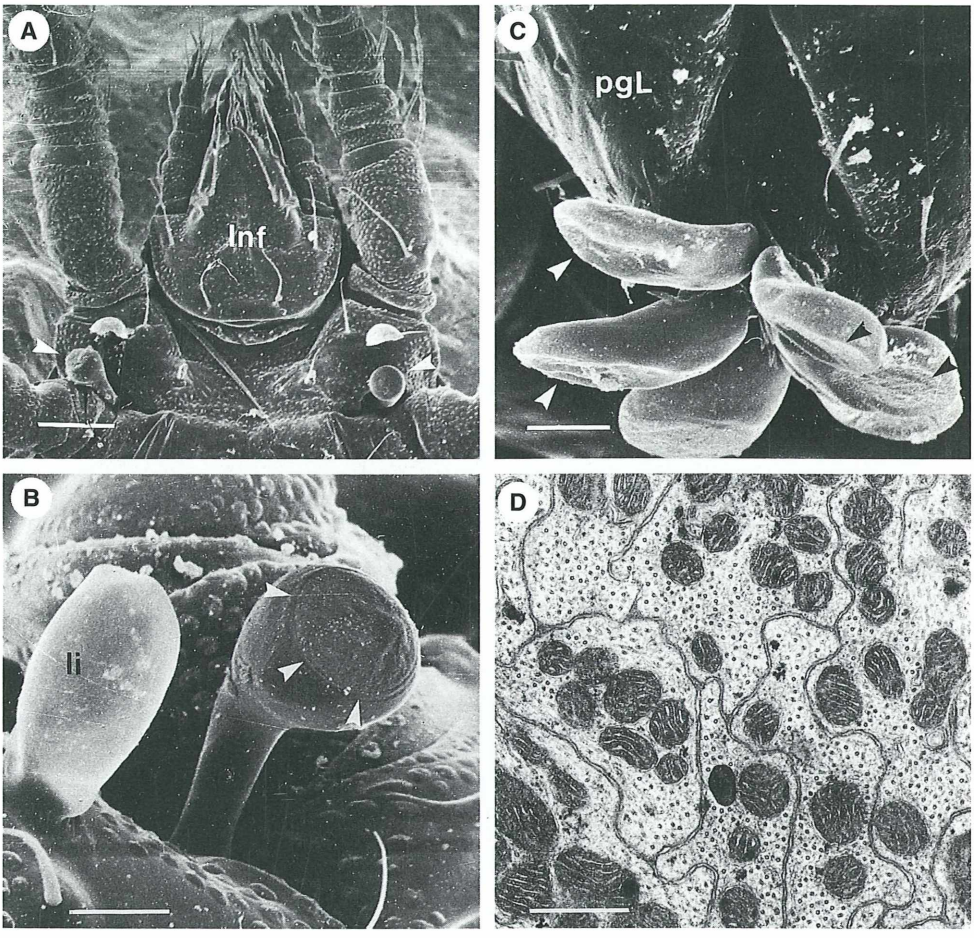


Fig. 15: Genital papillae and Claparède organs. A: Ventral view of larva of *Hypochthonius rufulus*. Note Claparède organs between legs I and II (arrowheads). Scale bar 20µm. B: Enlarged view of one Claparède organ of the same specimen. Note cuticular lid and stalked organ terminating with a modified distinct apical cuticle (arrowheads indicate its border). Scale bar 5µm. C: Protruded papillae of an adult specimen of *Hypochthonius rufulus*. Note that apically papillae are provided with a modified cuticle (arrowheads). Scale bar 10µm. D: Apical labyrinth of genital papilla of the freshwater-inhabiting oribatid mite *Hydrozetes lemnae* (Hydrozetidae). Note folds of plasmalemma, adjacent mitochondria and numerous microtubules. Scale bar 0.5µm. Inf, infracapitulum; li, lid of Claparéde organ; pgL, progenital lip. (A-C: After LÖWENFELD 1987; D: After ALBERTI and LÖWENFELD 1990).

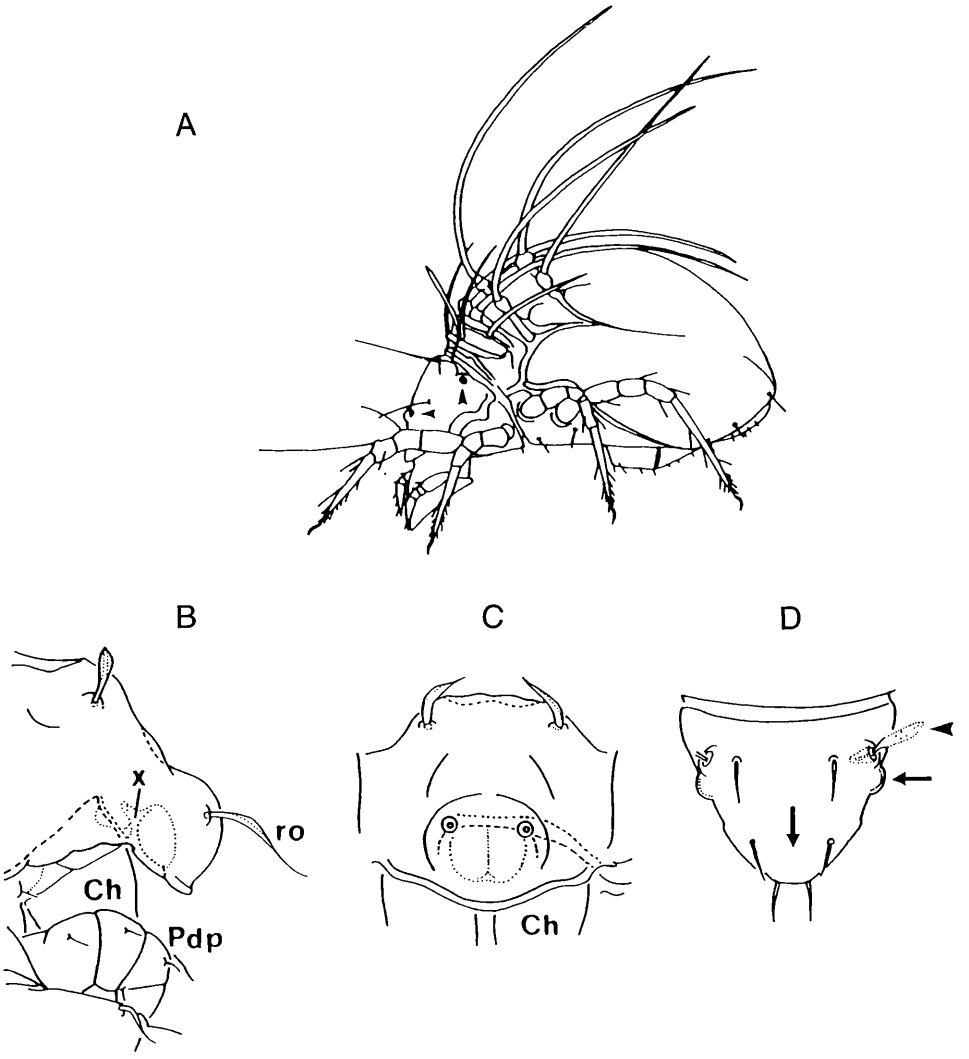


Fig. 16: Prodorsal eyes in early derivative oribatid mites: A: *Heterochthonius gibbus* (Heterochthoniidae) is an oribatid mite with an unpaired median eye and a pair of lateral eyes (arrowheads). (After GRANDJEAN 1928). B: Naso and median eye of the oribatid mite *Brachychthonius* sp. (Brachychthoniidae) in lateral view. x indicates invaginated space behind the median eye. (After GRANDJEAN 1958). C: The same in frontal view. Note that the median eye is divided into two by a fine suture. Rostral setae have been omitted (cf. Fig. B: ro). (After GRANDJEAN 1958). D: Naso and (paired) median as well as lateral (!) eyes (arrows) in *Eobrachychthonius* sp. Arrowhead indicates left trichobothrium. (After TRAVÉ 1968). Ch, chelicera; Pdp, pedipalp ro, rostral seta.

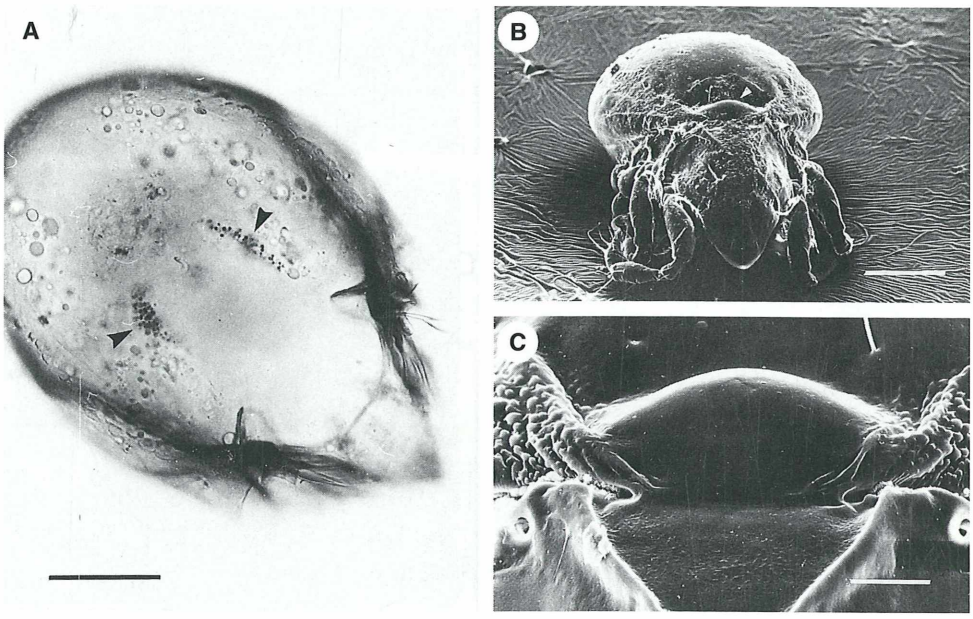


Fig. 17: Clear spots and lenticuli in Oribatida. A: Macerated specimen of *Chamobates borealis* (Chamobatidae) showing racemiform organ (= mineral granules/ spherites in proventricular glands; arrowheads) lateral of the region of the brain over which the cuticle would be less dark. Under this region lamellated bodies have been demonstrated by TEM closely attached to the brain in *Chamobates voigtsi* (see Fig. 20A; after LUDWIG et al. 1992). Scale bar 50µm. B: *Hydrozetes lemnae* in frontal view. Arrowhead points to lenticulus. Note cerotegument does not cover the elevation. Scale bar 100µm. C: Enlarged detail of same species (cleaned with ultrasound). Scale bar 20µm (B, C after ALBERTI & FERNANDEZ 1988).

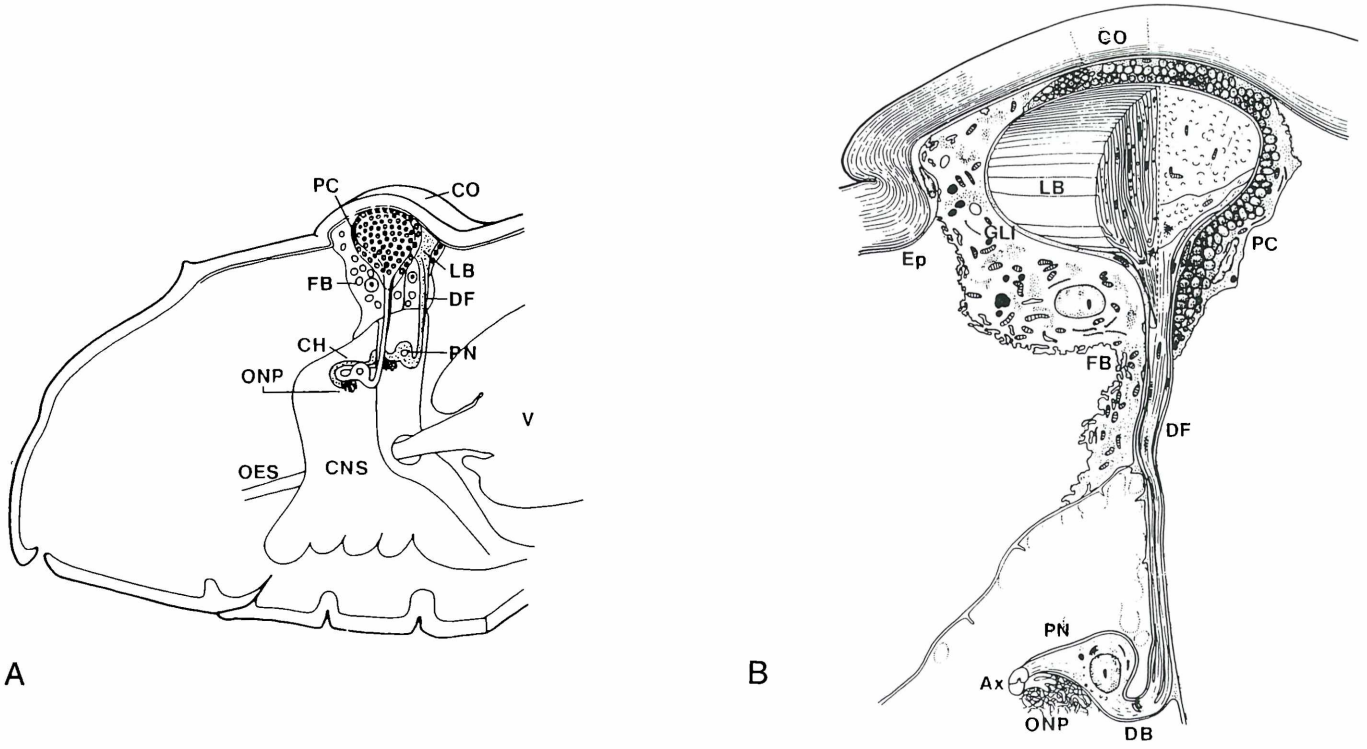


Fig. 18: Line drawings demonstrating components of the lenticulus in *Hydrozetes lemnae* (compare Fig. 17 and 19). A: Overview demonstrating position of the photoreceptor organ within the propodosoma and its relation to the synganglion. Note relative size of lamellated bodies. The receptor cell of the right side has been dotted. B: Reconstruction of one receptor cell and adjacent cells of lenticulus. Ax, axons; CH, chiasma opticum; CNS, central nervous system (synganglion); CO, cornea; DF, dendritic fibres; Ep, epidermis; FB, fat body cell; GLI, glial cell; LB, lamellated body; OES, esophagus; ONP, optic neuropil; PC, pigment cell; PN, perikaryon of photoneuron; V, ventricle. (After ALBERTI & FERNANDEZ 1988).

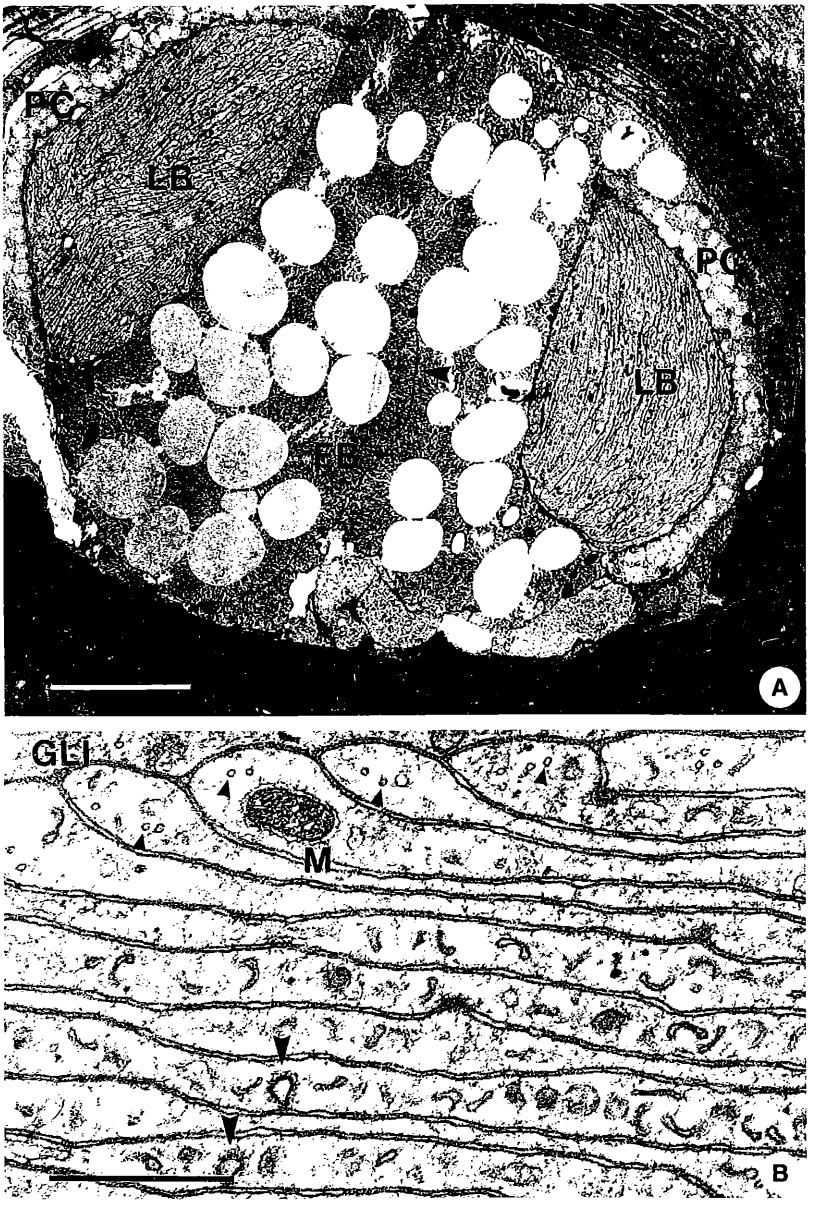


Fig. 19: Details of lenticulus of *Hydrozetes lemnae*. A: Horizontal section. Note pair of lamellated bodies and adjacent pigment cells. Arrowhead points to intercellular cleft separating the two fat body cells. Scale bar 10μm. B: Part of lamellated body in transverse section. Note numerous and characteristic cup-shaped vesicles. Large arrowheads point to coated vesicles (partly in formation?), small arrowheads indicate microtubules. Scale bar 0.5μm. Cu, cuticle; FB, fat body cell; GLI, glial cell; LB, lamellated body; M, mitochondrion; PC, pigment cell. (After ALBERTI & FERNANDEZ 1988).

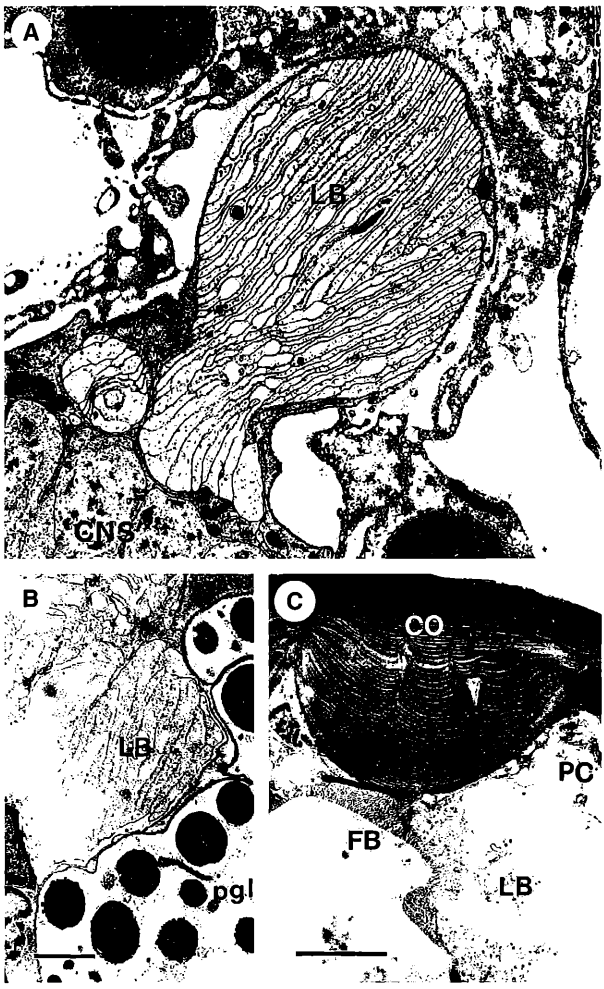


Fig. 20: Secondary light receptor organs in other oribatids. A: One lamellated body (transverse section) of *Chamobates voigtsi*, a species with clear spot. Note that it is not elevated under the dorsal surface by extensive dendritic fibres but is closely apposed to the synganglion. There is also no pigment cell. (After ALBERTI & FERNANDEZ 1990). Scale bar 4μm. B: One lamellated body of *Parapirnodus* sp. (Oripodidae). In this species the lamellated bodies are rather ventrally located and are partly embedded into extensions of the proventricular glands containing dense inclusions (modified spherites?). Scale bar 1μm. (After ALBERTI & FERNANDEZ personal observations.) C: Transverse section through lenticulus of *Scapheremaeus argentina* (Cymbaeremaeidae) showing biconvex cuticular lens. (After ALBERTI & FERNANDEZ personal observations.) Scale bar 10μm. CNS, central nervous system (synganglion); CO, cornea; FB, fat body cell; LB, lamellated body; PC, pigment cell; pgl, proventricular gland.