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Morphological adaptations of mite chelicerae to different trophic activities (Acari)

ABSTRACT

The authors briefly review the current knowledge on the structural organization and functional significance of the chelicerae and their sensory structures among mites of economical interest in agriculture that have been recently investigated for their gnathosoma.

The chelicerae of the polyphagous predatory mite *Typhlodromus exhilaratus* Ragusa (Gamasida, Phytoseiidae) have a rather unspecialized organization and are of chelate type. They function mainly in grasping the prey and other food, while the other mouthparts are adapted to prey wounding, salivary injection and juice suction.

In the Honey Bee parasite, *Varroa destructor* Anderson & Trueman (Gamasida, Varroidae), the chelicerae have almost completely lost the fixed digit while the movable digit is thinner and elongated. The chelicerae participate directly, along with the other mouthparts, only in the perforation of the Honey Bee integument.

In the plant-feeder, *Penthaleus major* (Dugès) (Actinedida, Penthaleidae), the movable digit is composed of a long and stout stylet-like structure, and a peculiar basal sclerite which activates the digit movements. During cheliceral protrusion, the stylets may work jointly or independently from each other in piercing the plant surface and causing deep and large wounds. The protruded stylets may justapose each other; they may delimit an intercheliceral channel and may be involved in salivary injection. The fixed digit is a large somewhat soft structure which covers dorsally the pre-oral and supralabral chamber, and is passively involved in juice sieving and sucking.

The movable digit of the fungivorous *Tarsonemus nodosus* Schaarschmidt (Actinedida, Tarsonemidae) is needle-like and articulated with a transverse lever to the second cheliceral article. The basal cheliceral articles are fused together forming a stylophore. The fixed digits partly envelop the movable digits and they are consolidated with the subcapitulum. The stylar morphology suggests an independent piercing action of the movable digits.

The phytophagous Two-Spotted Spider mite, *Tetranychus urticae* Koch (Actinedida, Tetranychidae), and False Red Spider mite, *Cenopalpus pulcher* (Canestrini & Fanzago) (Actinedida, Tenuipalpidae), have extensively protractable styliform chelicerae. The movable digits are very elongated and stylet-like, originating proximally from the stylophore (fused first cheliceral articles); the fixed digits are partially fused to each other. During cheliceral protrusion, the stylets are forced to be interlocked to each other to delimit an intercheliceral canal which is directly connected to the salivary duct. At the same time, the fused fixed digits are involved in salivary pump functioning. So, the chelicerae play a double role in piercing the plant surface and discharging saliva into the host tissue.

In the tiny phytophagous mites of the superfamily Eriophyoidea (Actinedida), the gnathosoma has a strongly derived organization. Fixed and movable digits are both styliform, laminar shaped, and included in a strict frame of nine stylets of different origin which function together in host piercing, salivary injection and juice suction. The short sliding movements of the cheliceral shafts are activated by the unpaired motivator. The chelicerae seem to be mainly involved in deeping the mouthparts into the wounds and partially in salivary injection.

In each of the investigated species, chelicerae are provided with putative chemoreceptive sensilla, in addition to other mechanoreceptors, which seem to be strictly involved in food perception and acceptance. As yet, however, an alternative perceptive function cannot be excluded.

Key words: Acari, gnathosoma, mouthparts, feeding mechanisms, sensory structures, digitus mobilis, digitus fixus, morphological adaptations, host piercing, salivary injection, basal sclerite, lever, motivator, stylophore.

INTRODUCTION

Up to the present, the Acari have become of increasing economic importance to human activities. Owing to their small size and ecological needs, they can live in diverse microenvironments. They display a great variety of trophic behaviours (EVANS, 1992), utilizing every kind of substrate and being involved in the cycle of organic matter. They have medical and veterinary as well as agricultural relevance for the direct and indirect (pathogen transmission) injuries they cause to man, domestic animals, edible fungi, stored products and plants. On the other hand, some species are useful for the positive roles they play against injurious insects, mites and nematodes. Therefore, they find considerable economic interest so as to be protected and actually applied in integrated pest management and biological control programs.

As a rule, structural and functional adaptations of the gnathosoma have evolved on the basis of mite feeding mechanisms and they can help in understanding mite trophic relationships. Of course, the injuriousness and symptoms resulting from feeding depend on the mouthpart frame-work, which surely needs a morphological approach to be understood in a thorough way. In particular, the chelicerae have undergone the most outstanding modifications in being chelate in typically predatory mites and, passing through the parasitic and fungivorous habits, they assume finally the specialized and derived stylet-like organization of the plant-feeding mites (KRANTZ & LINDQUIST, 1979; LINDQUIST, 1998; ALBERTI & COONS, 1999; RAGUSA & TSOLAKIS, 2000).

The present paper gives a brief account of the fine morphology of some acarine chelicerae, including remarks on their sensory structures, and updating and deepening previous short notes (NUZZACI, 1985 and 1994). In particular, it deals with the movable and fixed cheliceral digits, showing the similarity and diversity in some mites of agricultural interest which have received much attention by the authors of this paper in the last 25 years. In addition, a functional interpretation of the feeding mechanisms is advanced based on the morphological features.

FINE MORPHOLOGY OF THE CHELICERAE

The complex trophic sensory structure of the gnathosoma is conventionally composed of chelicerae, pedipalps, labrum, subcapitulum and their derived structures (i.e.: lateral lips, cervix, salivary styli, etc.). Unfortunately, there is no generally acceptable terminology for these parts and the same structures may be frequently considered under several different terms (VAN DER HAMMEN, 1980) even though a considerable and appreciable effort towards a common terminology has been done by LINDQUIST (1985, 1986 and 1996). This review mainly applies the terminology proposed by EVANS (1992).

1. *TYPHLODROMUS EXHILARATUS* RAGUSA (GAMASIDA, PHYTOSEIIDAE)

The detailed morphology and function of the mouthparts for *T. exhilaratus* females (figs 1.1-4) and other species of the family Phytoseiidae were reported by AKIMOV and YASTREBTSOV (1986), FLECHTMANN and MCMURTRY (1992b), and DE LILLO and ALDINI (1994). It is well known that phytoseiids have primarily predaceous habits and their chelicerae retain the original and underived acarine organization, being strongly sclerotized, chelate, more or less elongated and provided with teeth on the digits (CHANT, 1985; RAGUSA & TSOLAKIS, 2000). The chelicerae are dorsal to the hypostome, labrum and salivary styli (figs 1.1, 1.3-4), and show no particular morphological relationship with these parts.

The movable digit of *T. exhilaratus* is distally sharp and curved up forming a sort of hook which bears a subdistal tooth (figs 1.1, 1.3-4). The fixed digit is a bit longer than the movable digit, its sharp distal end is bent down. It bears ventrally a subdistal tooth, and the more proximal pilus dentilis (figs 1.1, 1.3-4). From its apex back to the level of the pilus dentilis, the movable digit is a bit mesally displaced so that its antiaxial surface partly apposes the fixed digit paraxial surface (figs 1.3, 1.5-6). In cross section, the movable digit is almost elliptical in its distal and subdistal part while, more proximally, it takes a triangular shape (figs 1.1, 1.5-9). At the level of the articulation with the second cheliceral segment, it becomes more elongated on the vertical plane (fig. 1.9) displaying, in cross section, a lateral concavity on each side (figs 1.1,

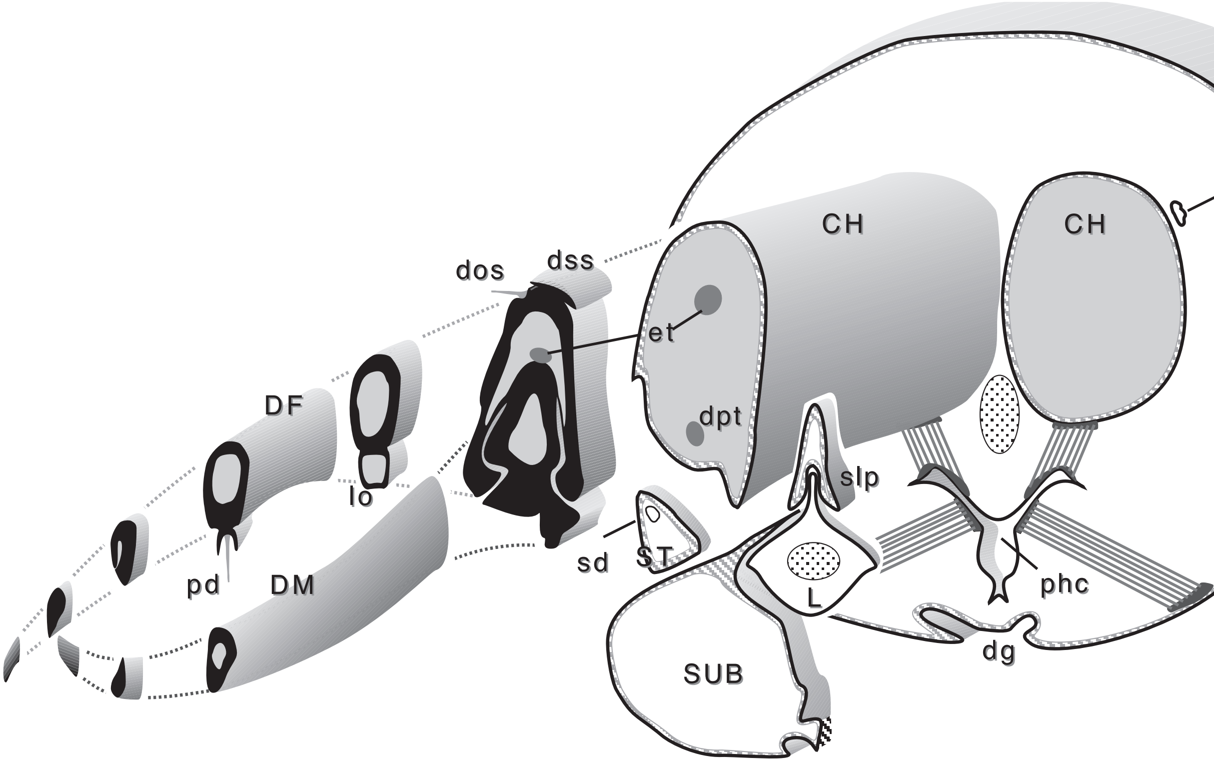
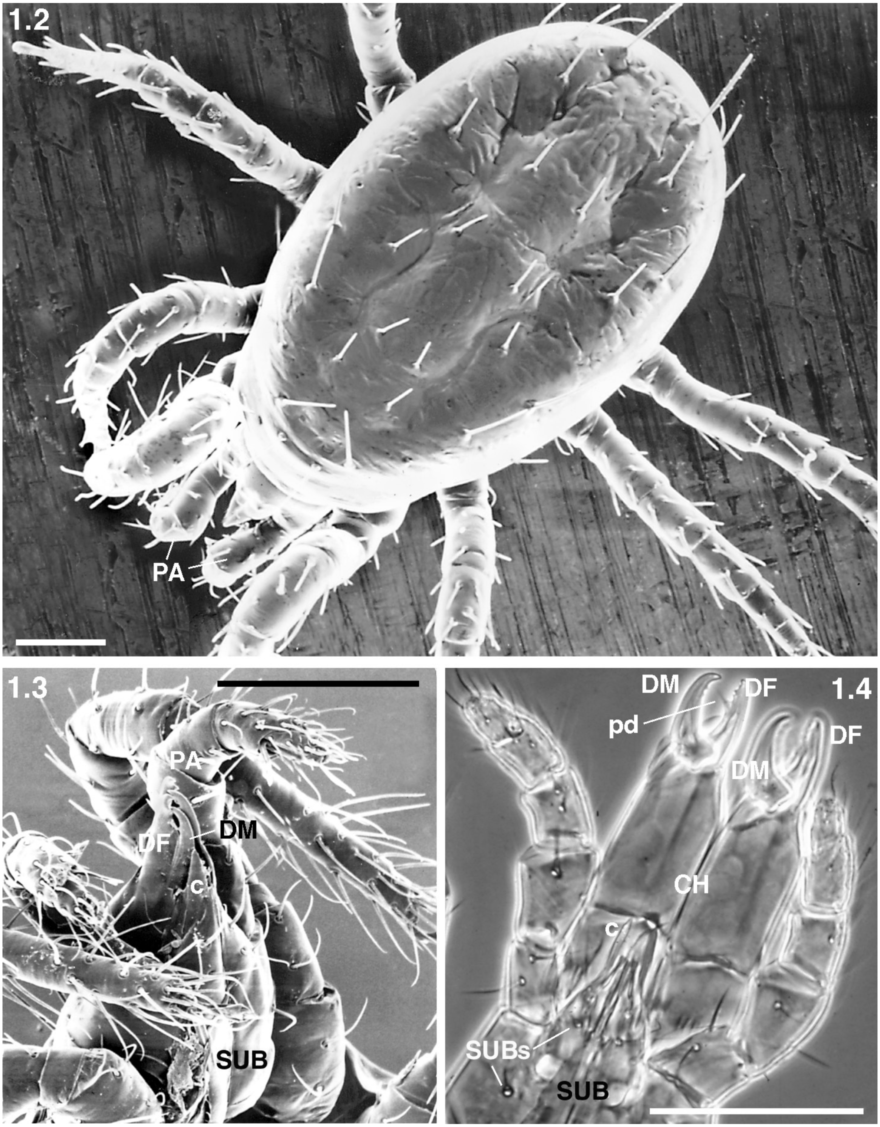
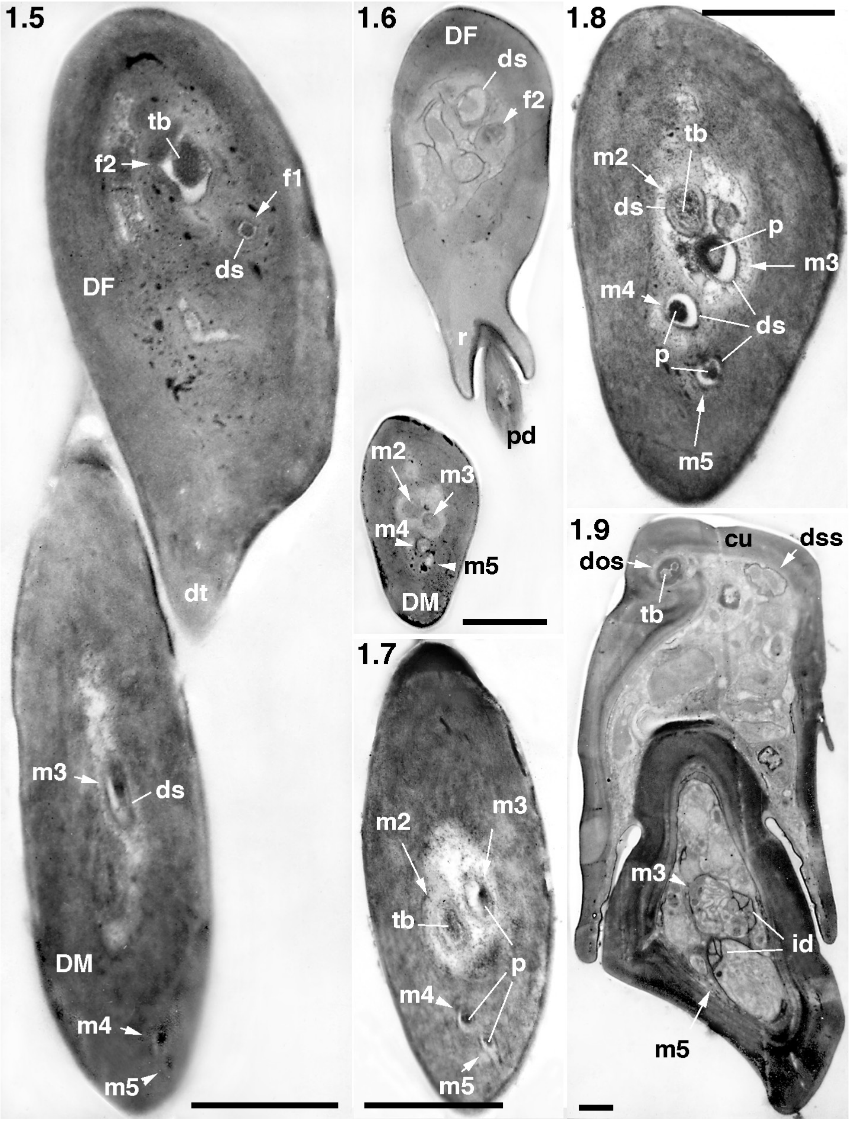


Fig. 1.1 - *Typhlodromus exhilaratus* Ragusa: semischematic drawing of the mouthparts from a latero-dorsal view. Subcapitular pieces, labrum and salivary styli are partly drawn. Abbrev.: CH, chelicera; DF, fixed digit; dg, deutosternal groove; DM, movable digit; dos, dorsal seta shaft; dpt, tendon of depressor muscles of the movable digit; dss, dorsal slit sense organ; et, tendon of elevator muscle of the movable digit; SUB, subcapitulum; L, labrum; lo, fixed digit lobe; pd, pilus dentilis; phc, pharyngeal chamber; sd, salivary duct; slp, supralabral process; ST, salivary stylus.



Figs 1.2-4 - *Typhlodromus exhilaratus* Ragusa: scanning electron micrograph of 2) an adult female from a dorsal view and 3) the gnathosoma from a ventro-lateral view; 4) phase contrast micrograph of the gnathosoma showing the protruded chelicerae. Scale bars = 50 µm. Abbrev.: c, corniculus; CH, chelicera; DF, fixed digit; DM, movable digit; SUB, subcapitulum; SUBs, subcapitular setae; PA, pedipalp; pd, pilus dentilis.



Figs 1.5-9 - *Typhlodromus exhilaratus* Ragusa, transmission electron micrographs of cheliceral cross sections: 5) both digits at a subdistal and 6) at pilus dentilis level; 7-8) movable digit at more proximal levels than the previous figures, showing nervous components; 9) movable digit articulation to the second cheliceral article. Scale bars = 1 µm. Abbrev.: cu, cuticle; DF, fixed digit; DM, movable digit; dos, dorsal seta shaft; ds, dendritic sheath; dss, dorsal slit sense organ; dt, digit tooth; id, inner dendritic segment; f1, fixed digit chemoreceptor; f2, fixed digit mechanoreceptor; m2, movable digit mechanoreceptor; m3, m4, m5, movable digit chemoreceptors; p, electron-dense plug; pd, pilus dentilis; r, rim; tb, tubular body.

1.10). More proximally, the movable digit is completely fused with the second cheliceral article (fig. 1.11) and is connected to the ventral and dorsal tendons, respectively, for the depressor and elevator muscles (figs 1.12-13).

The fixed digit is distally elliptical, in cross section, and gradually becomes larger towards its base (figs 1.1, 1.5-6, 1.14-15). More proximally, it displays a ventral “lobe” (according to FLECHTMANN & MCMURTRY, 1992b) provided with a thin and less electron-dense cuticle delimiting an electron-lucid and amorphous area (figs 1.1, 1.16). Basally, the fixed digit develops a lateral and ventral extension, on each side, which laterally envelops the movable digit (fig. 1.9). More proximally, each extension shows a bulbous which fits perfectly inside the lateral concavities of the movable digit (figs 1.1, 1.10).

Much further observations have been carried out by de LILLO *et al.* (1996) on the mouthpart sense organs. The following set of sensilla has been found on the chelicerae: 5 sensilla on the movable digit (4 chemo- and 1 mechanoreceptors), 3 on the fixed digit (2 mechano- and 1 chemoreceptors including the pilus dentilis), and 3 on the second cheliceral article (a dorsal seta, an antiaxial and a dorsal slit sense organ, according to ALBERTI & COONS, 1999).

The nerve cells of the digit chemoreceptors end at a subdistal level. They are evidently provided with such small pores (figs 1.5, 1.7) that they have not been detected on the cuticle by means of scanning electron microscopy. An electron-dense substance fills the sensillar lumina and mediates between the environment and the outer dendritic segments (figs 1.7-8). None of these sensilla display any outstanding cuticular structure, even if the fixed digit chemoreceptor lies at the base of a vestibulum connected to a “pit” located on the antiaxial surface of this part (figs 1.15, 1.17). The arrangement (mainly the cellular components) of these receptors accords perfectly with the conventionally classified terminal pore sensilla (figs 1.9-12, 1.16, 1.18-21).

A mechanical sensory structure (m2 and f2) is located about at the apex of both digits, and the outer dendritic segment of each of these sensilla is provided with a distal tubular body. One of them is just under the subdistal tooth on the fixed digit and the other one is close to the apical hook of the movable digit (figs 1.5, 1.8, 1.16, 1.18, 1.20, 1.22). The pilus dentilis is on the ventral side of the fixed digit at about half length of this part and is directed towards the antiaxial surface of the movable digit (figs 1.1, 1.4, 1.6, 1.23). The dorsal seta is antiaxially[1] located on the subdistal part of the second cheliceral article; it is directed forward and is beat very closely to the cuticular surface (figs 1.1, 1.10). Both sensilla are provided with a prominent hair-like

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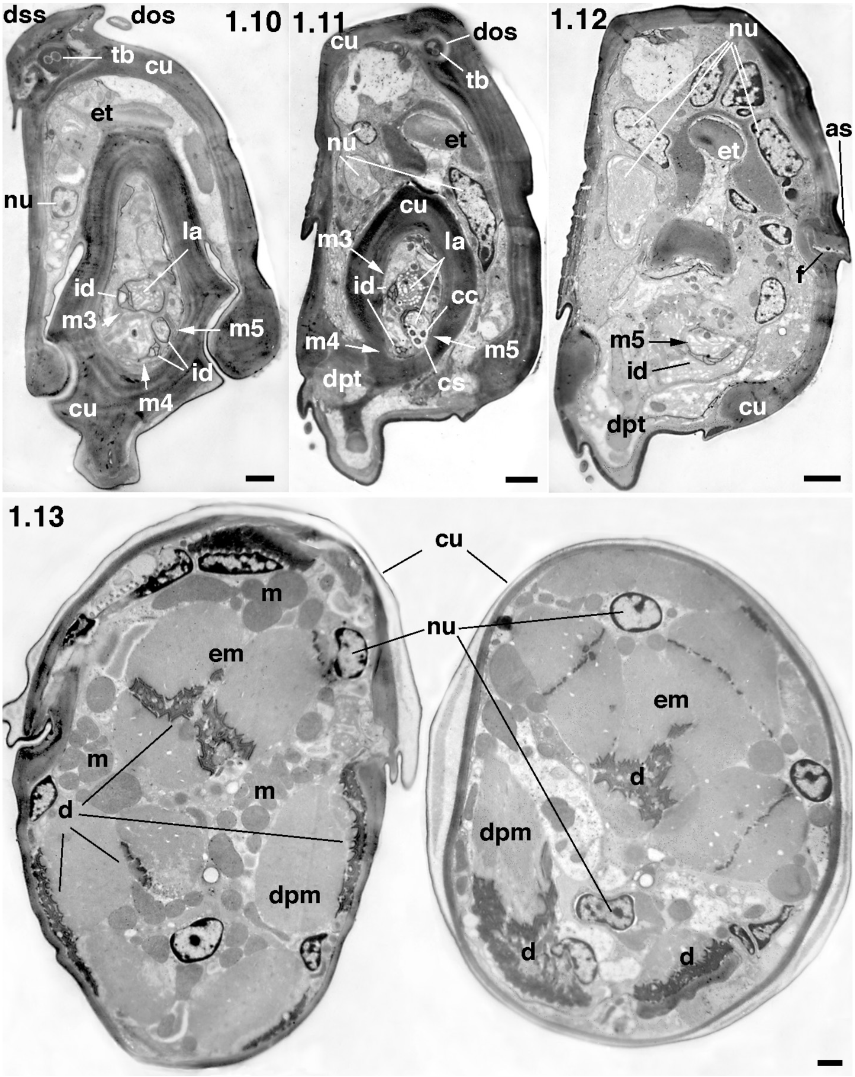
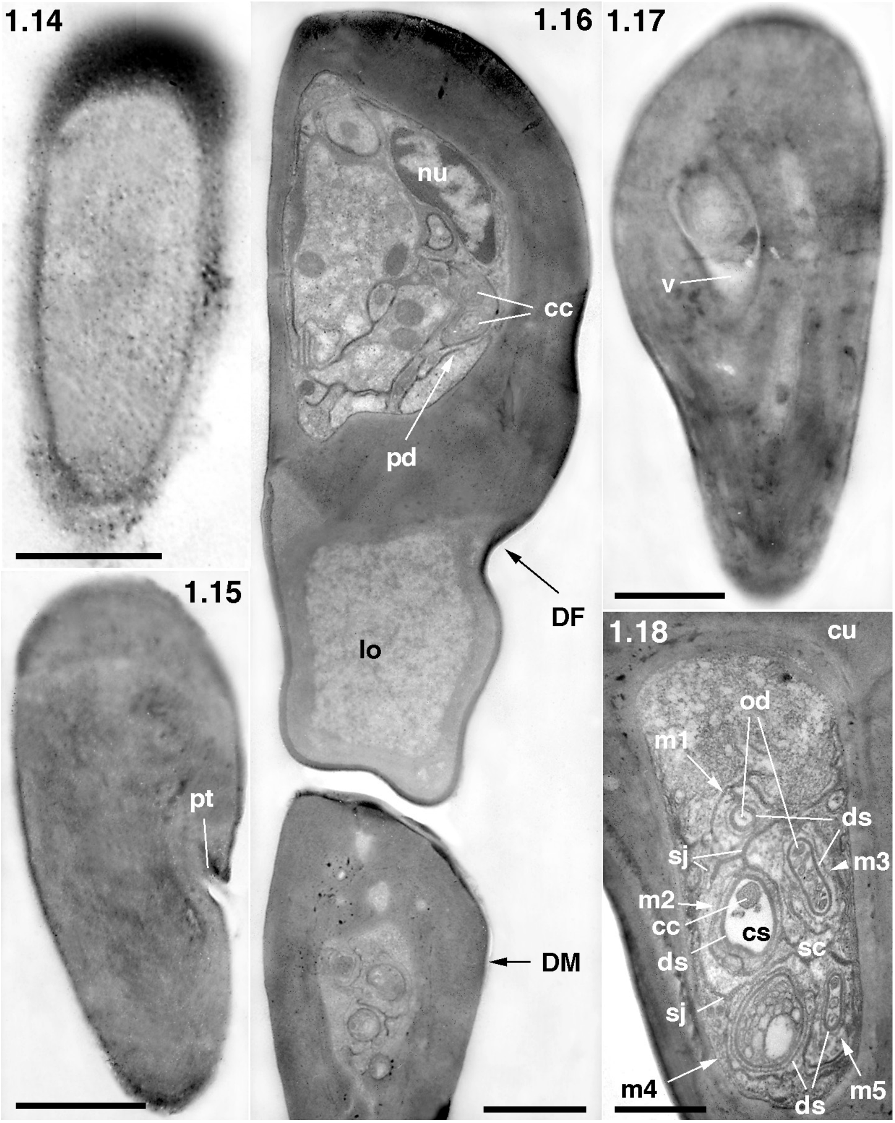
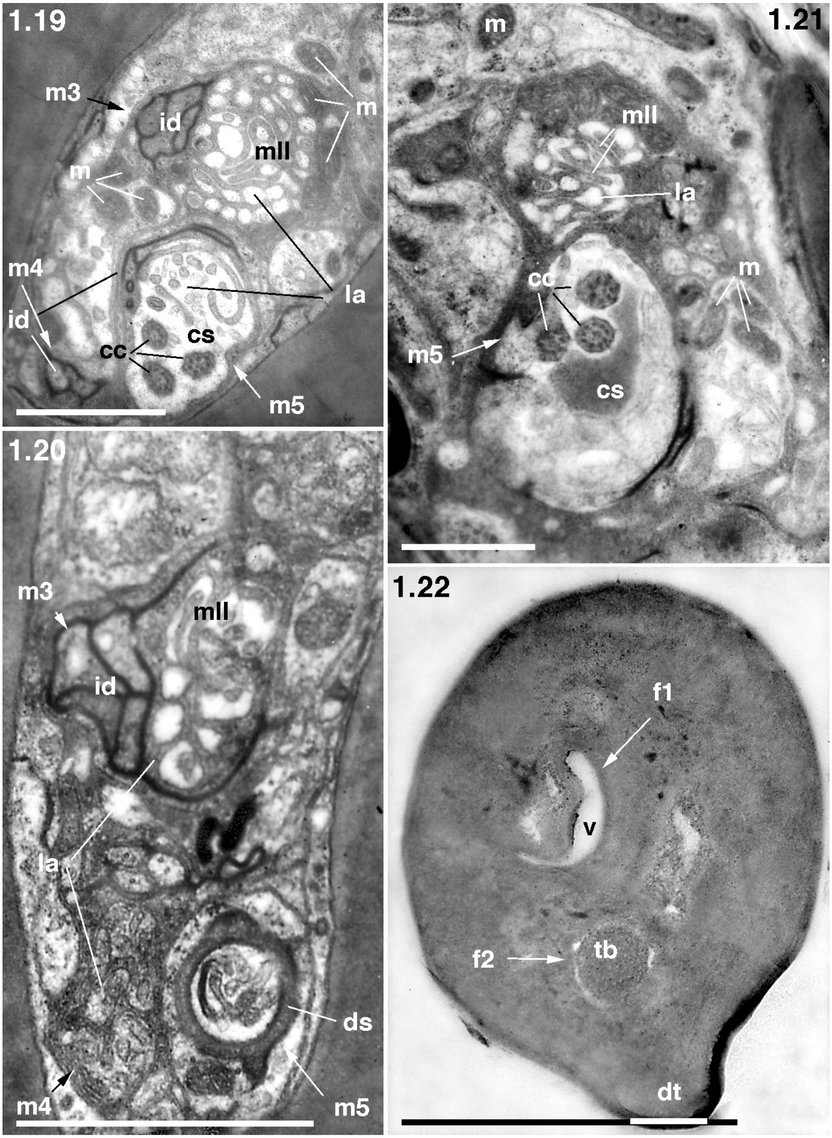
[1] This sensillum was erroneously indicated on the paraxial surface in de Lillo *et al.* (1996) and correctly reported on fig. 21 in de Lillo & Aldini (1994).



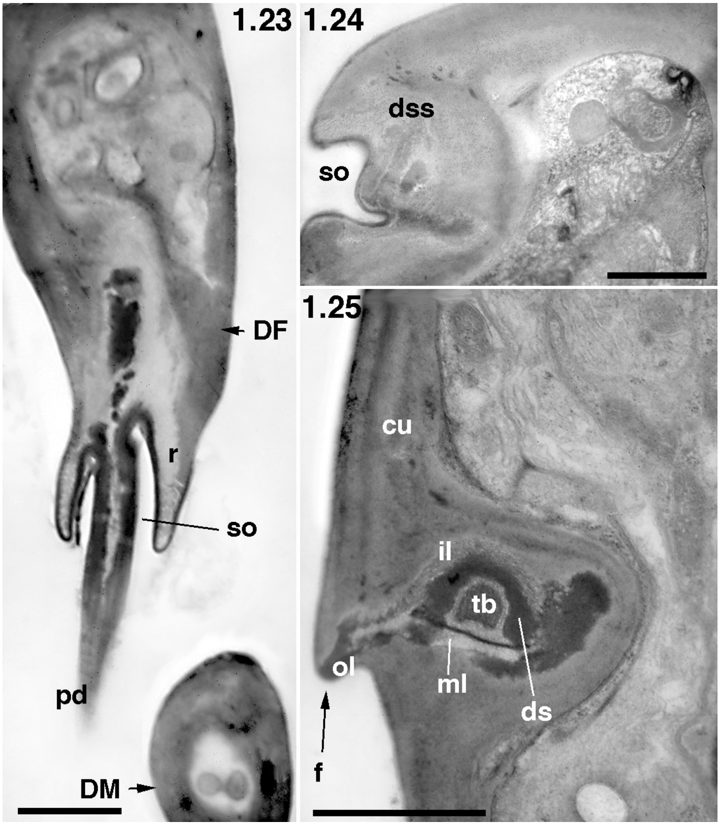
Figs 1.10-13 - *Typhlodromus exhilaratus* Ragusa, transmission electron micrographs of cheliceral cross sections: 10) movable digit articulation to the second cheliceral article; 11-13) gradually more proximal from 11 to 13 showing muscular and cuticular details of the movable digit articulation. Scale bars = 1 µm. Abbrev.: as, antiaxial slit sense organ; cc, ciliary constriction; cs, ciliary sinus; cu, cuticle; d, desmosome; dos, dorsal seta shaft; dpm, depressor muscles of the movable digit; dpt, tendon of depressor muscles of the movable digit; dss, dorsal slit sense organ; em, elevator muscles of the movable digit; et, tendon of elevator muscles of the movable digit; f, cuticular fold; id, inner dendritic segment; la, labyrinth; m, mitochondrion; m3, m4, m5, movable digit chemoreceptors; nu, nucleus; tb, tubular body.



Figs 1.14-18 - *Typhlodromus exhilaratus* Ragusa, transmission electron micrographs of cheliceral cross sections: 14-15) fixed digit at distal 14) and subdistal 15) levels; 16) both digits at “lobe” level; 17) more proximal than figure 15; 18) details of the cellular components of the movable digit sensilla. Scale bars = 0,5 µm. Abbrev.: cc, ciliary constriction; cs, ciliary sinus; cu, cuticle; DF, fixed digit; DM, movable digit; ds, dendritic sheath; lo, lobe; m1, m3, m4, m5, movable digit chemoreceptors; m2, movable digit mechanoreceptor; nu, nucleus; od, outer dendritic segment; pd, pilus dentilis shaft; pt, “pit sensillum”; sc, sheath cell; sj, septate junctions; v, vestibulum.



Figs 1.19-22 - *Typhlodromus exhilaratus* Ragusa, transmission electron micrographs of cheliceral cross sections: 19-21) details of the cellular components of the movable digit sensilla; 22) fixed digit at a subdistal level, showing the vestibulus, a tooth and the tubular body of the mechanosensillum. Scale bars = 1 µm. Abbrev.: cc, ciliary constriction; cs, ciliary sinus; ds, dendritic sheath; dt, digit tooth; f1, fixed digit chemoreceptor; f2, fixed digit mechanoreceptor; id, inner dendritic segment; la, labyrinth; m, mitochondrion; m3, m4, m5, movable digit chemoreceptors; mll, microlamellae; v, vestibulum.



Figs 1.23-25 - *Typhlodromus exhilaratus* Ragusa, transmission electron micrographs of cheliceral cross sections: 23) movable and fixed digit at pilus dentilis level; 24) at level of the dorsal and 25) lateral slit sense organ. Scale bars = 1 µm. Abbrev.: cu, cuticle; DF, fixed digit; DM, movable digit; ds, dendritic sheath; dss, dorsal slit sense organ; f, cuticular fold; il, inner layer; ml, middle layer; ol, outer layer; pd, pilus dentilis shaft; r, rim; so, socket; tb, tubular body.

seta arising from a socket delimited by a more or less evident rim (figs 1.6, 1.23-24). The shaft of both setae has smooth walls, without an innervated lumen (figs 1.10, 1.23) and its base is connected with two sensory cells provided with a discrete tubular body in the distal part of their outer dendritic segment (figs 1.9, 1.11).

The perceptive area of the slit sense organs consists of a transverse cuticular fold (figs 1.9-10, 1.12) composed of three layers with different electron-density. In half of the fold, the inner layer envelops two or one tubular bodies, respectively for the dorsal (figs 1.9-10) and the antiaxial slit sense organ (fig. 1.25) and thus indicating a mechanoreceptive role.

The hooked digits can grasp the food surface and penetrate distally into it (CHANT, 1985; DE LILLO & ALDINI, 1994). Then, the chelicerae can move independently tearing the food surface and causing wounds, or they can be retracted to allow the subcapitulum and its projections to penetrate into the food (FLECHTMANN & MCMURTRY, 1992a). The chelicerae are not involved either in the salivary discharge or in juice suction.

The chemoreceptors located on the digit tips have a typical gustative structure and they come in contact with the food. So, they should play an important role in the probing activity, but without electrophysiological evidences we cannot exclude an olfactory role. The digit mechanosensilla, the pilus dentilis and the dorsal seta are strategically located to perceive the contact between the digits and between the chela and the substrate (prey, pollen, fungal hyphae, etc.). In particular, the pilus dentilis is in a position to perceive the pressure applied by the movable digit on the grasped food, while the dorsal seta is in a position to perceive how close the fixed digit is to the food surface. The slit sense organs may work as proprioreceptors and morphologically resemble the insect campaniform sensilla. They may perceive stresses in the cheliceral cuticle during the up and down movement of the movable digits, being close to the articulation with the second cheliceral article.

2. *VARROA DESTRUCTOR* ANDERSON & TRUEMAN (GAMASIDA: VARROIDAE)

Detailed descriptions of the gnathosoma in females of *V. jacobsoni* Oudemans were done by GELBE and MADEL (1988), GRIFFITHS (1988), AKIMOV *et al.* (1988) and NUZZACI and DE LILLO (1995). The last paper surely refers to *V. destructor* (according to ANDERSON & TRUEMAN, 2000) even if it was attributed to *V. jacobsoni*. The species (fig. 2.1) is a typical Honey Bee ectoparasite being largely invasive into the hives. Its chelicerae are not chelate, the fixed digits appear to be considerably reduced (figs 2.2-3), and the second articles are quite elongated, such as in many other parasitic Dermanyssina. Chelicerae are located dorsally to the subcapitulum, labrum and salivary styli and they don't display any particular morphological relationship either with these mouthparts or with the pedipalps (figs 2.2-5). The movable digit is straight and spear-shaped, its size gradually increases from the apex, where it is ventrally rounded, to the proximal part. It is provided with a sharp ventral edge and two thin dorsal hook-like teeth (figs 2.2-8).

In cross section, it is wedge shaped at distal and subdistal levels and is lined by a very thick cuticle, especially on its distal part (figs 2.4, 2.6-9). Two short proximal processes are located laterally (one on each side) (figs 2.2, 2.9-10). They originate from the distal part of the second cheliceral article and seem to be residues of the movable digit articulation with the basal part of the fixed digit - the distal end of the second cheliceral article (compare them with the phytoseiid arrangement at this level). The proximal part of the movable digit is connected to the tendons (fig. 2.11) of the dorsal elevator and ventral depressor muscles (fig. 2.12).

Two chemosensilla on the movable digit, and two mechanosensilla on the second cheliceral article (a dorsal seta and a lateral antiaxial slit sense organ) have been found (AKIMOV *et al.*, 1988; NUZZACI *et al.*, 1992). The movable digit sensilla are each provided with a very reduced and blunt process (figs 2.3, 2.5, 2.13) and are distally located on the dorsal and ventral side of the cheliceral article. Each process displays a central pit (fig. 2.13) containing a roundish pore which is connected to a lumen filled with an electron-dense distal substance (figs 2.7, 2.14) that is placed between the dendrites and the surroundings. The outer dendritic segments of these sensilla don't contain any tubular bodies, and other ultrastructural details (figs 2.7-10, 2.15-17) indicate a uniporous sensillar status.

The dorsal seta (figs 2.18-22) and the antiaxial slit sense organ (figs 2.23-24) of *V. destructor* are ultrastructurally similar to the phytoseiid ones.

The movable digits look like blade structures provided with hard tips well adapted to pierce the Honey Bee integument along with the sharpened cor-

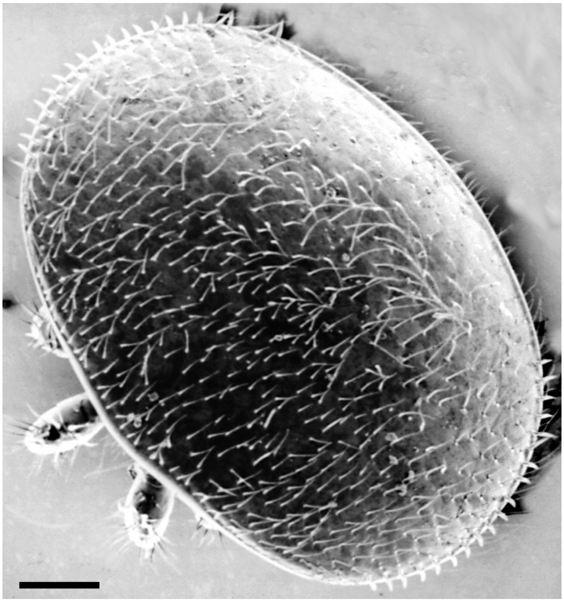


Fig. 2.1 - *Varroa destructor* Anderson & Trueman, scanning electron micrograph of an adult female from a dorsal view. Scale bars = 200 µm.

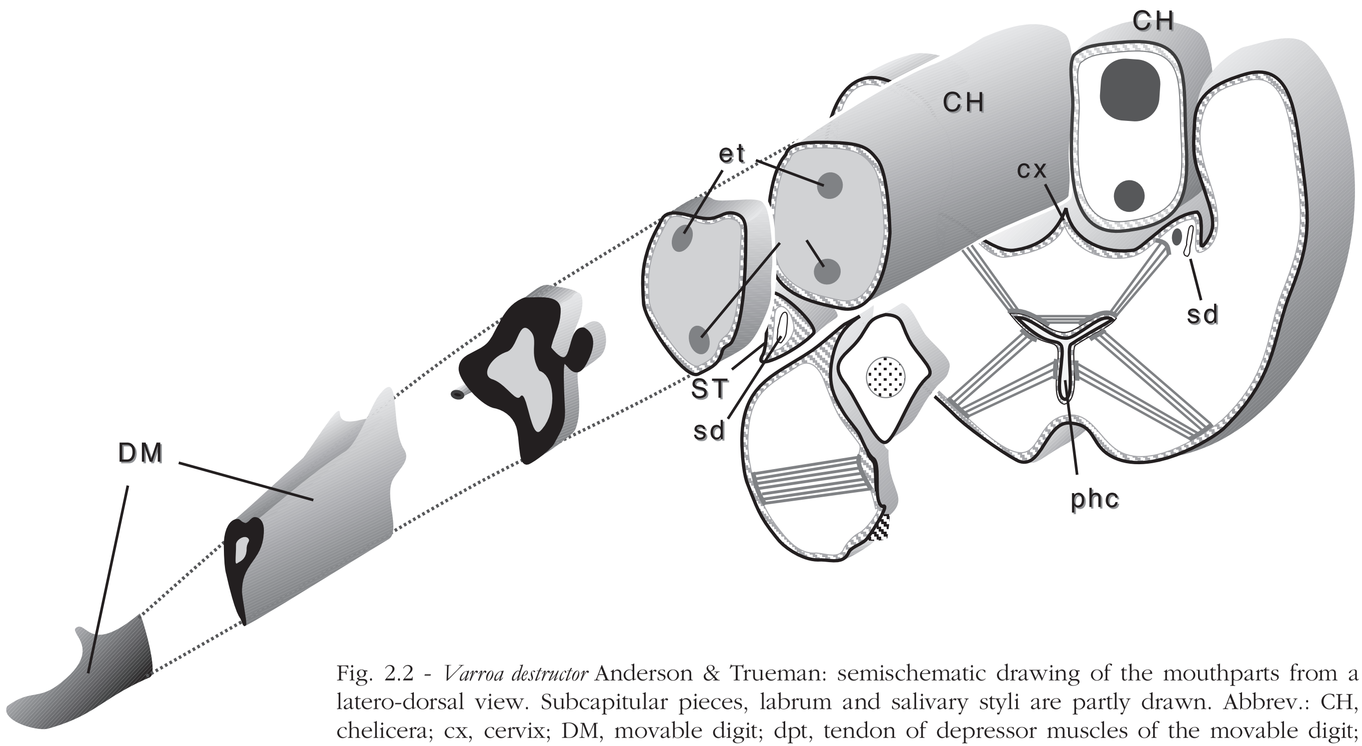
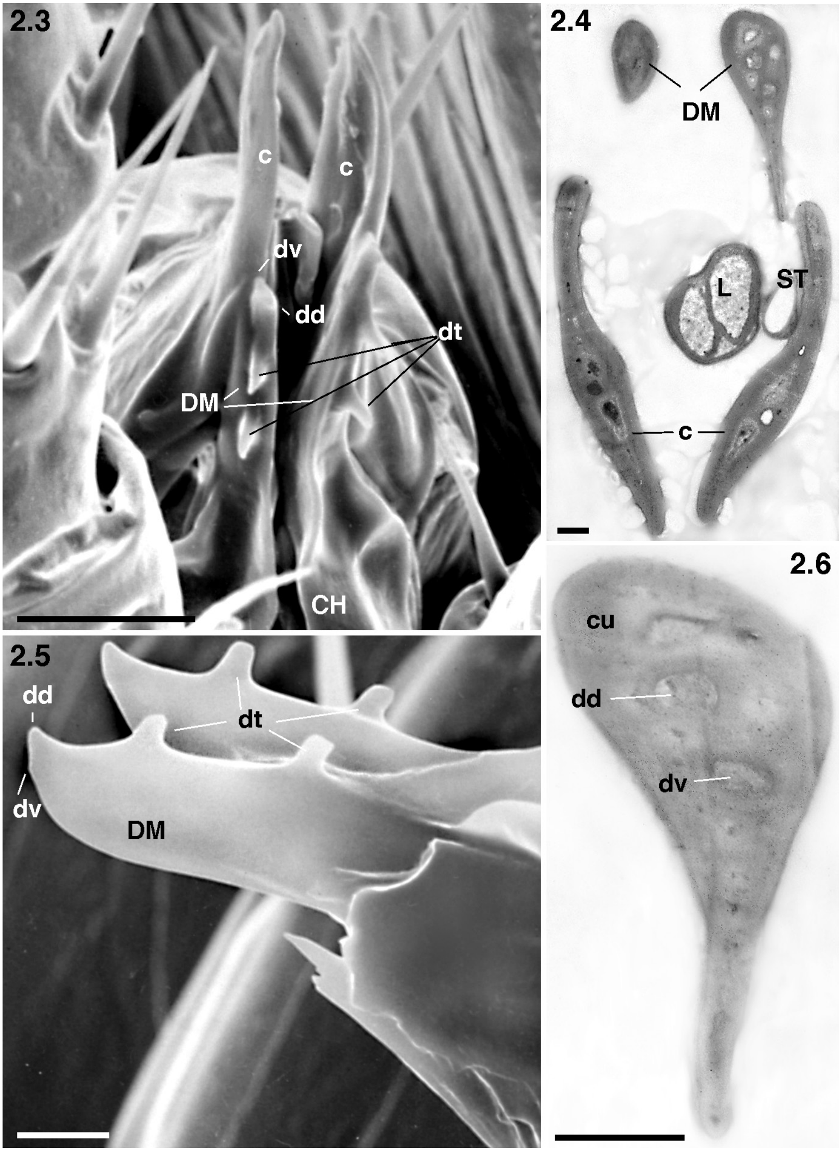
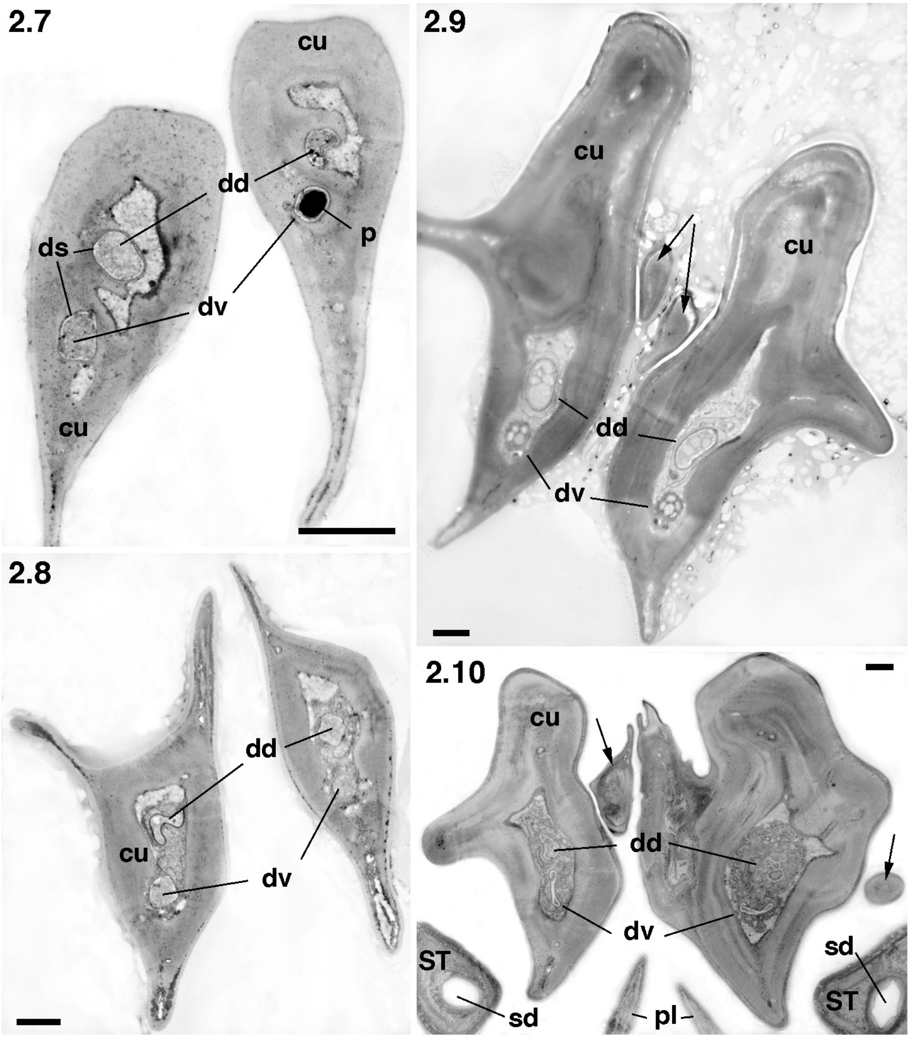


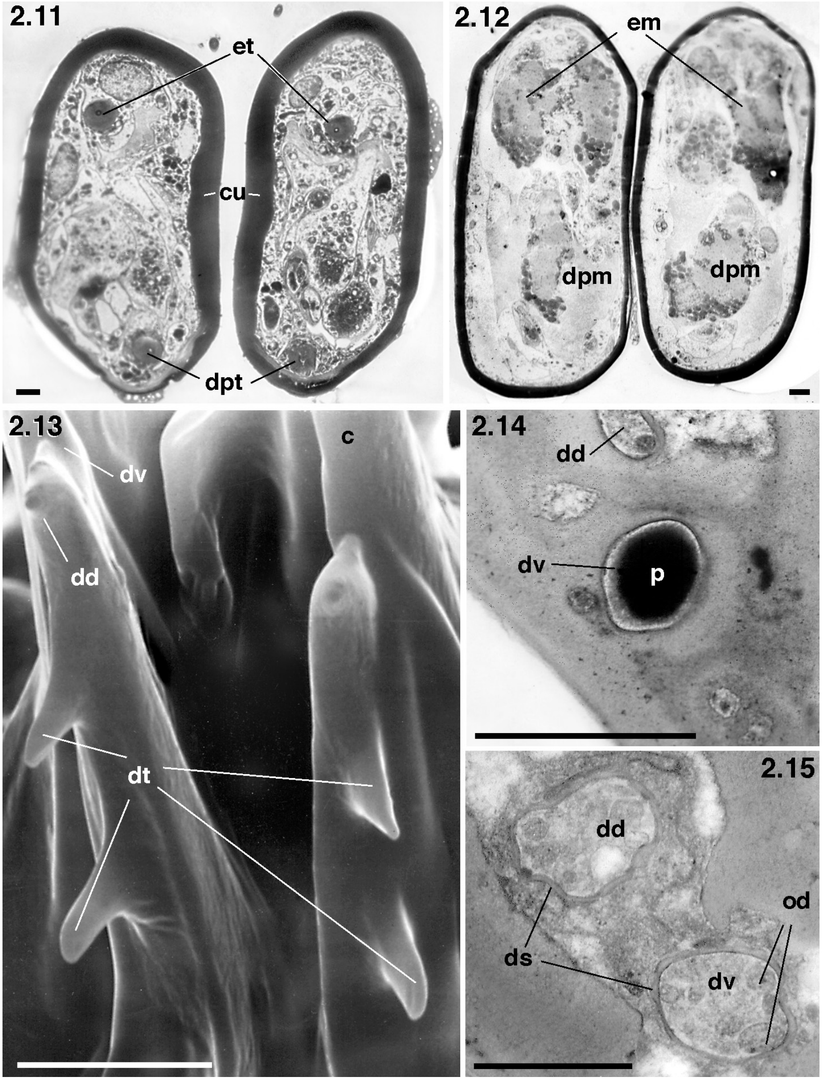
Fig. 2.2 - *Varroa destructor* Anderson & Trueman: semischematic drawing of the mouthparts from a latero-dorsal view. Subcapitular pieces, labrum and salivary styli are partly drawn. Abbrev.: CH, chelicera; cx, cervix; DM, movable digit; dpt, tendon of depressor muscles of the movable digit; et, tendon of elevator muscles of the movable digit; L, labrum; phc, pharyngeal chamber; sd, salivary duct; ST, salivary stylus.



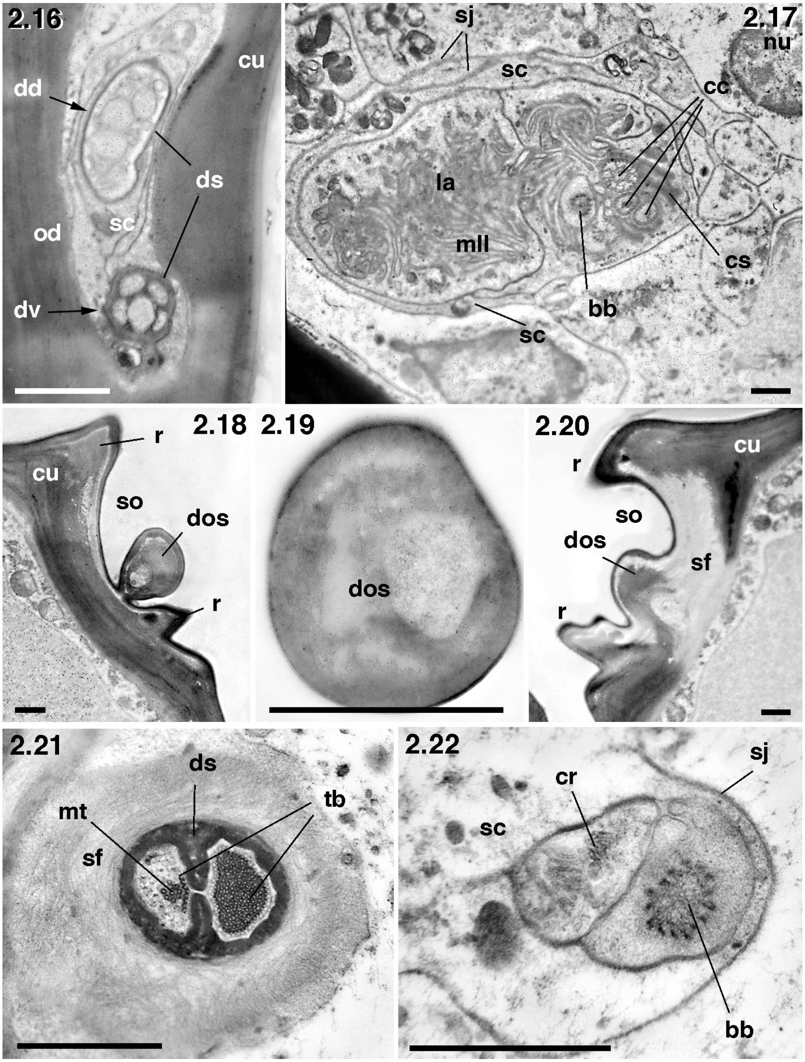
Figs 2.3-6 - *Varroa destructor* Anderson & Trueman. Scanning electron micrographs: 3) gnathosoma from a subdorsal view (Prof. N. Milani, courtesy), 5) movable digits from a sublateral view. Transmission electron micrographs: 4) gnathosoma subdistal cross section and 6) detail of a movable digit. Scale bars = 10 µm for figures 3 and 5, 1 µm for figures 4 and 6. Abbrev.: c, corniculus; CH, chelicera; cu, cuticle; dd, distal dorsal sensillum; DM, movable digit; dt, digit tooth; dv, distal ventral sensillum; L, labrum; ST, salivary stylus.



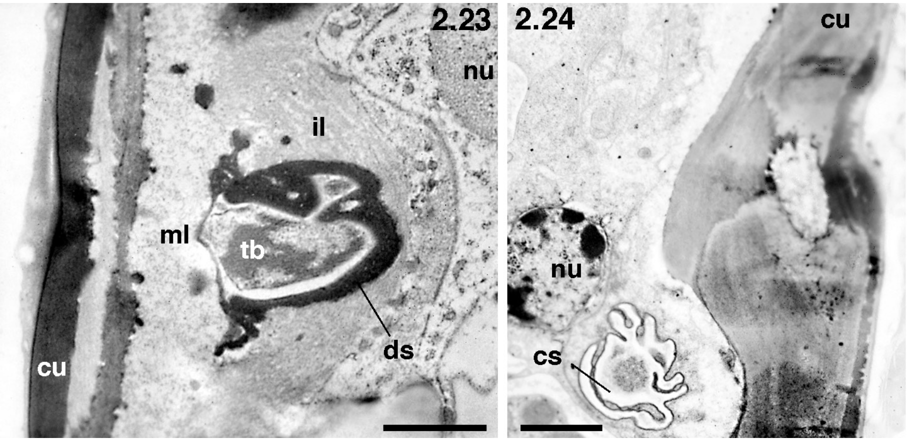
Figs 2.7-10 - *Varroa destructor* Anderson & Trueman, transmission electron micrographs of movable digit cross sections, gradually more proximal from 7 to 10. 9-10) The arrows indicate small processes on the antiaxial and paraxial surfaces which might be retained relict of the movable digit articulation to the second cheliceral article. Scale bars = 1 µm. Abbrev.: cu, cuticle; dd, distal dorsal sensillum; ds, dendritic sheath; dv, distal ventral sensillum; p, electron-dense plug; pl, paralabrum; sd, salivary duct; ST, salivary stylus.



Figs 2.11-15 - *Varroa destructor* Anderson & Trueman, transmission electron micrographs of cheliceral cross sections: 11-12) at level of the second cheliceral article close to the digit articulation; 14-15) detail of the digit sensilla at two close subdistal levels. 13) Scanning electron micrograph of the movable digits, a dorsal view (Prof. N. Milani, courtesy). Scale bars = 1 µm for figs 11-13 and 0,5 µm for figs 14-15. Abbrev.: c, corniculus; cu, cuticle; dd, distal dorsal sensillum; dpm, depressor muscles of the movable digit; dpt, tendon of depressor muscles of the movable digit; ds, dendritic sheath; dt, digit tooth; dv, distal ventral sensillum; em, elevator muscles of the movable digit; et, tendon of elevator muscles of the movable digit; od, outer dendritic segment; p, electron-dense plug.



Figs 2.16-22 - *Varroa destructor* Anderson & Trueman, transmission electron micrographs of cheliceral cross sections: 16) cellular components of the digit chemosensilla at a subdistal level; 17) ciliary region of the ventral movable digit sensillum at more proximal level; 18, 20) details of the dorsal seta at the level of the socket; 19) detail of the dorsal seta shaft, 21) its tubular bodies and 22) its ciliary region. Scale bars = 1 µm. Abbrev.: bb, basal body; cc, ciliary constriction; cr, ciliary rootlets; cs, ciliary sinus; cu, cuticle; dd, distal dorsal sensillum; dos, dorsal seta shaft; ds, dendritic sheath; dv, distal ventral sensillum; la, labyrinth; mll, microlamellae; mt, neurotubules; nu, nucleus; od, outer dendritic segment; r, rim; sc, sheath cell; sf, suspension fibres; sj, septate junctions; so, socket; tb, tubular body.



Figs 2.23-24 - *Varroa destructor* Anderson & Trueman, transmission electron micrographs of cheliceral cross sections: 23) tubular body of the antiaxial slit sense organ and details of the layers; 24) a more proximal section showing its ciliary region. Scale bars = 1 µm. Abbrev.: cs, ciliary sinus; cu, cuticle; ds, dendritic sheath; il, inner layer; ml, middle layer; nu, nucleus; tb, tubular body.

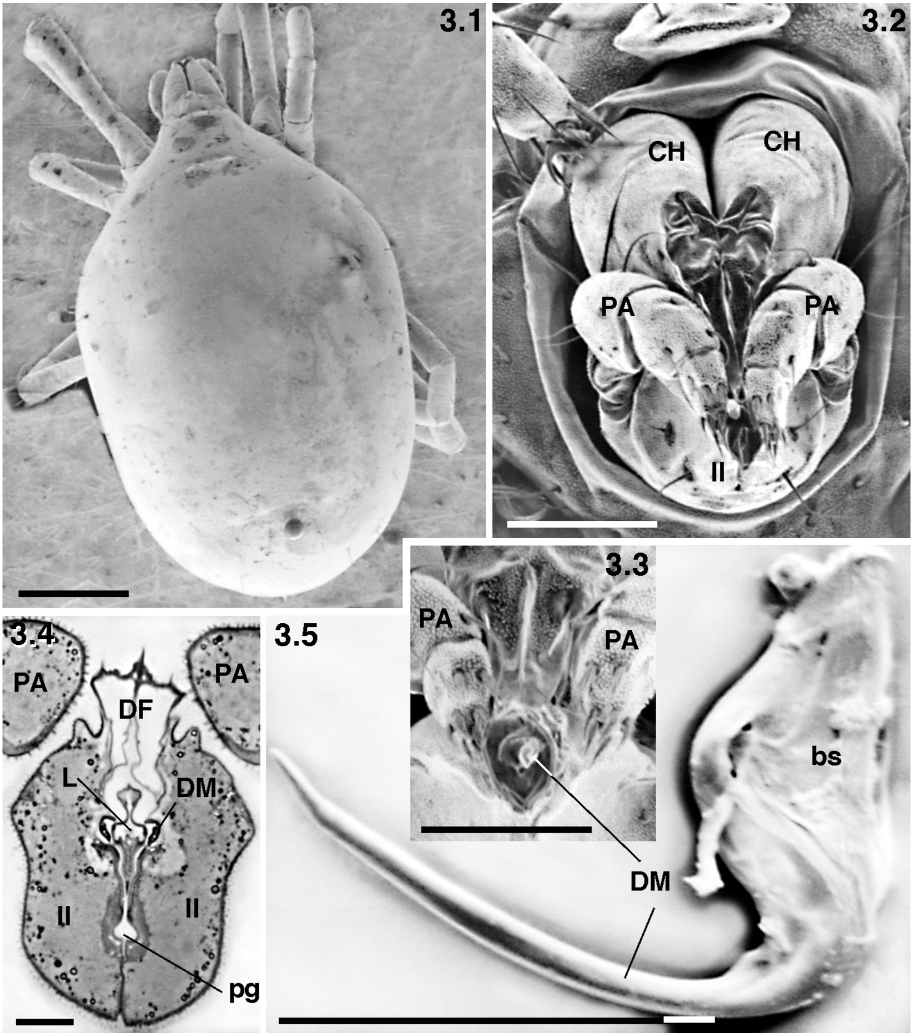
niculi. In such a way they can cause a wound through which the haemolymph comes out for sucking. Also for this species, chelicerae are not directly involved in salivary discharge and food intake.

The contact chemosensilla located distally on the movable digits are introduced into the Honey Bee body and immersed into the host haemolymph. So, they may taste the juices inside the host providing a sensory feedback on the quality of the food before and during pre-oral digestion. The dorsal seta and the lateral slit sense organ are homologues to the phytoseiid ones playing the same role.

3. *PENTHALEUS MAJOR* (DUGÈS) (ACTINEDIDA: PENTHALEIDAE)

The gnathosoma of this species (fig. 3.1), typically phytophagous on a wide host range, has been described by NUZZACI and DE LILLO (1991a) and DI PALMA (1995). It is conoid shaped with a large base (figs 3.1-2). The chelicerae are located dorsally to the subcapitulum and lie inside a supralabral cavity formed between the lateral lips (figs 3.3-4). The chelicerae are considerably modified with a stylet-like movable digit and a large fixed digit (figs 3.3-15). The movable digit is about 75 µm long, slightly arched, with a small blunt tip, and a paraxial furrow along its length (figs 3.5-9).

In cross sections, the movable chela is strongly electron-dense, its apex is subglobose (figs 3.6, 3.10-11), while more proximally it enlarges and assumes



Figs 3.1-5 - *Penthaleus major* (Dugès). Scanning electron micrographs of 1) an adult from a dorsal view, 2) the gnathosoma from a frontal view, 3) details of the previous figure, 5) the antiaxial surface of the movable digit including the basal sclerite. 4) Light micrograph of a subdistal gnathosomal cross section. Scale bars = 200 µm for fig. 1, 50 µm for figs 2-3, and 25 µm for figs 4-5. Abbrev.: bs, basal sclerite; CH, chelicera; DF, fixed digit; DM, movable digit; L, labrum; ll, lateral lips; PA, pedipalp; pg, preoral groove.

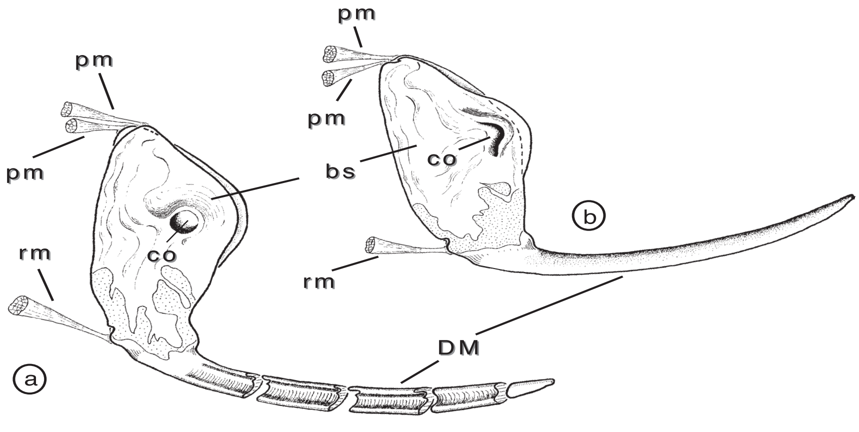


Fig. 3.6 - *Penthaleus major* (Dugès): semischematic drawing of the a) paraxial and b) antiaxial surfaces of the movable digit, included the basal sclerite and part of its muscles complex. Abbrev.: bs, basal sclerite; co, condyle; DM, movable digit; pm, protractor muscles of the movable digit; rm, retractor muscles of the movable digit.

a “c”-shaped aspect (figs 3.4, 3.7, 3.11-14) characterized by the paraxial surface notably concave and the antiaxial one always convex. Both surfaces are devoid of any special ornamentation but the paraxial one shows a small longitudinal ridge (fig. 3.12). No strict relationship has been recognized between the stylets, and among them and the other mouthparts. However, the stylets appear to slide one on the other, by means of the paraxial ridge, when they are protruded out of the supralabral cavity, and form an intercheliceral channel not perfectly interlocked (figs 3.4, 3.9, 3.12). Proximally, each stylet is set into a small gutter (figs 3.14-15) which is lateral to the labral base. The two gutters continue more proximally (fig. 3.16) and beyond the cervix where they are fused into a longitudinal medial furrow which lies under the second cheliceral articles (figs 3.17-18). Up to now, no salivary glands and salivary ducts have been described, but it is strongly expected that the said furrow is connected to a salivary gland complex.

The styliform part of the movable digit is connected to a basal sclerite (figs 3.5-6, 3.8, 3.16, 3.19-20) by means of a fibrous electron-dense structure (fig. 3.21). The sclerite is almost flat, oriented on the dorso-ventral and parasagittal

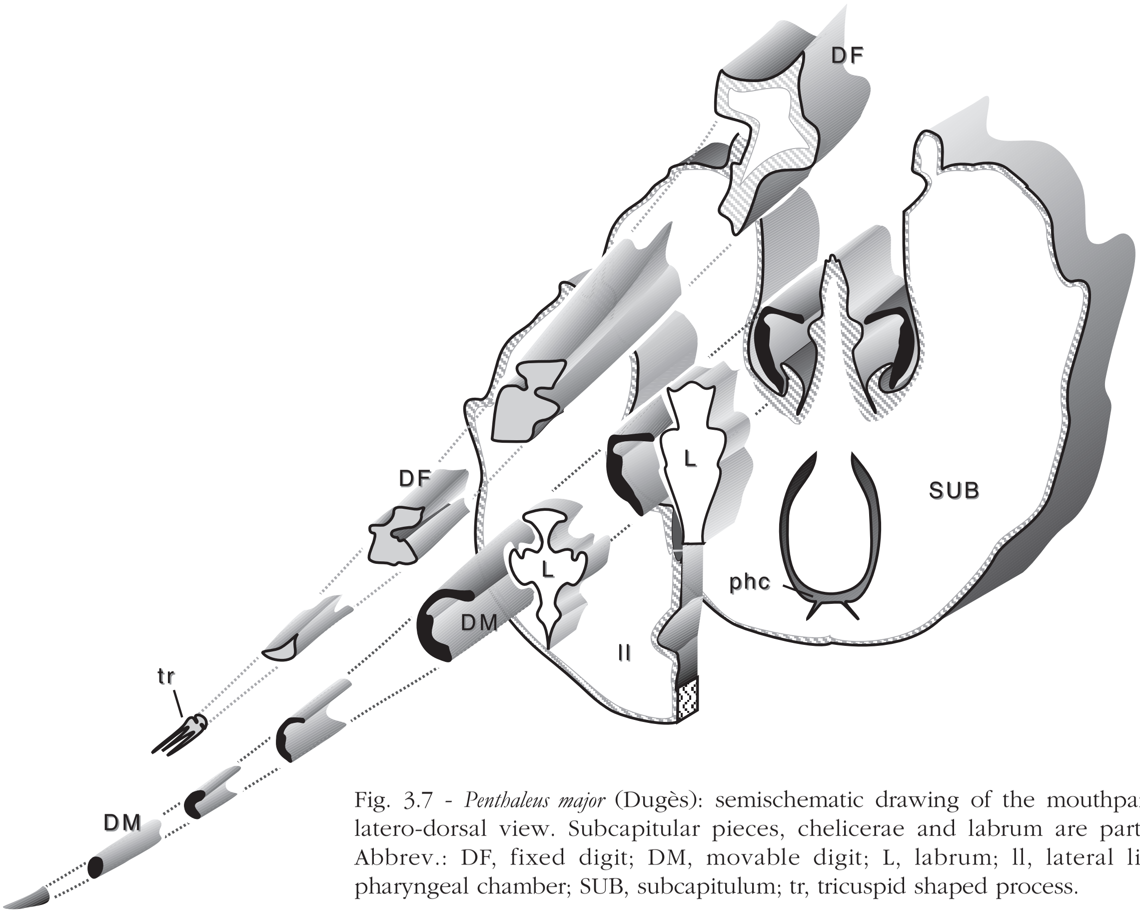
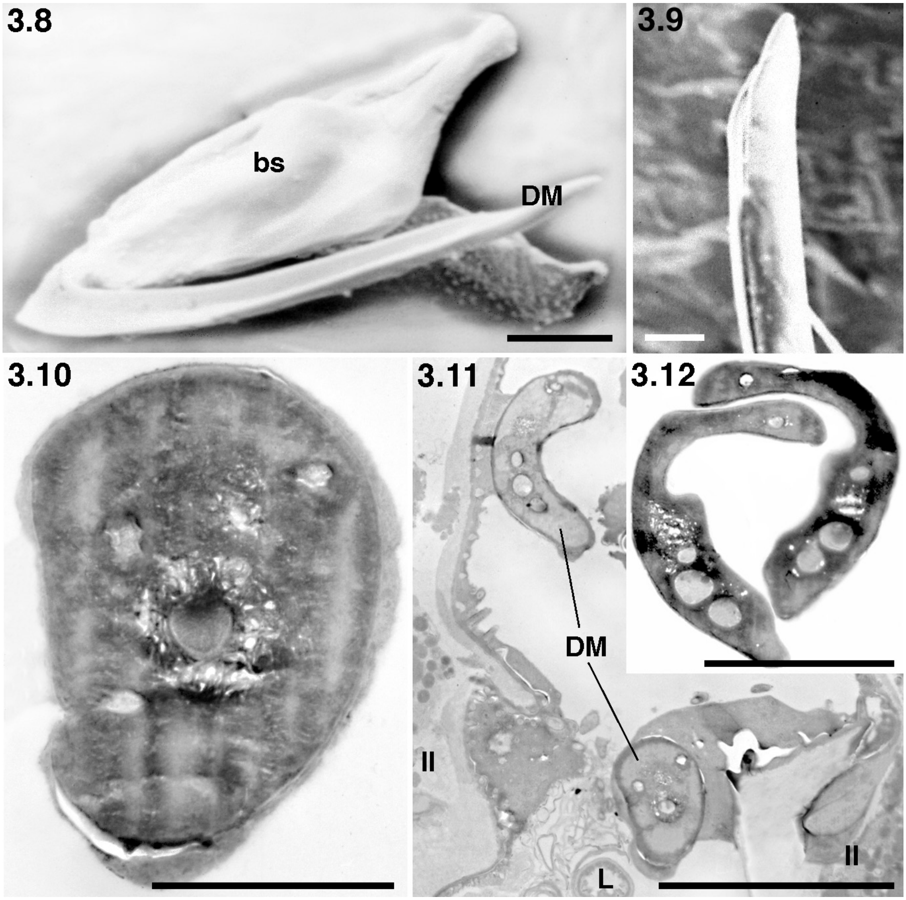
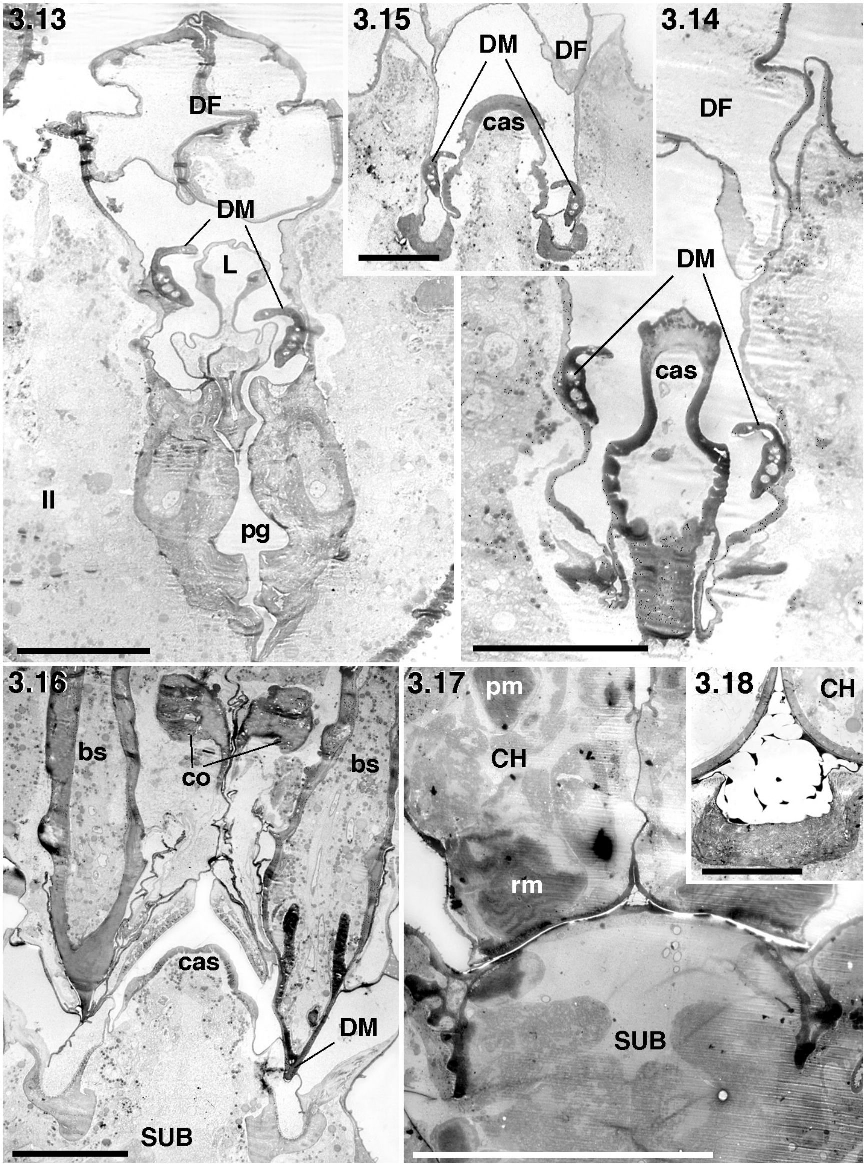


Fig. 3.7 - *Penthaleus major* (Dugès): semischematic drawing of the mouthparts from a latero-dorsal view. Subcapitular pieces, chelicerae and labrum are partly drawn. Abbrev.: DF, fixed digit; DM, movable digit; L, labrum; ll, lateral lips; phc, pharyngeal chamber; SUB, subcapitulum; tr, tricuspid shaped process.

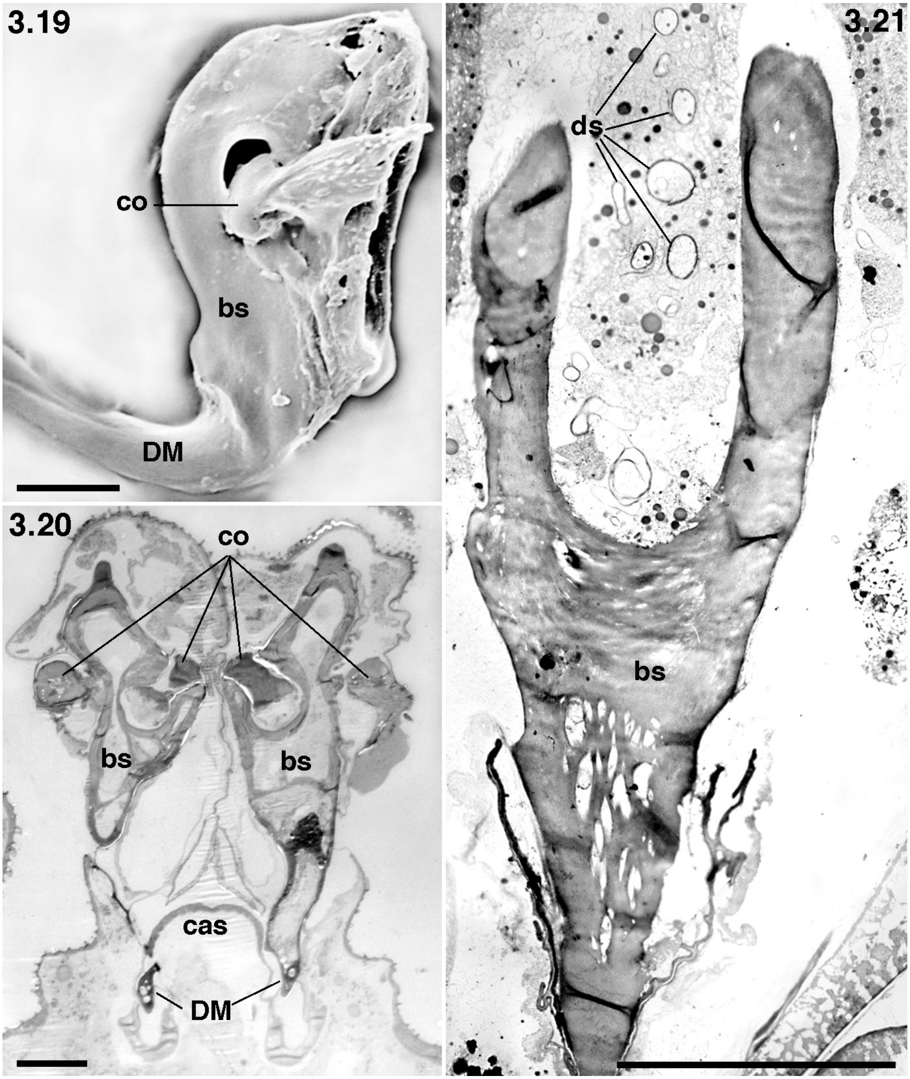


Figs 3.8-12 - *Penthaleus major* (Dugès) Scanning electron micrographs: 8) paraxial surface of the movable digit including the basal sclerite; 9) tip of the overposed movable digits. Transmission electron micrographs: 10) subapical cross section of the movable digit; 11) a more proximal section than the previous figure; 12) detail of the opposed movable digits (reconstruction by means of Photoshop™). Scale bars = 5 µm for figs 8-9, 11-12 and 1 µm for fig. 10. Abbrev.: bs, basal sclerite; DM, movable digit; L, labrum; ll, lateral lips.

plane, and composed of two strongly electron-dense plates fused together displaying small processes and a subdistal acetabulum on each side (figs 3.5-6, 3.8, 3.16, 3.19-20). The muscle arrangement of the basal sclerite (fig. 3.17) and the acetabular location cause the rotation axis of the articulation to be slightly oblique in respect to the horizontal and parasagittal planes (fig. 3.22).



Figs 3.13-18 - *Penthaleus major* (Dugès), transmission electron micrographs: movable and fixed digits, lateral lips, labrum and preoral groove, gradually more proximal from 13 to 18; 16) details at the level of the basal sclerite and 18) presumed salivary collector. Scale bars = 10 μm for figs 13-17, 1 μm for fig. 18. Abbrev.: bs, basal sclerite; cas, capitular saddle; CH, chelicerae; co, condyle; DF, fixed digit; DM, movable digit; L, labrum; ll, lateral lips; pg, preoral groove; pm, protractor muscles of the movable digit; rm, retractor muscles of the movable digit; SUB, subcapitulum.



Figs 3.19-21 - *Penthaleus major* (Dugès), 19) scanning electron micrograph of the antiaxial surface of the basal sclerite, 20-21) transmission electron micrographs of cheliceral cross sections 20) at the level of the basal sclerite and 21) detail of it with the movable digit. Scale bars = 10 µm. Abbrev.: bs, basal sclerite; cas, capitular saddle; co, condyle; DM, movable digit; ds, dendritic sheath.

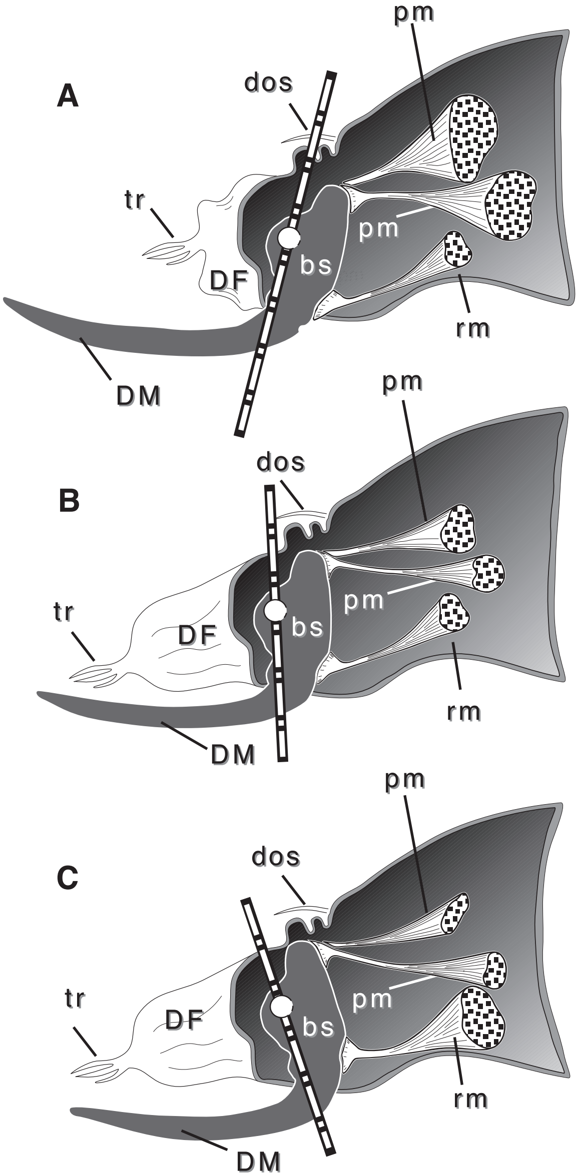
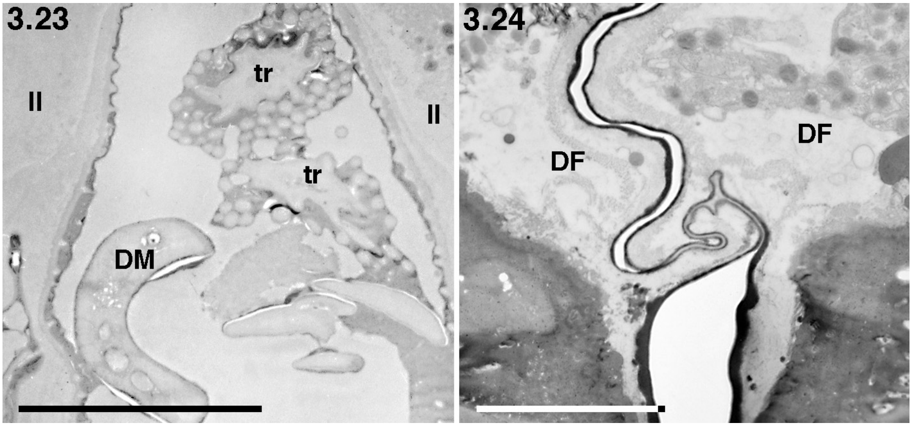


Fig. 3.22 - *Penthaleus major* (Dugès): semischematic drawings of the digitus mobilis and basal sclerite during A) protrusion, B) rest position and C) retraction. Abbrev.: bs, basal sclerite; DF, fixed digit; DM, movable digit; dos, dorsal seta shaft; pm, protractor muscles of the movable digit; rm, retractor muscles of the movable digit; tr, trifurcate process.



Figs 3.23-24 - *Penthaleus major* (Dugès), transmission electron micrographs of cheliceral cross sections: 23) details of the tricuspid shaped process inside the supralabral cavity; 24) detail of the fixed digit connection on their paraxial surfaces. Scale bars = 5 μm. Abbrev.: DF, fixed digit; DM, movable digit; ll, lateral lips; tr, tricuspid shaped process.

The fixed digits, which are lined mainly by a thin and electron-dense cuticle (figs 3.4, 3.7, 3.13-15), appear to be partly deformable, and are provided with a distal furcate process (figs 3.7, 3.22-23). Their paraxial surfaces are appressed to each other though not interlocking, even if a sort of furrow-ridge connection may be recognized at different levels (figs 3.13, 3.24). The ventro-lateral surfaces of the fixed digits fit perfectly on the dorsal edges of the lateral lips delimiting a large preoral (supralabral) cavity in which the stylets slide (figs 3.4, 3.7, 3.13-15).

The second cheliceral article is distally articulated with the basal sclerite acetabula by means of two strongly electron-dense condyles, one on each side (figs 3.16, 3.20). These articles contain the retractor and protractor muscles of the stylet which are connected from the basal sclerite respectively to the ventral and dorsal tendons (figs 3.6, 3.17, 3.22).

Finally, the first cheliceral articles are partly fused one to each other, mainly at the proximal level.

Very few data have been available on the mouthpart sensilla of this species (NUZZACI & DE LILLO, 1991a; NUZZACI *et al.*, 1991; DI PALMA, 1995). Five lumina have been observed into the cheliceral stylets. They can be recognized from the subdistal level of the stylet (figs 3.11-12) up to the movable digit articulation (fig 3.21) but the ultrastructural details have not been clearly detected. Outer dendritic segments of one or more sensory cells are strongly suspected to be inside the stylar lumina. At present, no sensorial structures have been pointed out on the fixed digits, and for the trifurcate process, previously called a seta, no nervous features have been detected even though the nature of this structure has not been ascertained yet.

The stylets are involved in piercing the plant surface and their movements are retained to function independently and possibly on different planes. The basal sclerite rotation allows the back and forth sliding of the stylets into the supralabral chamber. Because of the rather oblique rotation axis, the stylets are appressed to each other during protrusion but apart during retraction. The cheliceral stylets don't have apparently any strict relationship with their paraxial surfaces, so their vertical displacement during protrusion is limited only by the confines of the preoral chamber. Finally, the morphological and behavioural observations suggest a strong piercing activity which is repeated rapidly. The stylets do not play any role in suction mechanisms but an involvement in salivary discharge is suspected, even if there is scant information on the salivary gland arrangement.

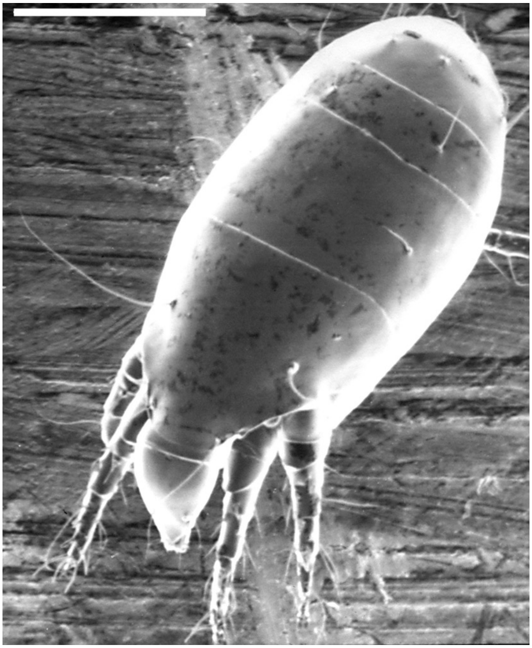


Fig. 4.1 - *Tarsonemus setifer* sensu Karl scanning electron micrograph: an adult female from a dorsal view. Scale bar = 50 µm.

4. *TARSONEMUS NODOSUS* SCHAARSCHMIDT (ACTINEDIDA: TARSONEMIDAE)

A detailed mouthpart description of this species has been only recently presented by NUZZACI *et al.* (in press), and few other data have been previously published for other Tarsonemina (KCRZAL, 1959; HISLOP & JEPPSON,

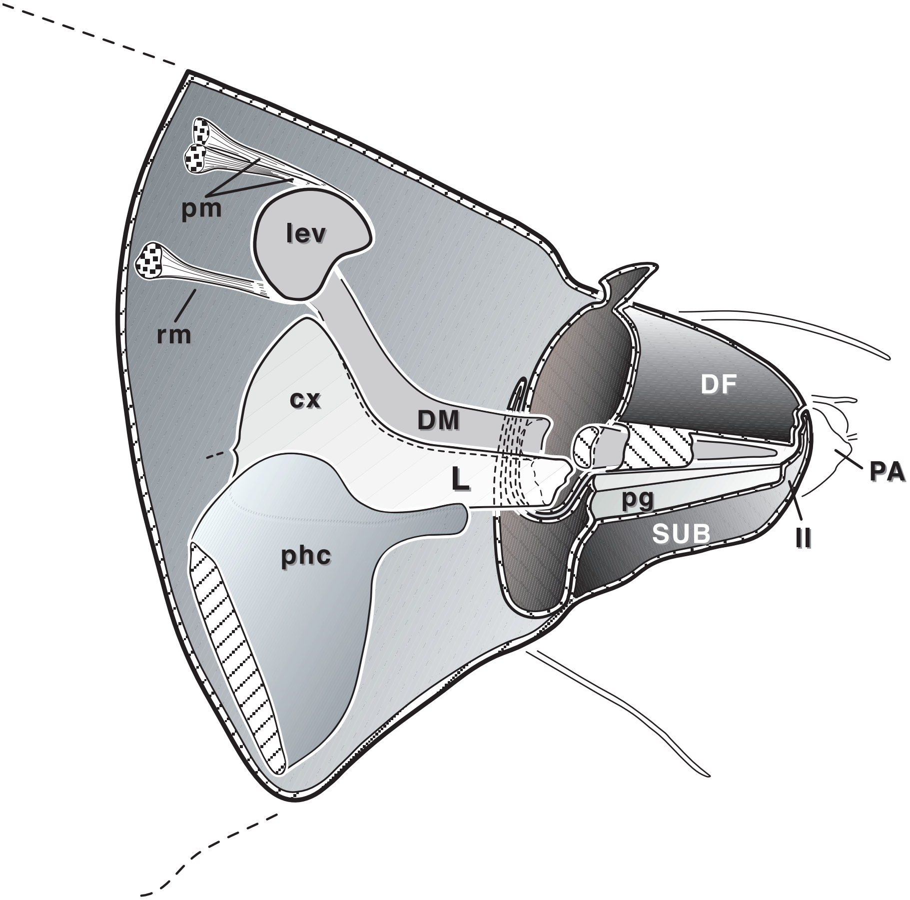


Fig. 4.2 - *Tarsonemus nodosus* Schaarschmidt: semischematic drawing of the mouthparts from a lateral view. Subcapitular pieces are partly drawn. Abbrev.: cx, cervix; DF, fixed digit; DM, movable digit; L, labrum; lev, lever; ll, lateral lips; PA, pedipalp; pg, preoral groove; phc, pharyngeal chamber; pm, protractor muscles of the movable digit; rm, retractor muscles of the movable digit; SUB, subcapitulum.

1976; Chow *et al.*, 1980; Lindquist, 1986; Bruce *et al.*, 1993). Tarsonemid mites (fig. 4.1) have a wide feeding range and *T. nodosus* has been observed to have a fungivorous habit (Suski, 1967; Kaliszewski *et al.*, 1983). Its chelicerae form a complex structure along with the labrum and the subcapitulum, and they are strongly modified as needle-like movable digits, fused fixed digits, and coalesced first and second articles forming a stylophore capsule (according to Lindquist, 1986) (figs 4.2-4).

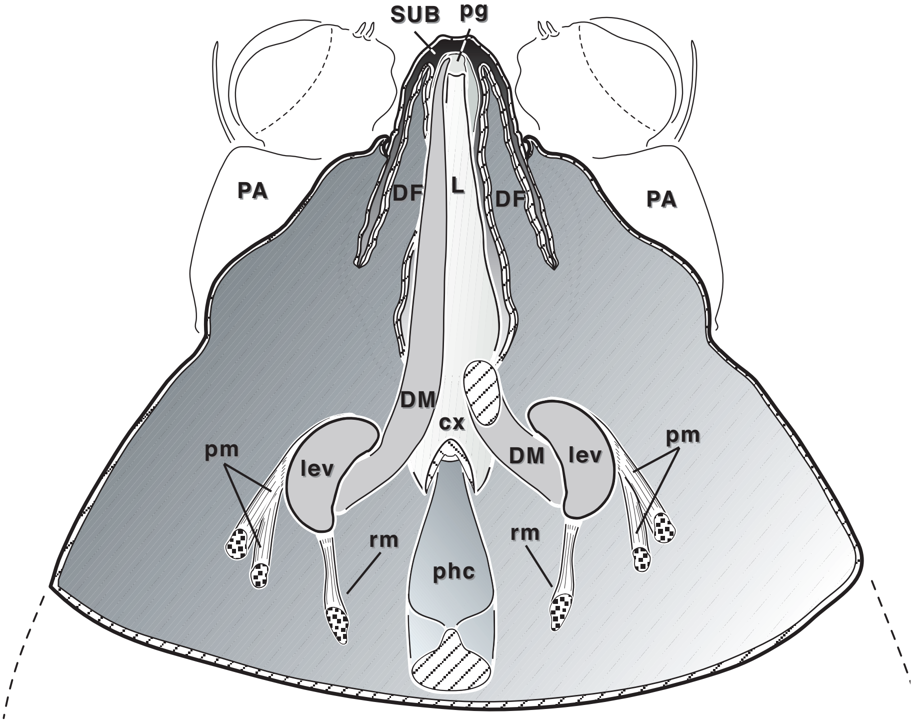
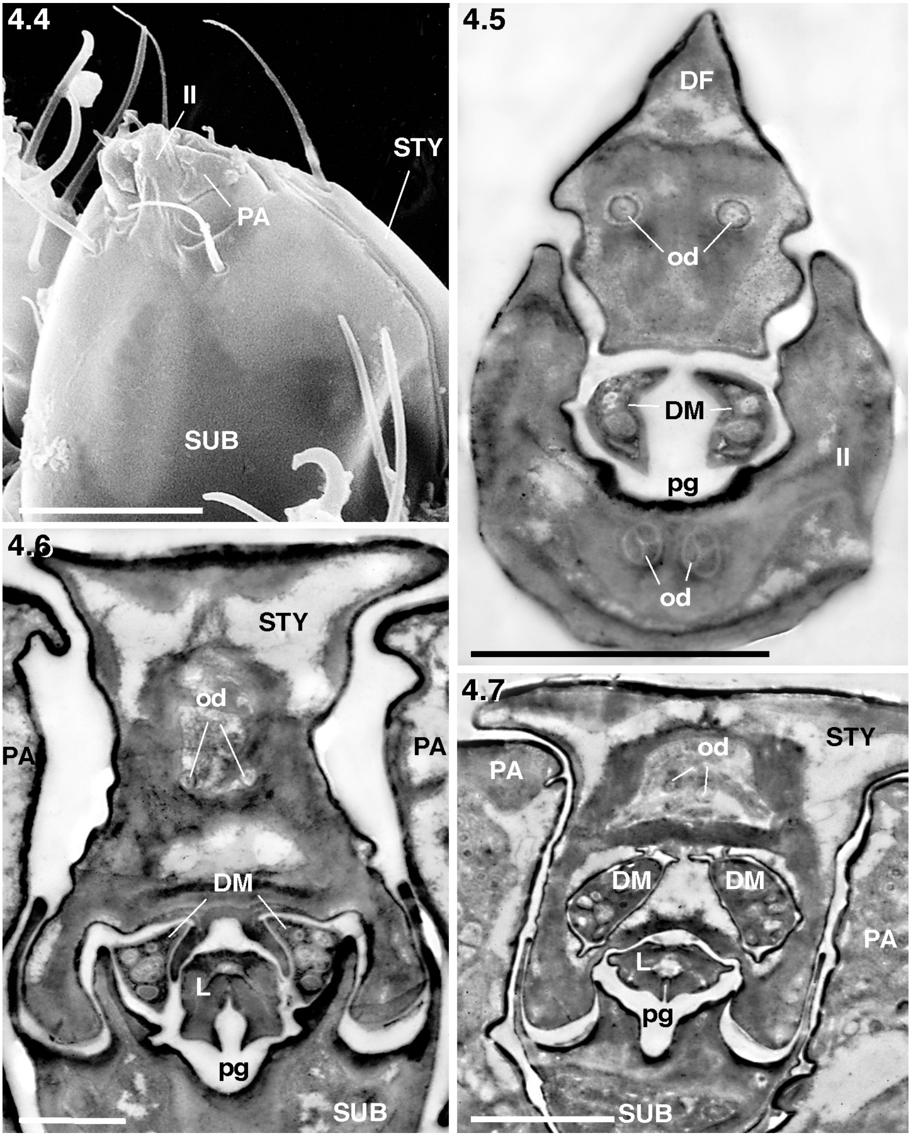
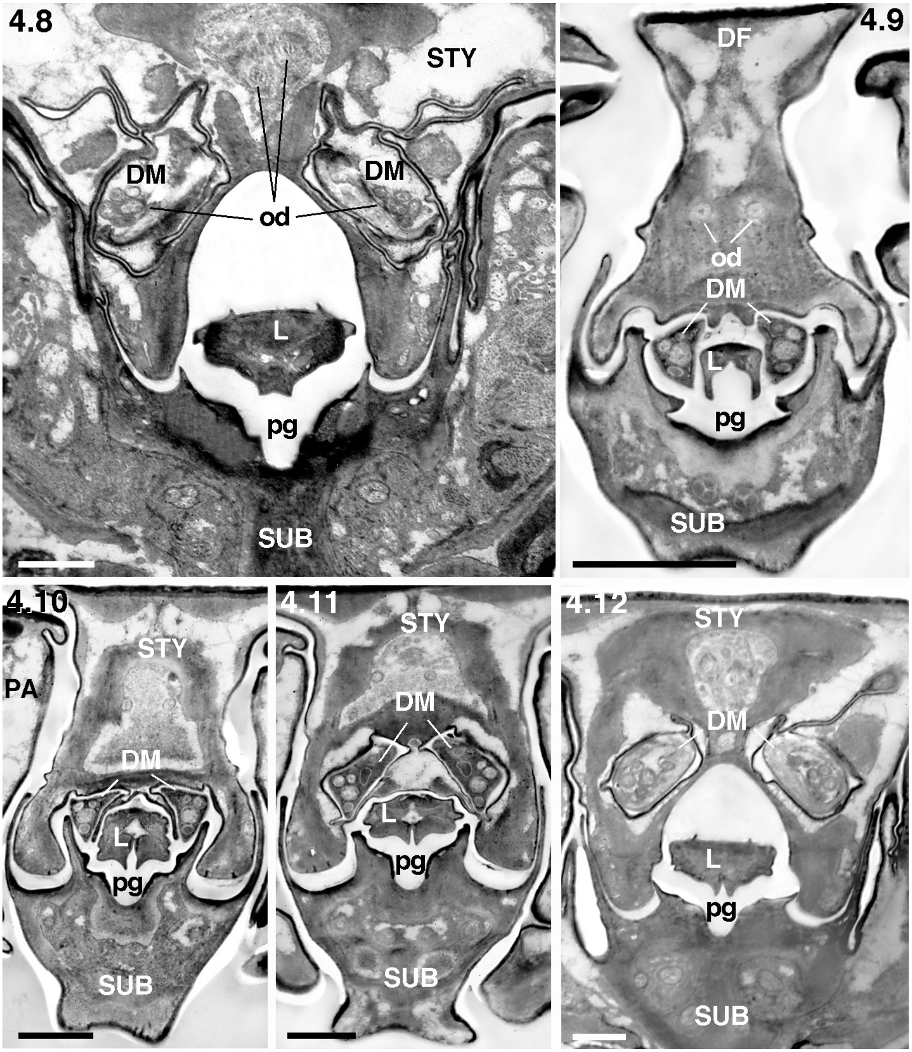


Fig. 4.3 - *Tarsonemus nodosus* Schaarschmidt: semischematic drawing of the mouthparts from a dorsal view. Abbrev.: cx, cervix; DF, fixed digit; DM, movable digit; L, labrum; lev, lever; PA, pedipalp; pg, preoral groove; phc, pharyngeal chamber; pm, protractor muscles of the movable digit; rm, retractor muscles of the movable digit; SUB, subcapitulum.

In distal cross sections, the movable digits appear strongly electron-dense, thin, sickle-like, and their paraxial surfaces are slightly concave (fig. 4.5). Proximally, they enlarge becoming almost subtriangular and face to the dorso-lateral sides of the labrum (figs 4.3, 4.6). More proximally, they display an elliptical outline (fig. 4.7) and electronlucid circular areas, especially at levels closer to the articulation with the second cheliceral article (fig. 4.8). No longitudinal ridges and complementary furrows are on the facing movable digit surfaces, so, they are not able to interlock with each other when protruded out of the subcapitulum (figs 4.5-11). At about their distal third, they lie ventrally in a medial subcapitular groove (a rather wide and not well defined cheliceral channel), and are dorsally covered by the fixed digits (figs

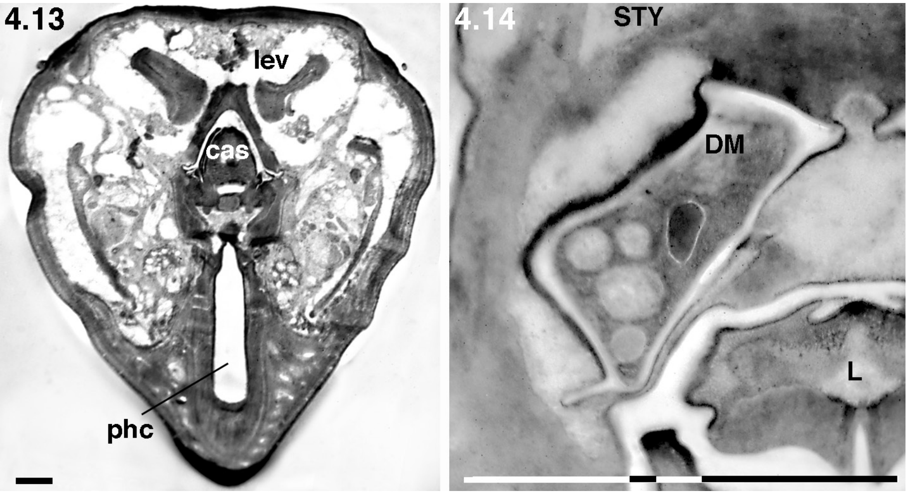


Figs 4.4-7 - *Tarsonemus nodosus* Schaarschmidt: 4) scanning electron micrograph of the gnathosoma from a latero-ventral view, 5-7) transmission electron micrographs of the gnathosoma cross sections gradually more proximal from 5 to 7, starting from a subapical level and showing the relationships between the movable digit, lateral lips and labrum. Scale bar = 10 µm for fig. 4, 1 µm for figs 5-7. Abbrev.: DF, fixed digit; DM, movable digit; L, labrum; ll, lateral lips; od, outer dendritic segment; PA, pedipalp; pg, preoral groove; STY, stylophore; SUB, subcapitulum.



Figs 4.8-12 - *Tarsonemus nodosus* Schaarschmidt, transmission electron micrographs of the gnathosoma cross sections: 8) very close to the movable digit articulation to the lever; 9-12) gradually more proximal from 9 to 12 starting from a subdistal level and showing the morphological relationships between the stylophore and the movable digits. Scale bar = 1 µm. Abbrev.: DM, movable digit; L, labrum; od, outer dendritic segment; PA, pedipalp; pg, preoral groove; STY, stylophore; SUB, subcapitulum.

4.5-6, 4.9-4.10). Proximally, the movable digits are gradually embedded into the fused fixed digits, by means of ventral and distal rims, and more proximally by laminar plates (figs 4.6, 4.9-10). More proximally, each laminar



Figs 4.13-14 - *Tarsonemus nodosus* Schaarschmidt, transmission electron micrographs of the gnathosoma cross sections: 13) at the level of the levers and the pharyngeal chamber; 14) detail of the supposed movable digit sensilla. Scale bar = 1 µm. Abbrev.: cas, capitular saddle; DM, movable digit; L, labrum; lev, lever; phc, pharyngeal chamber; STY, stylophore.

process extends laterally and envelops completely the stylets forming a sort of cheliceral sleeve (figs 4.2, 4.7-8, 4.11-12).

At the labral base level, each stylet comprises a spatulate sclerite (the cheliceral lever according to Lindquist, 1986), one on each side in the stylophore (figs 4.2-3). In cross section, the levers seem to be longer than wide and obliquely oriented on the plane of the gnathosoma (fig. 4.13). The stronger stylet protractor muscles are inserted on their dorsal antiaxial surfaces, while the retractor ones are inserted on their ventral posterior and paraxial surfaces (figs 4.2-3).

The fused fixed digits cover dorsally the subcapitulum, the labrum and the distal part of the movable digits. The ventro-lateral ridges of the fixed digits interlock with the complementary dorso-lateral furrows of the subcapitulum (figs 4.6-12). This arrangement, scarcely developed at the distal levels (fig. 4.5), allows the forwards and backwards sliding of the stylets and seals the pre-oral food channel. The coalesced cheliceral bases form a stylophore that is fully integrated with the subcapitulum to form a gnathosomal capsule. A dorso-median apodeme, including the median salivary duct, indicates the originally paired nature of the stylophore.

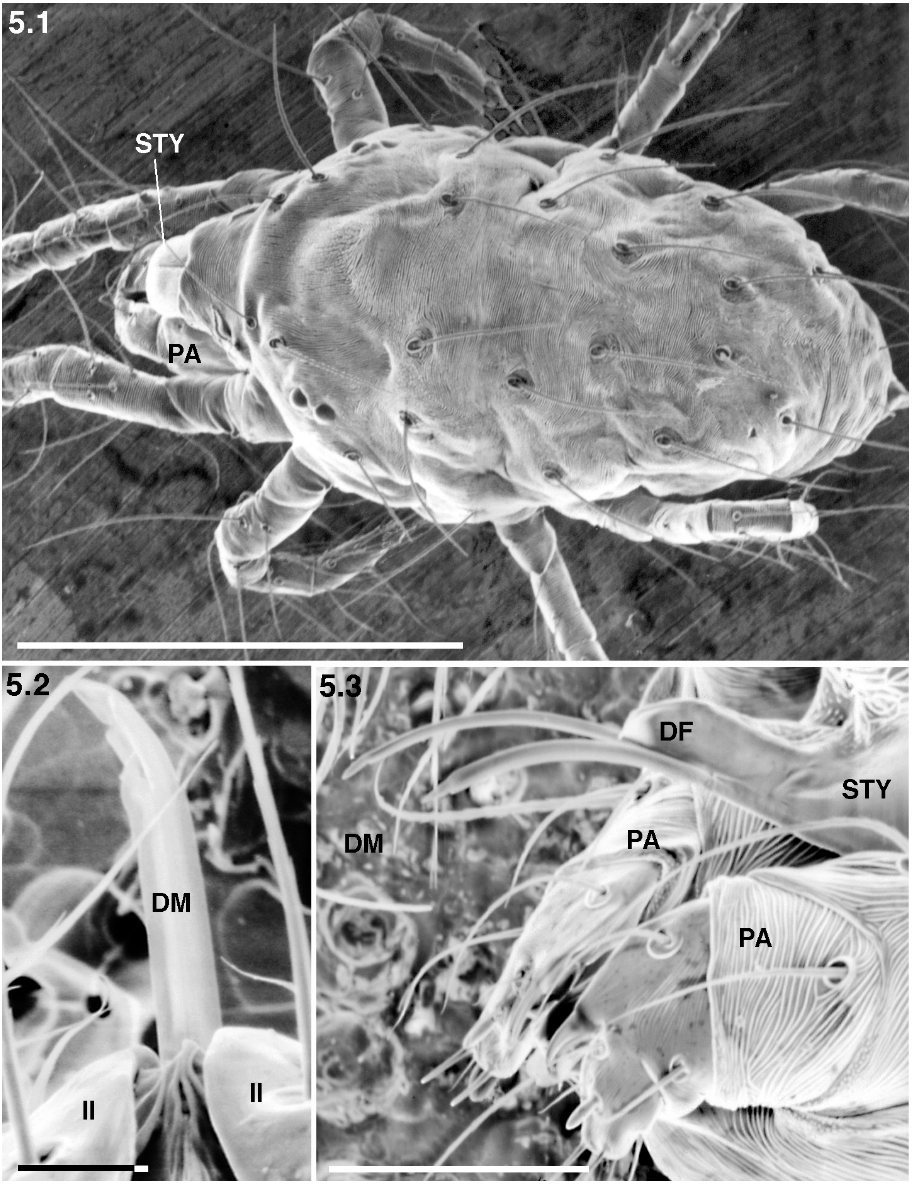
The ultrastructure of the cheliceral sensilla has not been clearly described even if there are evidences of an important receptor arrangement. Sensillar structures have been detected running lengthwise into the stylets: 4 at the distal level that become 5 at a more proximal level (figs 4.6-8, 4.14). In the apical region of the fused fixed digits, two sensilla have been observed, symmetrically located and close to the dorso-lateral wall (figs 4.5-9).

The tiny, short and needle-like cheliceral stylets are protruded by means of the cheliceral lever rotation and pierce the walls of the most delicate fungal or plant cells. The distribution of the stylet muscles and the oblique arrangement of the lever's long axis appear to activate a lever rotation in an oblique plane. During protraction and retraction, the stylets are held in position by the cheliceral sleeves and, distally, by the labrum and the lateral lip folds. The fact that the cheliceral stylets can not interlock with each other and the oblique rotation of the lever indicate that each stylet may slide and protrude independently from each other even though they may be closely approximated but never joined.

5. *TETRANYCHUS URTICAE* KOCH (ACTINEDIDA: TETRANYCHOIDEA) AND *CENOPALPUS PULCHER* (CANESTRINI & FANZAGO) (ACTINEDIDA: TENUIPALPIDAE)

There are several detailed descriptions for the gnathosoma of the Two-Spotted Spider mite (figs 5.1-3) (André & Remacle, 1984; Nuzzaci & de Lillo, 1991b) and many other related papers (Blauvelt, 1945; Baker & Connell, 1963; Summers *et al.*, 1973; Hislop & Jeppson, 1976; Akimov & Yastrebtsov, 1981; Lindquist, 1985; Alberti & Crooker, 1985, also for more references), or concerning the False Red Spider mite (Nuzzaci & de Lillo, 1989, 1991d). Both are specialized phytophagous species and their gnathosomal morphology is similar, displaying highly modified chelicerae. They are included in the subcapitulum, are surrounded by the lateral lips, and are situated dorso-laterally to the labrum and the median salivary duct with which they establish strict morphological and functional relationships (fig. 5.4).

The movable digits are styliform, greatly elongated, extensively protractable and deeply retractable (figs 5.3-5). They lie separately inside proper stylet channels (according to Alberti & Crooker, 1985) of the subcapitulum (figs 5.4, 5.6-8) which present thick and electron-dense walls. The stylets are proximally recurved into the second and first fused cheliceral article (stylophore) (figs 5.9). They are thicker in *T. urticae* than in *C. pulcher*, and in both species a lumen runs lengthwise into the stylet body (figs 5.7, 5.10). In cross section, the stylets are distally almost circular (figs 5.3, 5.11), while more proximally they display a half-moon outline in *T. urticae* (fig. 5.7) and become almost elliptical in *C. pulcher*



Figs 5.1-3 - *Tetranychus urticae* Koch, scanning electron micrographs of a 1) female from a dorsal view, 2) details of the interlocked cheliceral stylets, 3) details of the chelicera out of the rostral gutter and stylet channels. Scale bar 200 μm for fig. 1, 5 μm for figs 2-3. Abbrev.: DF, fixed digit; DM, movable digit; ll, lateral lips; PA, pedipalp; STY, stylophore.

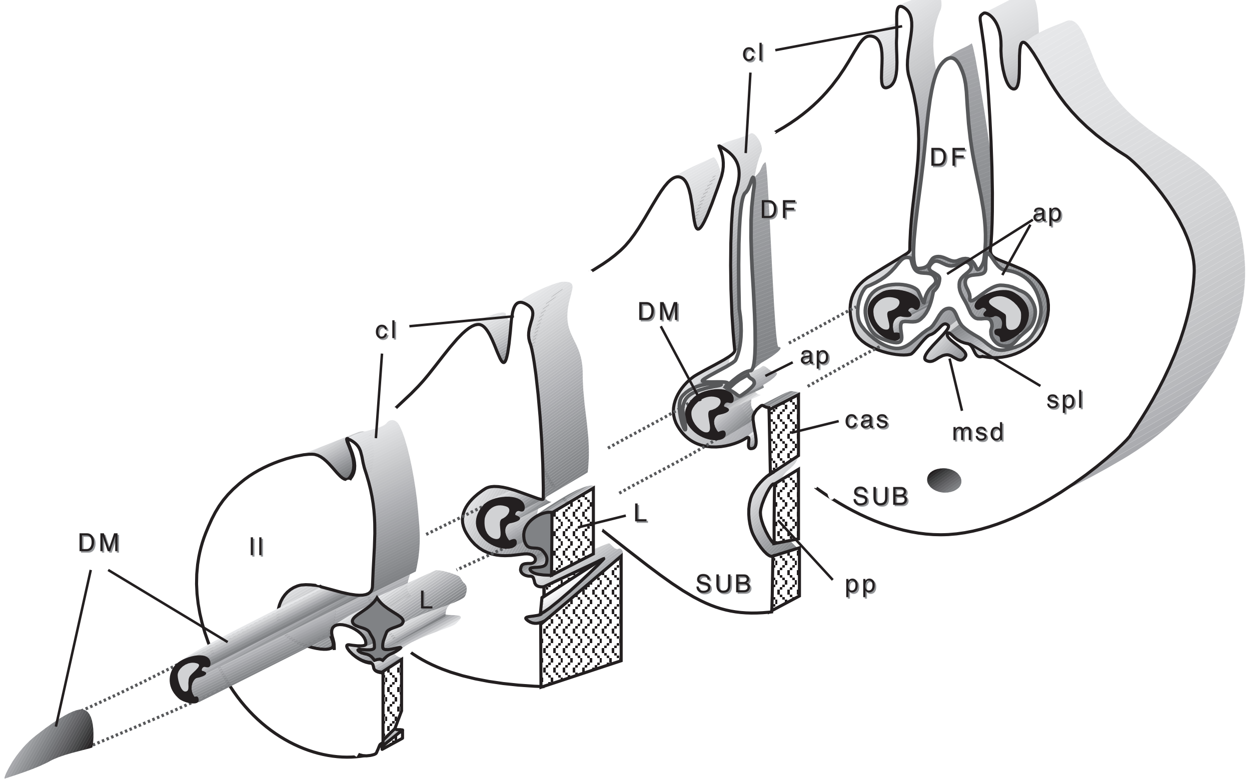


Fig. 5.4 – *Cenopalpus pulcher* (Canestrini & Fanzago): semischematic drawing of the mouthparts. Subcapitular pieces are partly drawn. Abbrev.: ap, fixed digit accessory pieces; cas, capitular saddle; cl, capitular lips; DF, fixed digit; DM, movable digit; L, labrum; ll, lateral lips; msd, median salivary duct; pp, pharyngeal pump; spl, plates of the salivary pump; SUB, subcapitulum.

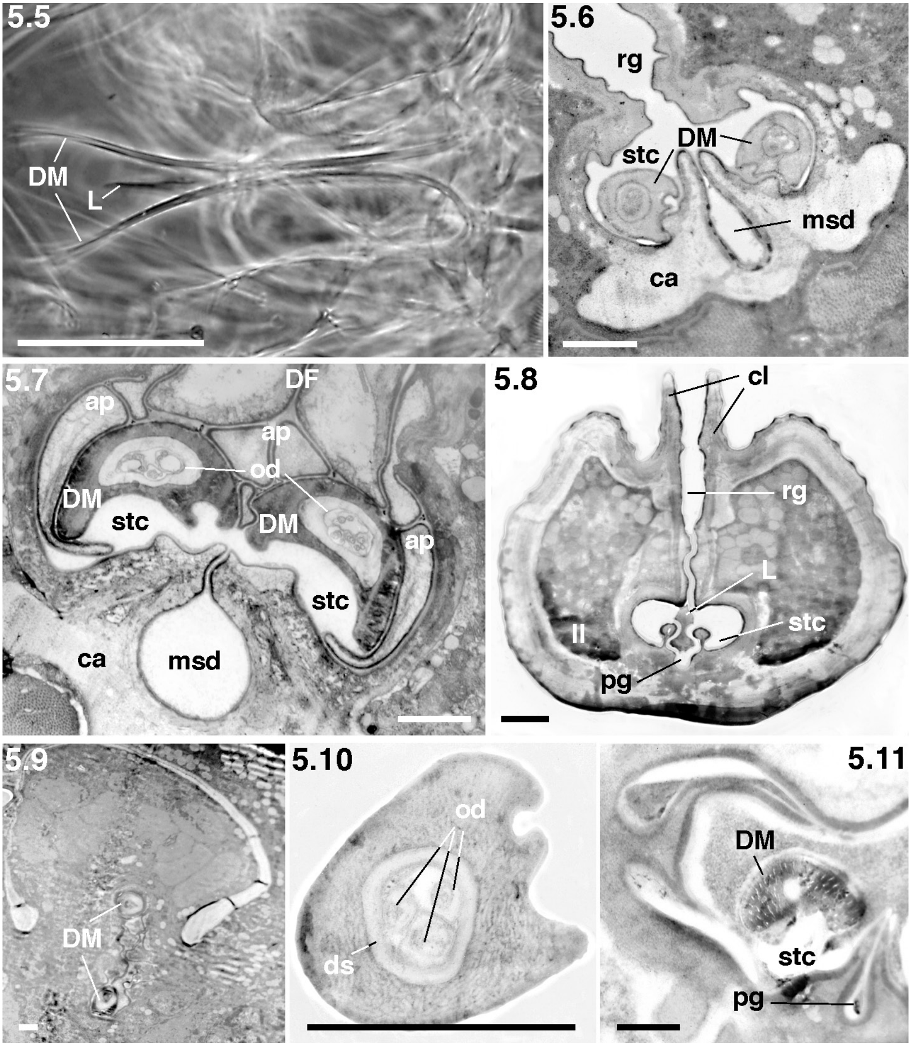


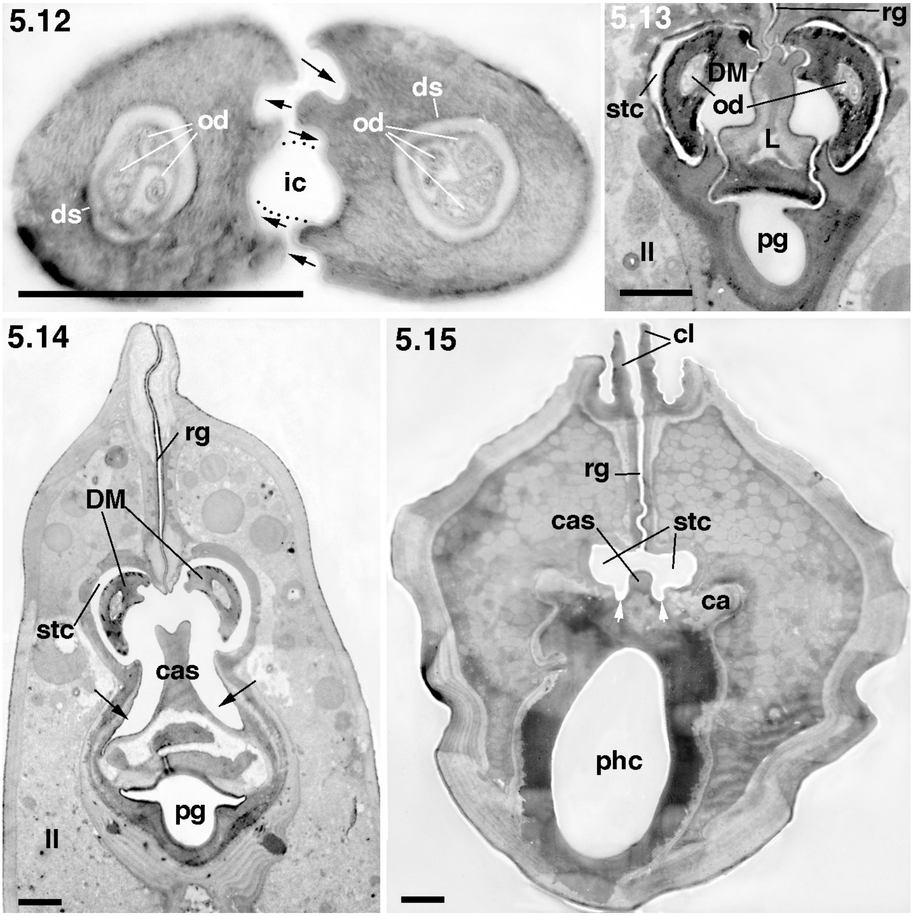
Fig. 5.5-11 - *Tetranychus urticae* Koch. 5) Light, micrograph of the chelicerae. Transmission electron micrographs of the gnathosoma cross sections: 6-7) details of the chelicerae at the level of the cervical apodeme; 8) subcapitulum and labrum at a subdistal level; 9) detail of the movable digits at a more proximal level; 10-11) details of the movable digits, showing subdistal micropore (11). *Cenopalpus pulcher* (Canestrini & Fanzago) for figs 6, 8-10, *Tetranychus urticae* Koch for figs 7, 11. Scale bar = 10 μm for fig. 5, 1 μm for figs 6-11. Abbrev.: ap, fixed digit accessory pieces; ca, cervical apodeme; cl, capitular lips; DF, fixed digit; DM, movable digit; ds, dendritic sheath; L, labrum; ll, lateral lips; msd, median salivary duct; od, outer dendritic segment; pg, preoral groove; rg, rostral gutter; stc, stylet channel.

(fig. 5.10). Three small ridges and two furrows (the ventral one larger than the dorsal one) are opposed along their paraxial surfaces which are complementary and strictly articulated between the protracted stylets (figs 5.2, 5.7, 5.12). In the protracted status, the median ridge fits perfectly into the dorsal furrow of the opposite stylet, much as a dovetail joint, ventrally delimiting a very small intercheliceral canal. Moreover, in *T. urticae* the labrum develops two small dorsal and longitudinal lobes and one of them fits perfectly in a dorsal stylet furrow (5.13). Proximally, two ventral depressions are present in each stylet channel (figs 5.14-15) flanking each side of the labral base. These structures appear to continue, more proximally, along with the median salivary duct (figs 5.6-7).

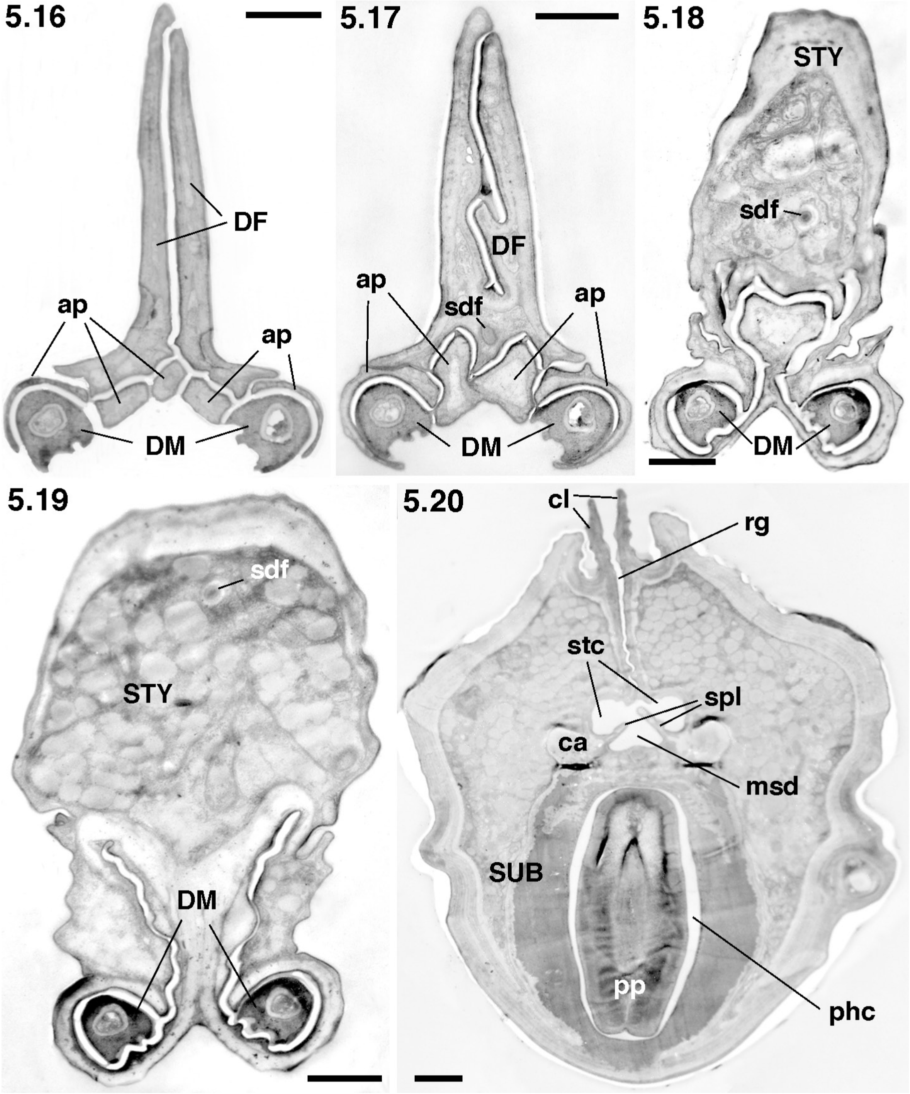
The fixed digits is formed by two vertical plates (thicker in *T. urticae* than in *C. pulcher*) which are ventrally enlarged and associated with the accessory projections (figs 5.3-4, 5.16-17). This complex is mesally located inside the subcapitulum, lying inside the rostral gutter, for the vertical parts, and inside the stylet channels, for the ventral part and the accessory pieces (fig. 5.7). More apically, they become gradually fused into a common structure which ensheathes the stylets and displays cuticular ridges complementary to the stylet furrows (figs 5.18-19). At the cervix level, the median salivary duct, its distal plates and the fixed digits form the salivary pump complex (fig. 5.20). An annular strong electron-dense (sclerotized) reinforcement of the stylet channels is distally located at the tip of the subcapitulum (figs 5.21-22).

Little ultrastructural work has been carried out on the sensillar arrangement of the tetranychoids. Up to now, the outer dendritic segments of three nervous cells have been detected inside the stylet lumen (figs 5.7, 5.10) and they are related to a subdistal microporous area observed in *T. urticae* (fig. 5.11) (MOTHES & SEITZ, 1981; ANDRÉ & REMACLE, 1984; ALBERTI & CROOKER, 1985; NUZZACI & DE LILLO, 1991b; ALBERTI & COONS, 1999). No other ultrastructural features are available, even if there may be retained chemoreceptors based on their position and presence of pores. Ventrally and mesally on the distal part of the fixed digit and stylophore of *C. pulcher*, a long electron-dense structure has been detected (figs 5.17-19). Its ultrastructure and function are still unknown even if a sensillar activity is presumed.

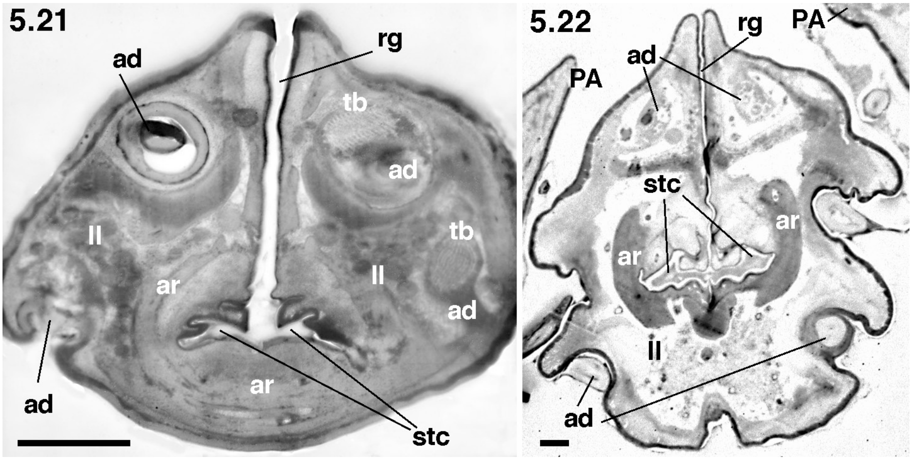
The longitudinal movement of each stylet is rigidly guided within the stylet channels. Actually, the stylets move back and forth in them, and during protrusion, they pass through the annular sclerotized reinforcement, at the tip of the subcapitulum, where forced to interlock with each other. In such a way, they cannot have any vertical displacement and they form a single and penetrating probing tube which contains an intercheliceral canal. Fixed digits



Figs 5.12-15 - Transmission electron micrographs of the gnathosoma cross sections: 12) details of opposed movable digits showing the interlocked position by means of arrows. Lines delimit the intercheliceral channels (reconstruction by means of Photoshop™); 13) detail of labrum, movable digits and stylet channels; 14) subcapitulum at the capitular saddle level. Arrows indicate the vestibula collecting saliva; 15) subcapitulum at the pharyngeal chamber level. *Cenopalpus pulcher* (Canestrini & Fanzago) for figs 12, 15, *Tetranychus urticae* Koch for figs 13-14. Scale bar = 1 µm. Abbrev.: ca, cervical apodeme; cas, capitular saddle; cl, capitular lips; DM, movable digit; ds, dendritic sheath; ic, intercheliceral channel; L, labrum; ll, lateral lips; od, outer dendritic segment; pg, preoral groove; phc, pharyngeal chamber; rg, rostral gutter; stc, stylet channel.



Figs 5.16-20 - *Cenopalpus pulcher* (Canestrini & Fanzago), transmission electron micrographs of the gnathosoma cross sections: 16-19) details of the fixed and movable digits gradually more proximal from 16 to 19; 20) subcapitulum at the level of the salivary pump complex and pharyngeal chamber. Scale bar = 1 µm. Abbrev.: ap, fixed digit accessory pieces; ca, cervical apodeme; cl, capitular lips; DF, fixed digit; DM, movable digit; msd, median salivary duct; phc, pharyngeal chamber; pp, pharyngeal pump; rg, rostral gutter; sdf, sensillum of the fixed digit; spl, plates of the salivary pump; stc, stylet channel; STY, stylophore; SUB, subcapitulum.



Figs 5.21-22 - Transmission electron micrographs of a subdistal cross section of the subcapitulum in: 21) *Cenopalpus pulcher* (Canestrini & Fanzago) and 22) *Tetranychus urticae* Koch. Scale bar = 1 µm. Abbrev.: ad, adoral setae; ar, annular reinforcement; ll, lateral lips; PA, pedipalp; rg, rostral gutter; spl, plates of the salivary pump; stc, stylet channel; tb, tubular body.

and their accessory pieces slide backwards and forwards along the rostral gutter, for the dorsal parts, and along the stylet channels, for the ventral part and the accessory pieces along with the stylets. They may possibly apply a pressure on the flexibile salivary plates to cause a salivary flow from the median salivary duct into the intercheliceral canal via the stylet channel depressions. The stylet retraction allows food juice to be sucked through the pre-oral food channel. In addition, the labrum appear to be pushed ahead by means of the stylet-labrum articulation during cheliceral protrusion. Therefore, the stylets are involved both in piercing plant tissues and in injecting saliva into the plant cells to allow a pre-oral digestion.

The sensilla located in the stylets are thought to be related to the tasting of host cell juices but we cannot exclude a volatile perception, especially considering the cheliceral movements during partner and food searches. Unfortunately, information on the putative sensory organ on the fixed digits of *C. pulcher* is too scanty. One might hypothesize that it is part of a proprioreceptor (could it derive from a slit sense organ?) and may perceive the pressure exerted on the salivary pump complex or the position of the fixed digits inside the rostral gutter.

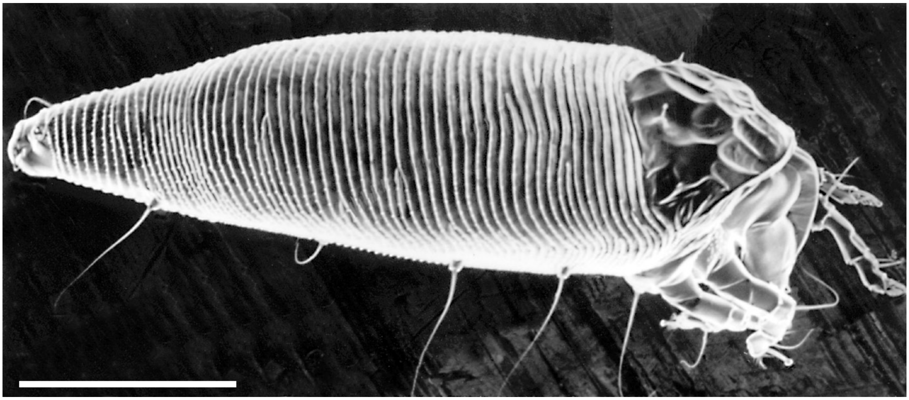


Fig. 6.1 - *Diptacus hederiphagus* Nuzzaci, scanning electron micrograph of a female from a dorso-lateral view. Scale bar = 50 µm.

6. ERIOPHYOIDEA (ACTINEDIDA: ERIOPHYOIDEA)

The mouthparts of some eriophyoids (fig. 6.1) have been described in much detail by NUZZACI (1979) and further data can be found in several related papers (KEIFER, 1959; SHEVTCHENKO & SILVERE, 1968; HISLOP & JEPPSON, 1976; LINDQUIST, 1996; NUZZACI & ALBERTI, 1996, also for other references). Their gnathosoma is strongly modified, showing a highly complex arrangement of nine stylet-like structures deriving from the chelicerae, pedipalps and labrum. The cheliceral stylets are flanked antiaxially by the outer subcapitular stylets and latero-ventrally placed on the styliform labrum (figs 6.2-5). Their surfaces don't display any specific features suitable for a distal interlocking with the other mouthparts, and all the pieces are just overposed to one another. The chelicerae are not protractable; fixed and movable digits are both styliform, long and stout in diptilomiopids, and short and fine in phytoptids and eriophyids. In cross sections, the fixed digits are larger than the movable digits (figs 6.2-6). They lie together in a mesal stylet sheath which is deeply U-shaped (figs 6.2-5). The sheath derives from the subcapitulum and envelops the cheliceral, subcapitular and labral stylets, driving them into the wound (figs 6.2-5). Its walls are distally very thin forming dorsal overlapping cuticular extensions, while proximally they are thicker on the ventral surface (figs 6.2-5). More proximally, the movable digit is connected to the fixed digit and each cheliceral shaft lies in a discrete stylet channel (figs 6.6-7). This channel is delimited ventro-mesally by the labrum, and ventro-laterally by elevated lips which are derived from the subcapitulum (figs 6.6-8) and distally connected to the subcapitular stylets (fig. 6.2).

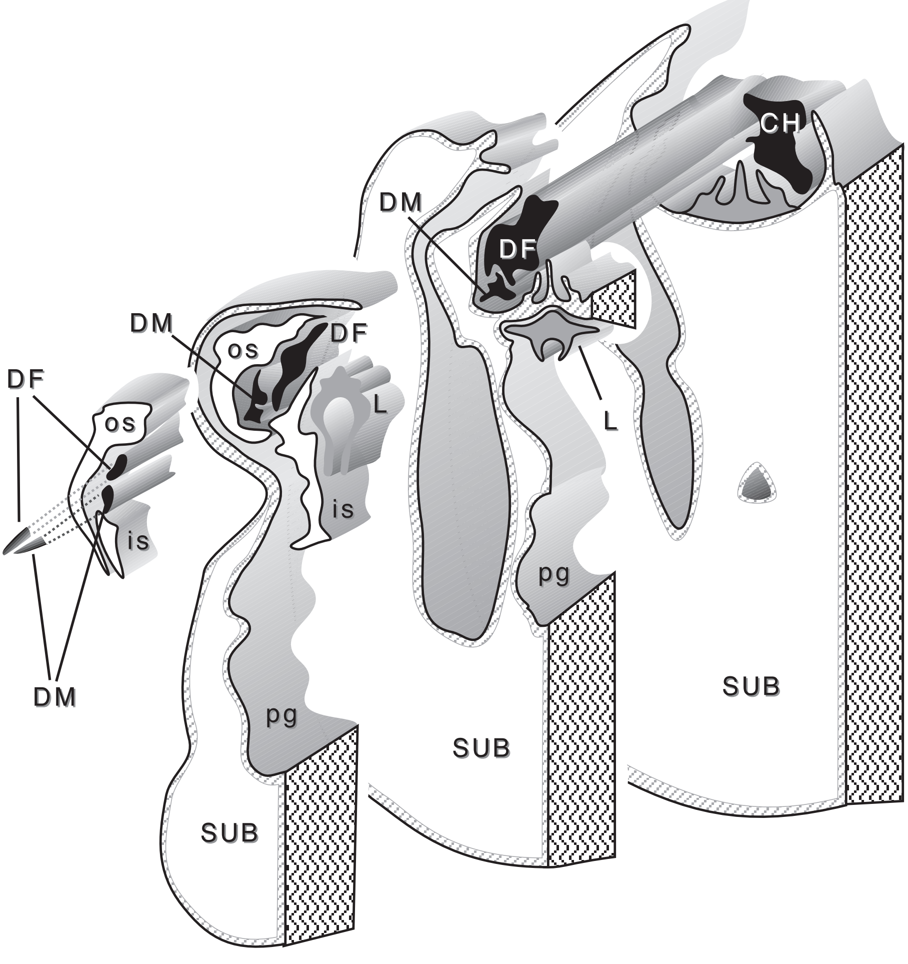
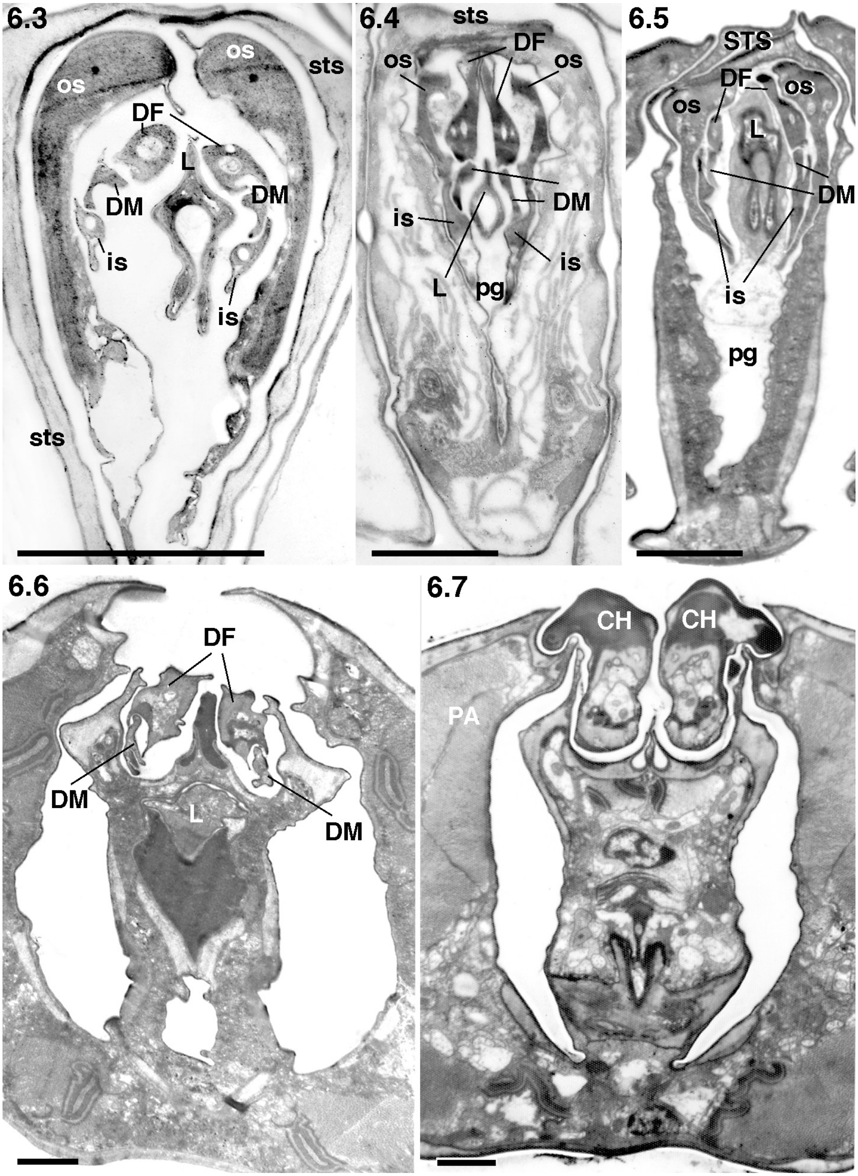


Fig. 6.2 - Eriophyoid mites: semischematic drawing of the mouthparts. Subcapitular pieces and chelicerae are partly drawn. Abbrev.: CH, chelicera; DF, fixed digit; DM, movable digit; is, inner subcapitular stylet; L, labrum; os, outer subcapitular stylet; pg, preoral groove; SUB, subcapitulum.

A stylophore, or a structure therefrom derived, is not detectable proximally. The cheliceral shafts are directly linked and hinged to the electron-dense motivator. This peculiar structure is passed through by the median salivary duct, which issues from the unpaired salivary gland and reaches the dorsal labral surface (fig. 6.10). Moreover, a large plate-like



Figs 6.3-7 - Transmission electron micrographs of the gnathosoma cross sections: details of the stylet complex gradually more proximal from 3 (subdistal section) to 7 (at the level of the pharyngela pump). *Diptacus hederiphagus* Nuzzaci for fig. 3, *Phytoptus avellanae* (Nalepa) for figs 4-7. Scale bars = 1 µm. Abbrev.: CH, chelicera; DF, fixed digit; DM, movable digit; is, inner subcapitular stylet; L, labrum; os, outer subcapitular stylet; PA, pedipalp; pg, preoral groove; sts, stylet sheath.

Figs 6.8-11 - *Phytoptus avellanae* (Nalepa), transmission electron micrographs of the gnathosoma cross sections: 8-9, 11) details of very close sections at the level of the motivator; 10) details of the motivator. Scale bars = 1 µm. Abbrev.: CH, chelicera; mo, motivator; pdc, podocephalic canal; t, tendon. Arrow indicates the salivary duct coming from the unpaired salivary gland.

tendon originates mesally on the motivator anterodorsal surface (fig. 6.10) and inserts on the dorsal surface of each basal cheliceral segment (figs 6.8-9).

The sensillar arrangement of the chelicerae is still not well understood. Both cheliceral stylets are innervated and contain outer dendritic extensions of sensorial cells. In particular, two small lumina have been detected for each fixed digit stylet starting in different position (figs 6.3-5) in a subdistal level. More proximally and in both lumina, a dendritic sheath, neurotubules and

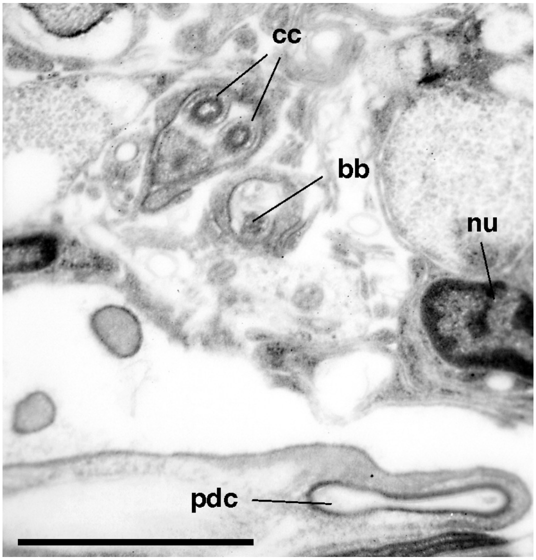


Fig. 12 - *Phytoptus avellanae* (Nalepa), transmission electron micrograph of the gnathosoma cross section at the level of the ciliary regions of the cheliceral sensilla. Scale bars = 1 µm. Abbrev.: bb, basal body; cc, ciliary constriction; nu, nucleus; pdc, podocephalic canal.

two ciliary constrictions have been found, while no tubular body is evident (figs 6.8, 6.11-12).

The cheliceral stylets have a slight, alternate, back-and-forth movement, resulting from the combined action of the retractor cheliceral muscles, motivator and pedipal length contraction. The cheliceral stylet retractor muscles may induce a rotation of the motivator which plays an important role in the cheliceral stylet deepening into the host plant cells. The wound production seems to depend mainly on the telescopical retraction of the pedipalps (KEIFER, 1959; KRANTZ, 1973; MCCOY & ALBRIGO, 1975; NUZZACI, 1976; NUZZACI & ALBERTI, 1996) and on the piercing by the subcapitular stylets. Cheliceral stylets move separately, and may be simply appressed to the other mouthparts, deepen into the plant cell and are involved in salivary discharge. The motivator and cheliceral stylets complex should be directly involved in pushing saliva from ducts up to the wound. All stylets together delimit a sort of chamber, partially surrounded by the stylet sheath, through which salivary secretions and plant juices may be transported. Actually, it is assumed that the saliva collected at the level of the dorsal surface of the labrum is delivered into the pierced plant cell between the cheliceral stylets and labrum, whereas the plant cell contents are sucked through the pre-oral canal formed by the ventral side of the labrum and the subcapitular stylets.

DISCUSSION AND CONCLUSIONS

The fine morphology of the chelicerae and other mouthparts shows clearly an evolutionary trend with structural adaptations that strictly depend on a large number of nutritional patterns, even if the different grades of specialization have probably arisen independently (THERON, 1974; KRANTZ & LINDQUIST, 1979; NUZZACI, 1985; NUZZACI & DE LILLO, 1991c; LINDQUIST, 1998; ALBERTI & COONS, 1999). Unfortunately, few anatomical studies have been conducted to describe the morphology and explain the function of the mouthparts, mainly limited to the most economically important taxa (for more references see ALBERTI & COONS, 1999). Based on our research and other literature, the chelicerae may grasp or pierce the food surface and inject specifically or not the saliva into the wound, but alone they cannot participate directly to the suction.

The mouthpart arrangement of the adult females of *V. destructor* generally resembles that of other parasitic Gamasida, mainly belonging to the Dermanyssina (EVANS & TILL, 1965; EVANS & LOOTS, 1972), and it should be considered derivative from the predaceous typically chelate form, of which phytoseiids are good examples (EVANS & LOOTS, 1972; BOURDEAU-GORIROSSI, 1989; EVANS, 1992). The varroid and phytoseiid chelicerae don't have any specialized morphological relationship with the labrum and the mouth, and the salivary apparatus has separate devices for injecting saliva. The chelicerae are not forced by the other mouthparts in assuming a particular position and they are not functionally associated with each other. Instead, from a functional point of view, the chelicerae of these taxa are surely involved in food grasping (phytoseiids) and in food surface cutting (phytoseiids and varroids), the latter sometimes also performed by the corniculi.

In the studied actinedid mites, the fixed and movable digits are often deeply transformed and play different roles. Among different superfamilies the relationship between the stylet-like movable digits has a different degree of complexity. It is really strict in the tetranychid and tenuipalpid mites, whereas it is simpler in the other taxa, even if the stylet position into the gnathosomal frame depends on the morphology of the fixed digits, labrum and subcapitular derivative parts. In addition, the development of a longitudinal dovetail between the paraxial walls of the styliform movable digits of tetranychids and tenuipalpids allows them to form a well adapted tube-like unit for piercing. Moreover, the salivary apparatus discharges saliva at the base of the labrum, at its dorsal or lateral position, and it utilizes the stylets for bringing the secretion into the plant cells. This action is more specifically realized by means of the intercheliceral canal produced by the interlocked and protracted tetranychid and tenuipalpid stylets, with a larger canal in the first taxon. The stylet involvement in salivary injection is less specific for the other taxa, where both stylets and labrum participate actively without any particular tube-like structure.

By contrast, the greatly elongated styliform chelicerae of the deutonymphal and adult smaridid have lost their movable digit and this follows the adaptive transformation in the stem-lineage of the Erythraeoidea (WITTE, 1998).

Though the movable digits tend towards a unique structure and function in the investigated species, the fixed digits display different morphological characteristics, relationships with the other mouthparts and, therefore, functions. In the most specialized form of tetranychid and tenuipalpid mites, they are part of a salivary pump apparatus set just beyond the labral base and at the distal part of the salivary median duct. In the eriophyoids, even if the fixed digits are stylet-like, they don't display any morphological relationship with the other pieces. They apparently don't participate in salivary discharging in a specific way, even thought the motivator induces a back and forth movement with respect to the labrum and this action may help in the salivary debouchment. In the penthaleid and tarsonemid mites, the fixed digits close dorsally the supralabral chamber without an interlocking connection with the other pieces even though a sort of sliding apparatus occurs between the subcapitular lateral lips and the digits. The consequence is the formation of a hermetic supralabral chamber that can be invaded by the food juices.

Of considerable interest is the movable digit articulation with the distal part of the second cheliceral article which exhibits large modifications in the studied groups. Its most simple and typical form is the bicondylar articulation in phytoseiid chelicera. Otherwise, in *V. destructor*, as shown also by AKIMOV *et al.* (1988), the fixed digit is strongly reduced to the antiaxial and paraxial processes at the base of the movable digits and these processes can be considered to be traces of this articulation. A complex arrangement is preserved also for the penthaleid basal sclerite (DI PALMA, 1995), which appears to be homologous to the structure (variously named) found in Tetranychidae (SUMMERS *et al.*, 1973; ALBERTI & CROOKER, 1985; ALBERTI & COONS, 1999), Cheyletidae (SUMMERS & WITT, 1971; AKIMOV & GORGOL, 1990), Anystidae (AKIMOV & BADANIN, 1999), Ereynetidae (BADANIN, 2000), Demodicidae (DESH

& Nutting, 1977), Cheyletiellidae (Hallas, 1982), Stigmaeidae (André, 1977), Tarsonemidae (Sachs, 1951; Lindquist, 1986; Lindquist, 1998; Nuzzaci *et al.*, in press), Pyemotidae (Krczal, 1959), Trombididae (Mathur & LeRoux, 1965) and in an oribatid Gustaviidae (Wolley, 1979). Moreover, in *P. major* and *T. nodosus* the rotation of their cheliceral sclerite is realized obliquely, as in pyemotid mites (Kcrzal, 1959). The plane of rotation varies considerably among other tarsonemid taxa from vertical in *Acarapis* (Sachs, 1951) to horizontal in *Steneotarsonemus* (Lindquist, 1986).

Finally, the homology of the eriophyoid motivator is still a matter of conjecture. It partly works in the same way as the tarsonemid lever and penthaleid basal sclerite from which it is distinguished by the absence of muscles directly inserted and involved in the up-and-down movement of the movable digit. The hypothesis that the motivator may be a relict of the movable digit articulation to the second cheliceral article seems to be intriguing.

A considerable lack of knowledge is evident concerning the sensilla of acarine mouthparts. Most of the fine morphological descriptions concern Ixodida (see references in Nuzzaci, 1995; Alberti & Coons, 1999; Coons & Alberti, 1999) because of their medical and veterinary importance and their greater size. So, in a few cases, they have been also studied by electrophysiological means giving evidence of their functional role. There are very few exhaustive investigations about other groups of Acari, and, often, the information is fragmentary. This is due to the different economic importance of the taxa, the scarcity of financial support for such important studies and, mainly to the very small size of the mites which deeply hinders behavioural and electrophysiological research. More recently (more or less in the last decade), original and specific contributions have been published on this topic (see references in Nuzzaci, 1995 and Alberti & Coons, 1999; de Lillo & Aldini, 2001; de Lillo & Aldini, in press; Nuzzaci *et al.*, in press) and most of those observations are summarized in the present paper.

The gnathosoma may bear various mechanical, chemical and putative thermo/hygroreceptors. The first two kinds of sensilla have been found on the chelicerae of some Gamasida (Nuzzaci *et al.*, 1992; Nuzzaci & de Lillo, 1995; de Lillo & Aldini, 1994; de Lillo *et al.*, 1996), Ixodida (Waladde & Rice, 1977; Waladde, 1982), Actinedida (Nuzzaci & de Lillo, 1989, 1991a, b, d, e; Di Palma, 1995; Nuzzaci & Alberti, 1996; Nuzzaci *et al.*, in press), and Oribatida (Walzl, 1987) following a common scheme. Without speculating on the sensillar fine morphology, a gustatory role has been electrophysiologically demonstrated only for *Boophilus microplus* (Canestrini) (Waladde & Rice, 1977).

For other studied taxa, it is reasonable to suppose a gustatory function for cheliceral sensilla on the basis of their ultrastructure. This supposition may be supported also by their strategic location at the digit tips, which allows them to come in contact with the food earlier than the sensilla located on the other mouthparts. Their presence is highly significant for the feeding activity as these chemoreceptors are introduced into the prey or plant or other host tissues, and provides to the mites a first sensory feedback to the acceptability of the food juices.

Moreover, some different types of mechanoreceptors have always been considered on the second cheliceral article and its fixed digit (pilus dentilis, slit sense organs, dorsal setae, putative proprioreceptor in tetranychid and tenuipalpid mites), while a mechanoreceptor has been detected on the movable digit only in Gamasida. Their structural aspect and their distal position suggest an involvement in the food surface contact during grasping and tearing activity (phytoseiids), or their role in perceiving the reciprocal digit position or their position in respect to the food surface during cheliceral movements (proprioreceptors and dorsal setae).

Despite some remarkable contributions made during the last few years, the functional morphology of the chelicerae and their sensilla are, for the most part, one of the most poorly known aspects in acarology. Much additional and comparative work is needed regarding closely related groups and other species of considerable economic interest to learn more about the gnathosoma and its sensory patterns, mainly to understand their trophic relationships and find applications of this knowledge.

ACKNOWLEDGMENTS

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RIASSUNTO

Morfologia dei cheliceri e comportamento trofico in acari di interesse economico

Gli autori raccolgono le attuali conoscenze sulla organizzazione strutturale e sul significato funzionale dei cheliceri e delle strutture sensoriali tra gli acari di interesse economico in agricoltura e per i quali lo gnatosoma è stato più recentemente studiato.

I cheliceri del predatore polifago *Typhlodromus exhilaratus* Ragusa (Gamasida, Phytoseiidae) mostrano una organizzazione alquanto primitiva e di tipo chelato. Essi sono preposti alla presa della preda, o altro tipo di alimento, mentre le altre parti boccali intervengono nel praticare la lesione dei tessuti della preda, immettere saliva e suggere l'alimento.

In *Varroa destructor* Anderson & Trueman (Gamasida, Varroidae), il digitus mobilis è sottile e allungato, mentre il digitus fixus è fortemente ridotto. I cheliceri partecipano direttamente, insieme alle altre parti boccali, solo alla puntura del tegumento dell'ape.

Nell'acaro fitofago *Penthaleus major* (Dugès) (Actinedida, Penthaleidae), il digitus mobilis è distalmente stilettiforme, lungo e robusto, e prossimalmente si articola allo sclerite basale. Durante la protrusione dei cheliceri, gli stiletti possono agire insieme o separatamente nella puntura della superficie vegetale e causare grandi e profonde lesioni. Gli stiletti protrusi potrebbero appaiarsi a formare un canale interchelicerale non perfettamente definito e si presume possano, così, essere implicati nella immissione salivare. Il digitus fixus è relativamente grande e non rigido, ricopre dorsalmente la camera preorale sopralabrale ed è passivamente implicato nel setacciamento e suzione dei succhi cellulari.

Nell'acaro micofago *Tarsonemus nodosus* Schaarschmidt (Actinedida, Tarsonemidae), il digitus mobilis è aghiforme e articolato tramite un lever al secondo articolo chelicerale. Il digitus fixus avvolge parzialmente il digitus mobilis ed è articolato con il subcapitulum. Gli articoli basali dei cheliceri sono fusi in uno stiloforo che forma una capsula gnatosomale con il subcapitulum. L'organizzazione e la morfologia dello gnatosoma suggeriscono che i digiti mobili pungano le cellule fungine indipendentemente e senza stabilire una stretta relazione tra loro.

I fitofagi *Tetranychus urticae* Koch (Actinedida, Tetranychidae), ragnetto rosso comune, e *Cenopalpus pulcher* (Canestrini & Fanzago), falso ragnetto rosso (Actinedida, Tenuipalpidae), sono provvisti di cheliceri stilettiformi notevolmente modificati e adatti ad essere protrusi considerevolmente. Il digitus mobilis è molto allungato e stilettiforme, terminando prossimalmente nello stiloforo (articolo chelicerale basale fuso). I digiti fixi sono prevalentemente fusi tra loro. Durante la protrusione dei cheliceri, gli stiletti sono forzati ad articolarsi tra loro formando un fine canalicolo il quale è direttamente connesso al dotto salivare. Contemporaneamente i digiti fixi intervengono nell'attivazione della pompa salivare. Pertanto, i cheliceri svolgono un duplice ruolo nel pungere i tessuti e nell'immettere saliva in questi.

Nei piccoli acari fitofagi della superfamiglia Eriophyoidea (Actinedida), lo gnatosoma ha una organizzazione fortemente modificata. Il digitus fixus e mobilis sono entrambi stilettiformi, laminari ed entrano a far parte di una struttura composta da nove stiletti di differente origine che opera come un tutt'uno nella puntura della superficie dell'ospite, immissione della saliva e suzione dei succhi cellulari. In particolare, i cheliceri sembrano implicati in una ulteriore penetrazione del complesso delle parti boccali nella lesione e nella immissione della saliva.

In ognuna delle specie indagate, i cheliceri sono dotati di sensilli chemo e meccanorecettori che sembrano essere implicati nella percezione e scelta del substrato alimentare. Una percezione del partner non può però essere esclusa.

Parole chiave: Acari, gnatosoma, parti boccali, meccanismi alimentari, strutture sensoriali, digitus mobilis, digitus fixus, adattamenti morfologici, puntura, immissione di saliva, lever, motivator, stiloforo.

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