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Mouthparts of a tydeid mite: an ultrastructural and functional investigation*

ABSTRACT

The gnathosoma of a tydeid mite (*Tydeus* sp.) shows the subcapitulum and the cheliceral segments not fused to each other though closely appressed. The lateral lips are provided with a well defined system of grooves and rims for interlocking. The pre-oral groove has very electron-dense walls; it is tightly shaped and covered dorsally by the labrum only distally. More proximally it becomes a channel (food channel), dorsally sealed. The labrum is an unpaired structure involved in keeping the cheliceral stylets into the cheliceral groove and in covering the pre-oral groove distally. The fixed digits and the basal segments of the chelicerae are shaped to adhere to the lateral lips and mesally to each other; they are not fused to form a stylophore. The movable digits are stylet-like, reach the tip of the gnathosoma and are proximally articulated with a large lever provided with two strong knobby apodemes.

A pharyngeal pump connected to the food channel activates and controls the intake of the alimentary fluids.

Some sensorial structures associated with the mouthparts components have been observed and described.

Key words: stylets, gnathosoma, lever, fixed digits, labrum, functional morphology.

INTRODUCTION

The gnathosoma is among the most distinctive features in the group of Acari; moreover adaptations of mouthparts to many nutritional patterns are comparable to the great adaptational diversity found in insects (EVANS, 1992; ALBERTI & COONS, 1999). In general, these adaptations are known only from the perspective of external morphology and, for several taxa, observations are limited to light microscopy while in only few groups have functional aspects been comprehensively interpreted.

Tydeids represent one of those taxa whose gnathosomal anatomy and functional morphology is completely unknown but for the systematic and taxonomic drawings primarily by light microscopy. Information on this group

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is lacking in several aspects. Little is known about the biology of its species (BAKER, 1965; KRANTZ, 1978). These mites can be found on plants, on fungi, in mosses and lichens on trees, in soil and litter, bird nests, stored foods, and associated with plant feeding mites as phytophages or predators (ANDRÉ, 1986; BIGNOTTE *et al.*, 1987; WHITFORD, 1996; ESTEBANES-GONZALES, 1997; ZDARKOVA, 1998; ABOU-AWAD *et al.*, 1999; NORTON *et al.*, 2000; RIPKA, 2000). A number of tydeid species have been reported to have a general life style, a supposition that would account for the difficulty in analysing tydeid behaviour; however the interaction between this group and their habitats remains unclear. Thus different trophic behaviours have been described for the same species (BAKER & WHARTON, 1952; FLESCHNER & ARAKAWA, 1953).

In view of this lack of knowledge the aim of this paper is to give an ultrastructural description and a functional interpretation of the mouthparts for a species of the genus *Tydeus* (maybe *T. californicus*) belonging to the family Tydeidae.

Finally, our comprehension of evolutionary trends in the modifications and adaptations of gnathosomal components to different trophic habits needs to fill some gaps among the already described groups of mites. In this respect tydeid mites may represent a very interesting group, thanks to their relatively unspecialized trophic habits (thus a kind of intermediary towards the modifications of more specialized groups), so that a better understanding of their gnathosomal anatomy may help in hypothesizing a phylogenetic path among Actinotrichida mites.

MATERIAL AND METHODS

Mites of the genus *Tydeus* sp. were found in the calyx of *Cotoneaster horizontalis* Decne fruits collected, during winter, in Bari, Apulia, Southern Italy.

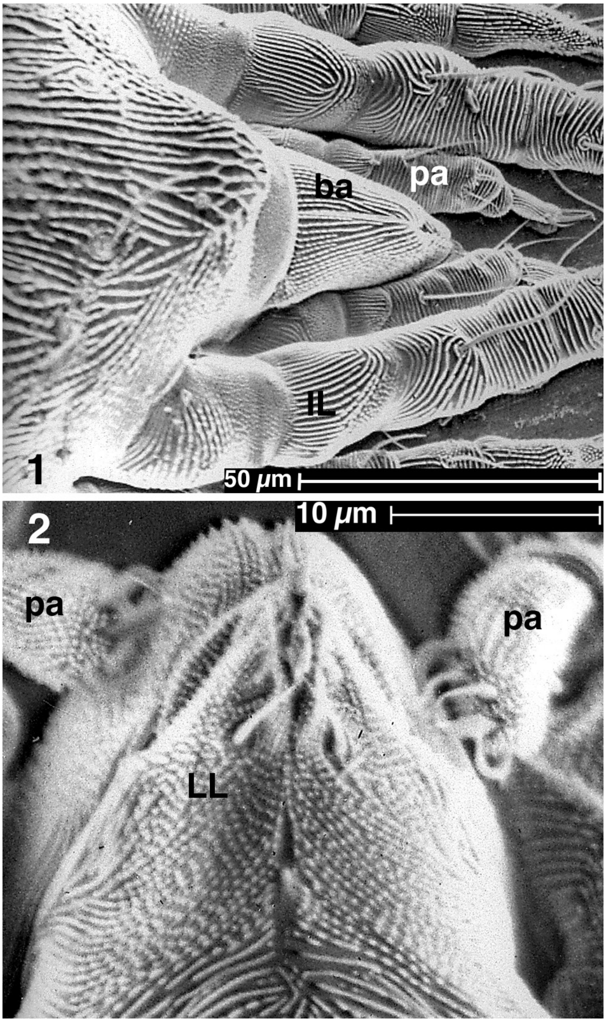
Specimens for TEM were cut and fixed in a Karnovsky's (1965) solution for three hours at 4°C; then they were rinsed with a cacodylate buffer solution for two hours and post fixed in 2% OsO_4 buffer solution for another two hours. After being rinsed again the specimens were dehydrated in graded ethanols up to absolute alcohol, then embedded in Araldite medium using propylenoxide as intermedium. Ultrathin sections were cut using a LKB III ultramicrotome provided with a diamond knife. Sections were stained in uranylacetate and lead citrate (REYNOLDS, 1963). Observations were performed using a Zeiss EM109T transmission electron microscope.

Specimes for SEM were processed according to Nuzzaci and Vovlas (1976). Observations were realized with a stereoscan Cambridge S100.

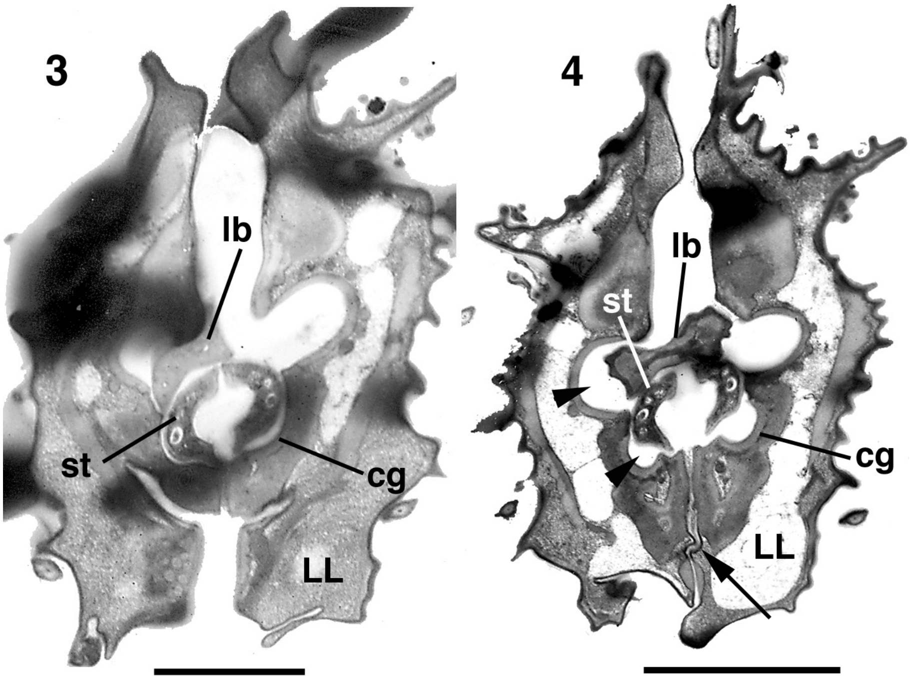
RESULTS

GNATHOSOMA AND PEDIPALPS

The gnathosoma is conically-shaped (figs 1-2), and consists of the cheliceral segments, dorsally located, and the subcapitulum. Distally the subcapitular lateral lips form the ventral tip of the gnathosoma. The pedipalps are linear and simple, relatively long projecting well beyond apex of other gnathosoma structures (fig. 1).



Figs 1-2 - SEM micrographs of the gnathosoma: 1) dorsal view; 2) ventral view. Abbr.: ba, basal articles of chelicerae; IL, first leg; LL, lateral lips; pa, pedipalp.



Figs 3-4 - TEM micrographs: subdistal cross sections at the level of the lateral lips. Abbr.: cg, cheliceral groove; lb, labrum; LL, lateral lips; st, stylet. Arrow points to the interlocking system of the lateral lips. Arrowheads indicate the two mesial grooves. Scale bar: 1 µm in fig. 3; 5 µm in fig. 4.

LATERAL LIPS AND SUBCAPITULUM

The lateral lips are never fused either dorsally or ventrally. Distally they are simply opposed but not morphologically adapted to each other (fig. 3); slightly more proximally the adoral walls of the lateral lips are ventrally provided with corresponding folds and ridges that make them tightly appressed (fig. 4). On the other hand, the two dorsal regions of the lateral lips do not show this kind of adaptation but they are simple mirror images of each other (fig. 4). Each lateral lip shows two grooves mesially located, one dorsal to the other (fig. 4 arrowheads). The ventral groove is shaped to receive the cheliceral stylets (cheliceral groove), while the dorsal one accommodates the labrum. Finally, the cuticle of the adoral walls is thicker and very electron-dense in the ventral and dorsal region of the lateral lips such as at the level of the cheliceral groove (fig. 4).

More proximally the dorsal walls of the lateral lips are shaped to accomodate the ventral region of the fixed digits of the chelicerae. At this level also the dorsal region of the lateral lips shows a system of rims and folds (fig. 5). Slightly more proximally the lateral lips develop a real interlocking system composed of furrows and rims to accommodate the ventral part of the basal cheliceral segments (fig. 6).

Pre-oral groove, labrum and mouth

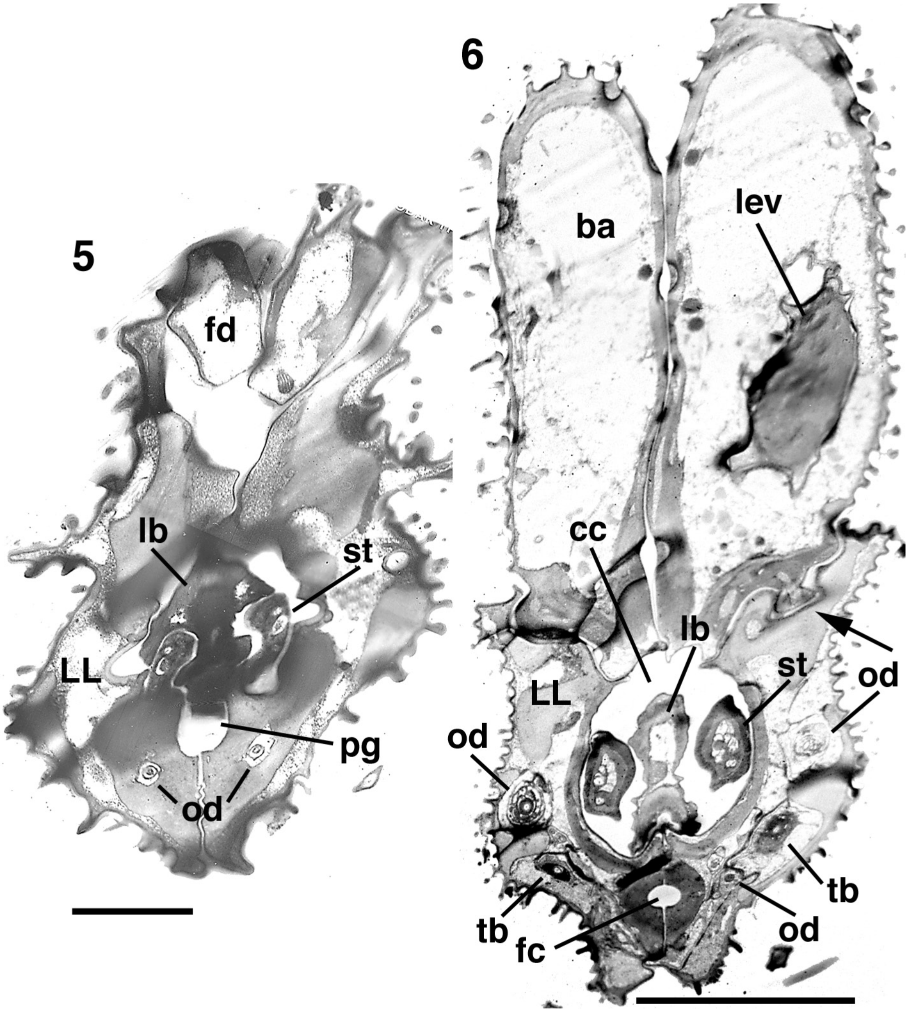
The pre-oral groove does not reach the apex of the gnathosoma. At its apex it is a kind of wide depression in the electron-dense walls of the lateral lips (fig. 7) At this level the pre-oral groove is closed dorsally by a central process of the labrum while ventrally it is delimited by the adoral walls of the lateral lips (fig. 7). More proximally the pre-oral groove acquires U-shaped cross section while the labrum still covers it dorsally (fig. 5). Moving more posteriorly the pre-oral groove shows a circular cross section with both dorsal and ventral mesial walls still not fused (fig. 8). The labrum is dorsally appressed to the pre-oral groove. More proximally, the pre-oral groove becomes a channel (food channel), dorsally sealed while ventrally still opened (figs 6, 9-13). A thick ring of electron-dense cuticle surrounds the food channel. Finally, at the level of the mouth, the lateral lips are completely fused to form the subcapitulum. Then the food channel leads into the lumen of the pharynx (fig. 14).

The labrum shows a different morphology along its length. It is an unpaired projection dorsally located to the cheliceral stylets (figs 3-4) and provided with two lateral furrows and one ventral process (figs 5-10). The lateral furrows tightly accommodate the stylets while the ventral process covers the distal tract of the pre-oral groove (figs 5, 7-8). Just posterior to the mouth, the labrum consolidates with the cervix (fig. 11).

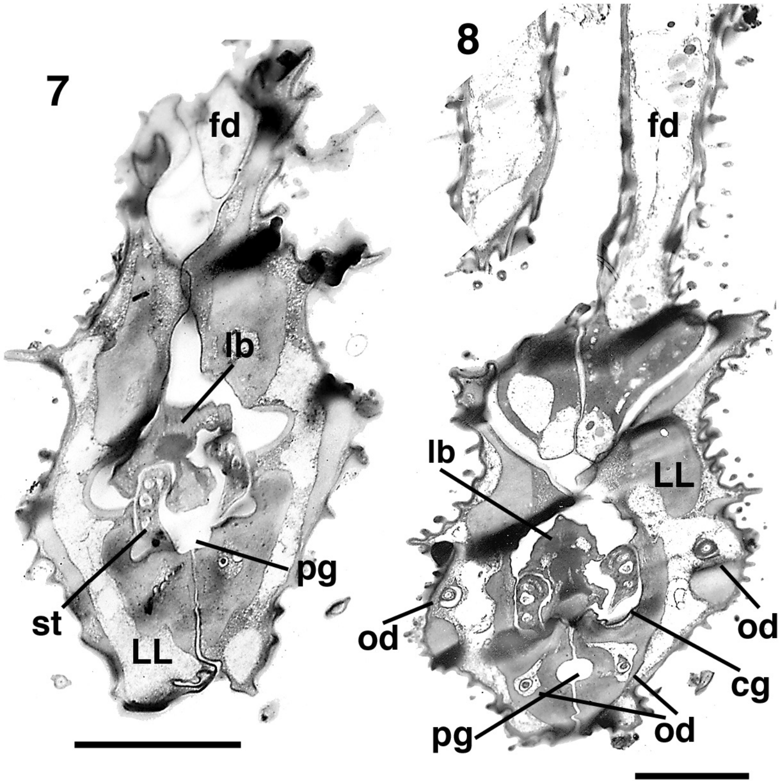
Chelicerae

The fixed digits constitute the distal and dorsal part of the gnathosoma (figs 5, 7-8) even though they do not reach the apex of gnathosoma (fig. 3). They are dorso-ventrally elongated; their ventral walls are structurally adapted to adhere to the dorsal walls of the subcapitulum and their adoral walls are shaped to be appressed to each other (fig. 8).

The movable digits are stylet-like; at the tip of the gnathosoma they are sickle-shaped in cross section (fig. 3). No corresponding rims and furrows are

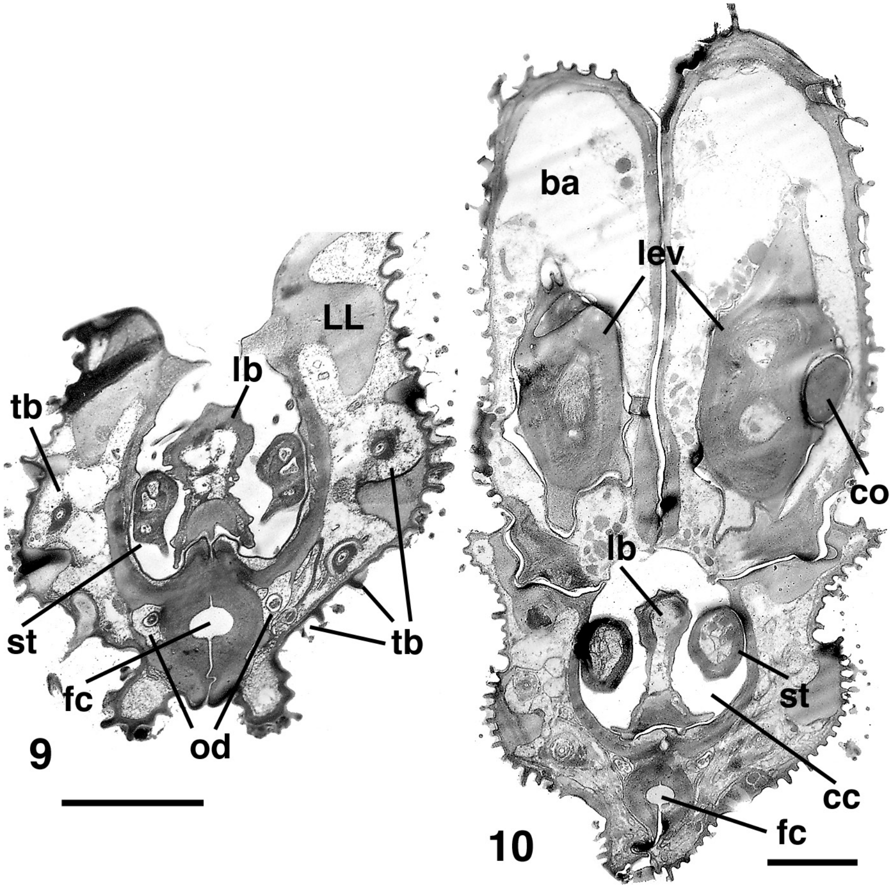


Figs 5-6 - TEM micrographs at the level of: 5) the pre-oral groove and 6) the food channel. Abbr.: ba, basal articles of chelicerae; cc, cheliceral chamber; fc, food channel; fd, fixed digit; lb, labrum; lev, lever; LL, lateral lips; od, outer dendritic segment; pg, pre-oral groove; st, stylet; tb, tubular body. Arrow points to the guide system between the lateral lips and the basal segments of chelicerae. Scale bar: 1 µm in fig. 5; 2 µm in fig. 6.



Figs 7-8 - TEM micrographs: cross sections of the pre-oral groove, 8) is more proximal than 7). Abbr.: cg, cheliceral groove; fd, fixed digit; lb, labrum; LL, lateral lips; od, outer dendritic segment; pg, pre-oral groove; st, stylet. Scale bar: 2 µm.

observed in the axial surfaces of the stylets. Distally they are located in the cheliceral grooves (figs 3-4) while, more proximally, they are held in position by both the cheliceral grooves and the dorsal lobes of the labrum that are shaped to accommodate them (figs 5-10). At the level of the food channel, the stylets look almost circular in cross section and are located in a cheliceral chamber (figs 6, 9-10, 12). A ring of very electron-dense cuticle surrounds the chamber (figs 6, 9-10, 12). Stylets are proximally connected to a basal spatulate sclerite (lever) (figs 6, 10). In the distal region the lever is roundish in cross section (figs 6, 10) while more proximally, it is elongated dorso-



Figs 9-10 - TEM micrographs: cross sections at the level of the food channel (fig. 9) and, more proximally, of the cheliceral chamber (fig. 10). Abbr.: ba, basal articles of chelicerae; cc, cheliceral chamber; co, condile; fc, food channel; lb, labrum; lev, lever; LL, lateral lips; od, outer dendritic segment; st, stylet; tb, tubular body. Scale bar: 5 µm in fig. 9; 2 µm in fig. 10.

ventrally and provided with a peripheral layer of thick and electron-dense cuticle (fig. 13). The lever is articulated with two knob-like apodemes on which it pivots (figs 10, 13). One apodeme originates from the aboral wall of the basal segment of the chelicerae and the other from the adoral wall.

The cheliceral basal segments are dorsally located to the subcapitulum and form the basal and dorsal region of the gnathosoma; they are never fused either to each other or to the subcapitulum (figs 6, 10-11, 13). Their mesial walls are appressed and seem to be able to coalesce to each other even though they do not show a real interlocking system (figs 6, 10-11, 13). Moreover, at the level of the two knob-like apodemes, the ventral walls of the basal segments of the chelicerae show a cuticular cleft to allow the articulation of the lever to the basal segments themselves (figs 13, 18).

The ventral walls of the basal segments of the chelicerae and the dorsal walls of the subcapitulum are intimately appressed by means of variously shaped ridges or processes (figs 6, 10-11, 13).

Pharynx and pharyngeal chamber

The food channel leads into the lumen of the pharynx. At this level the lumen looks elongated dorso-ventrally in a vestigial furrow derived from the fusion of the lateral lips. An electron-dense large area is present in the ventral region of the subcapitulum and it surrounds the pharyngeal chamber (fig. 14). All around the pharyngeal chamber the electron-dense area shows a non-homogeneous cuticle that looks like a spongyform layer (fig. 14). Slightly more proximally where the lumen of the pharynx becomes wider, the electron-dense area is still present while a tendinous process appears dorsally to the lumen (fig. 15). The dorsal wall of the pharynx is folded and connected to the tendinous structure (fig. 15) for insertion of the dilator muscles of pharynx.

Sensorial structures

Several sensorial structures are observed associated with the mouthpart components. A complete description is not reported here for all of them but for the following we present some details.

Lateral lips

One dendritic segment is observed in the ventral region of each lateral lip, at the level of the pre-oral groove, lying just laterally to it (fig. 5). It runs posteriorly and is still present at the level of the food channel, located dorso-laterally to the food channel itself (figs 6, 8-9, 16). At the level of the cervix, the labyrinths of the accessory cells are observed (fig. 11).

Three outer dendritic segments belonging to three different sensorial structures are observed at the level of the food channel on each ventral side of the subcapitulum. They end with three tubular bodies connected to ventral setae (figs 6, 8-9, 12).

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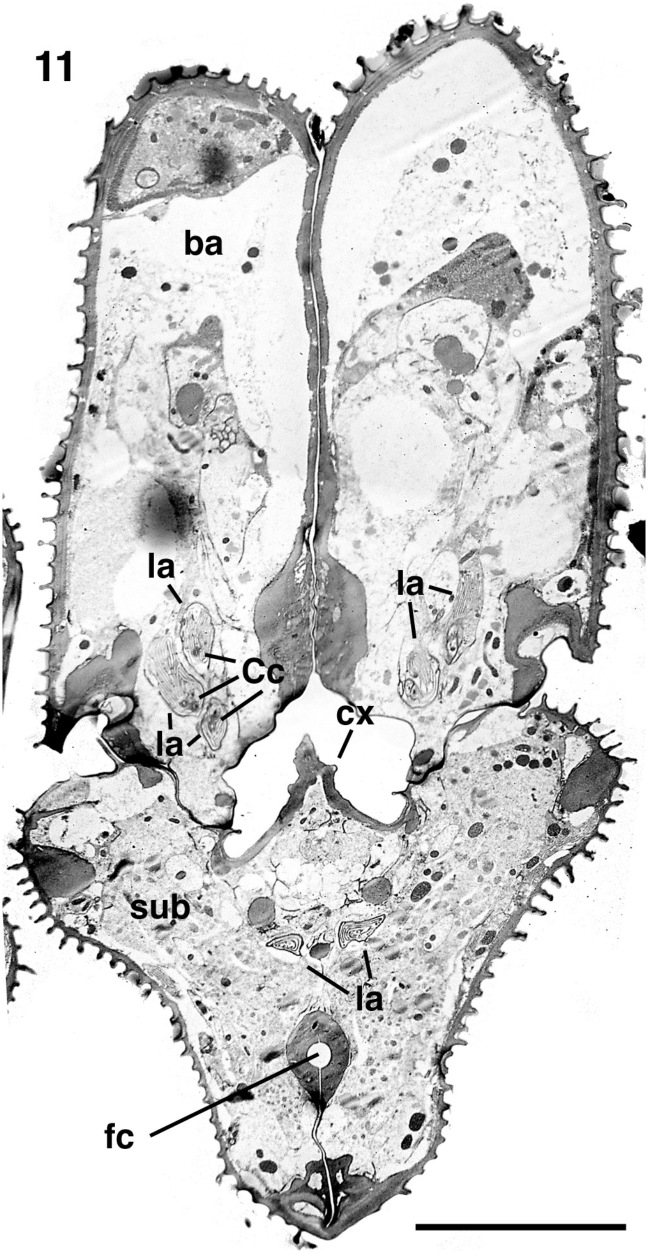

Fig. 11 - TEM micrograph: cross section at the level of the cervix. Abbr.: ba, basal articles of chelicerae; Cc, ciliary constriction; cx, cervix; fc, food channel; la, labyrinth; sub, subcapitulum. Scale bar: 5 µm.

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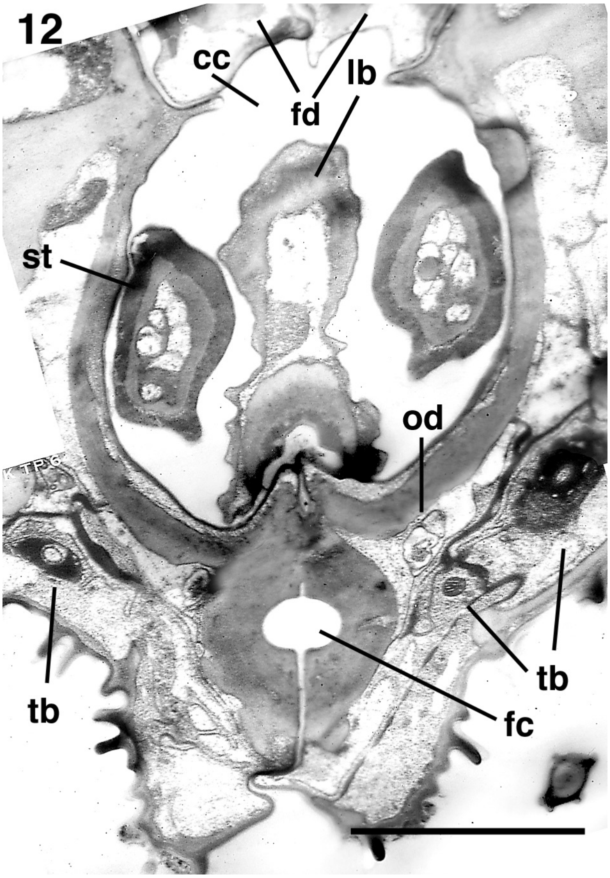

Fig. 12 - TEM micrograph: cross section showing the food channel and the cheliceral chamber. Abbr.: cc, cheliceral chamber; fc, food channel; fd, fixed digit; lb, labrum; od, outer dendritic segment; st, stylet; tb, tubular body. Scale bar: 1 µm.

PHARYNX

Ventro-laterally to the pharyngeal chamber some outer dendritic segments, connected to the pharynx lumen, are observed (fig. 17). Moreover, the labyrinths of two accessory cells are detected associated with the tendinous structure of the pharyngeal chamber, (fig. 15 detail in the right upper corner).

CHELICERAL STYLETS

Outer dendritic segments are observed running lengthwise in the stylet cross sections. At least three single outer dendritic segments are observed in

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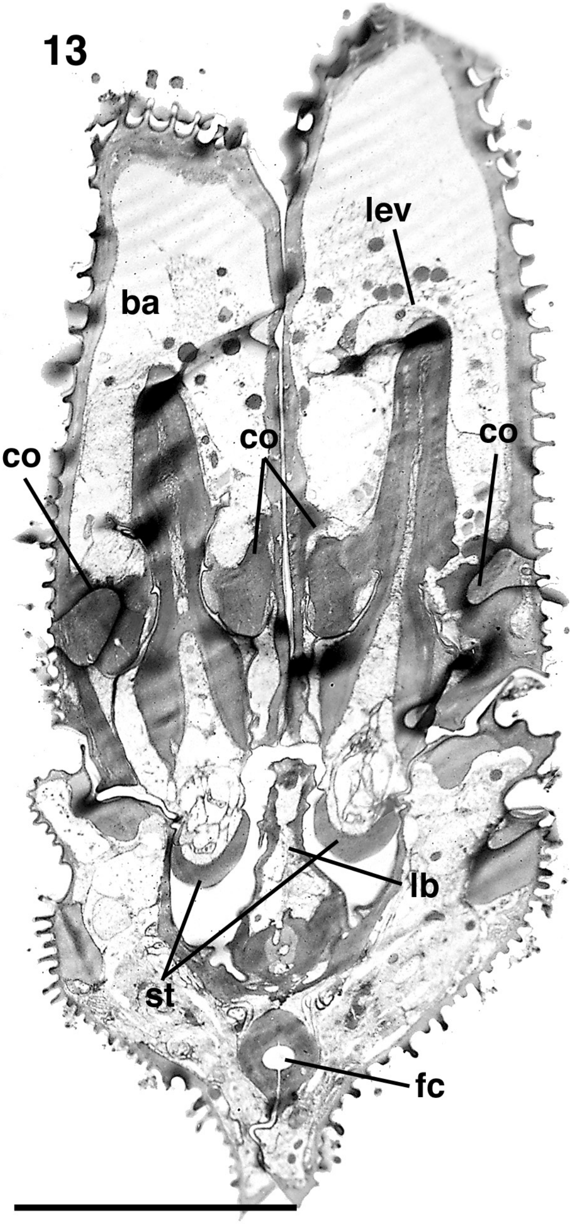
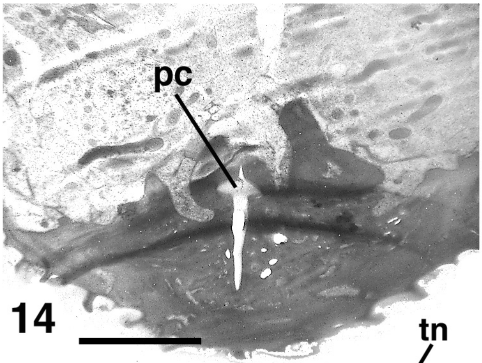
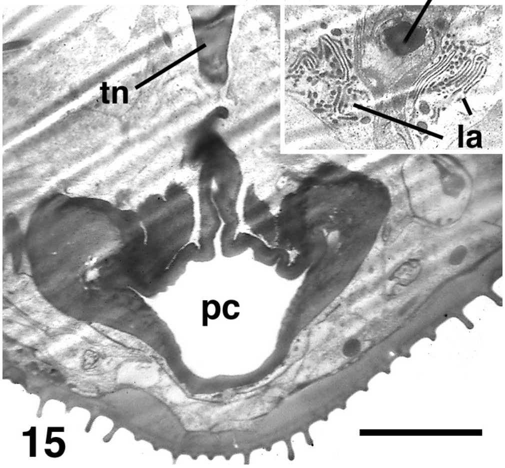


Fig. 13 - TEM micrograph: cross section at the level of the cheliceral lever showing the two knobby-like apodemes. Abbr.: ba, basal articles of chelicerae; co, condile; fc, food channel; lb, labral base; lev, lever; st, stylet. Scale bar: 5 µm.





Figs 14-15 - TEM micrographs of cross sections at the level of the pharyngeal chamber. Fig. 14 is slightly more distal then fig. 15. Note in fig. 14 the very electron-dense area surrounding the lumen of the pharynx. In fig. 15 in the right upper corner a detail of the labyrinth observed close to the tendineous structure of the pharynx. Abbr.: la, labyrinth; pc, pharyngeal chamber; tn, tendon. Scale bar: 2 µm.

the cross section of the levers (fig. 18). More proximally the ciliary constrictions and the labyrinths of the ciliary sinuses are present (figs 11, 19). Distally, it seems that these dendritic segments branch extensively (figs 6-10, 12) but only three dendritic branches reach the tip of the stylets (figs 3-5).

DISCUSSION AND CONCLUSIONS

This paper represents the first attempt to give an ultrastructural description and a functional interpretation of the mouthparts in a *Tydeus* species.

Considering the wide trophic range of this family (André, 1986; Bignotte *et al.*, 1987; Whitford, 1996; Estebanes-Gonzales, 1997; Zdarkova, 1998; Abou-Awad *et al.*, 1999; Norton *et al.*, 2000), it could be reasonable to predict different morphological adaptations to diverse feedings habits. On the other hand, according to the idea that considers these mites as generalists (Castagnoli *et al.*, 1984; Ripka, 2000), it is possible that not deeply specialized mouthparts may be involved in different feeding behaviours.

In the observed genus *Tydeus* the gnathosoma is composed of paired fixed digits and basal segments of chelicerae, styliform movable digits, paired

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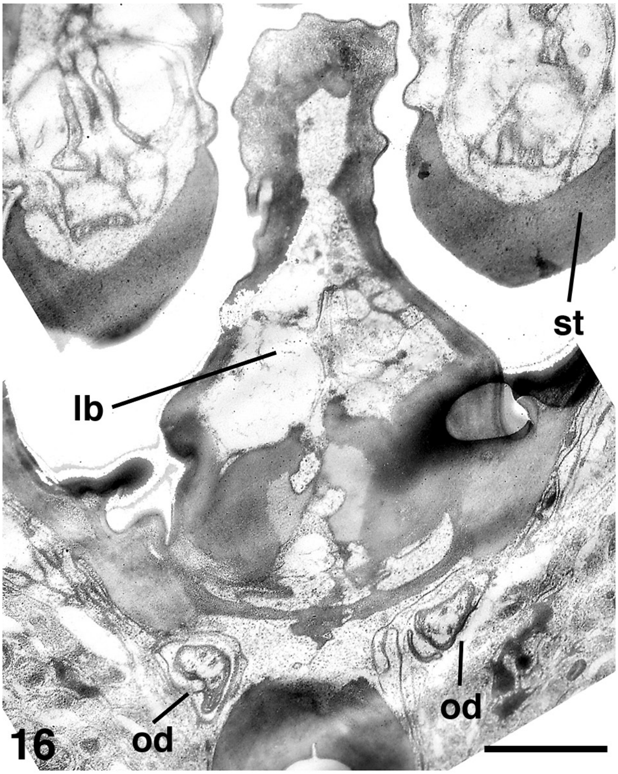

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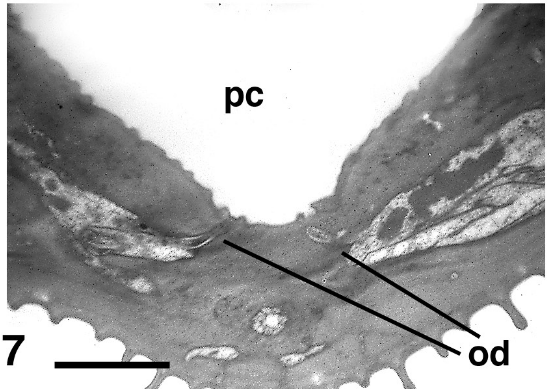

Figs 16-17 - TEM micrographs. 16) Cross section at the level of the labral base. Note the outer dendritic segments just beneath the labrum and above the food channel. 17) Detail of the pharyngeal chamber wall. The dendritic segments connected with the lumen of the pharyn are evident. Abbr.: lb, labral base; od, outer dendritic segment; pc, pharyngeal chamber; st, stylet. Scale bar: 1 µm.

lateral lips and elements of the subcapitulum. Mouthparts seem modified to pierce a variety of tissues (perhaps both animal and vegetable) and in this respect analogies and homologies with other mite groups are evident. The lateral lips are still not fused, a stylophore is not present nor a stylophore capsule; cheliceral stylets are short and not comparable to the slender and elongated stylets described in the spider mites and false spider mites (BLAUVELT, 1945; BAKER & CONNELL, 1963; SUMMERS *et al.*, 1973; HISLOP & JEPPSON, 1976; AKIMOV & YASTREBTSOV, 1981; ANDRÉ & REMACLE, 1984; LINDQUIST, 1985; ALBERTI & CROOKER, 1985; NUZZACI & DE LILLO, 1989; 1991b, d; DE LILLO *et al.*, 2001); no interlocking system has been observed to allow them to form a single tube. In this respect *Tydeus* stylets are more comparable with the ones described in *Tarsonemus nodosus* Schaarschmidt by Nuzzaci *et al.* (2002), which are short and seem to be protruded independently one from the other. Protraction and retraction of stylets in *Tydeus* is allowed by a basal sclerite (lever) (figs 6, 10, 20) articulated by means of two condyles (figs 13, 20) like the ones reported for *Penthaleus major* (Dugès) (NUZZACI & DE LILLO, 1991a; DI PALMA, 1995; DE LILLO *et al.*, 2001). A similar structure is described for several mite groups (SACHS, 1951; KRCZAL, 1959; SUMMERS & WITT, 1971; SUMMERS *et al.*, 1973; ANDRÉ, 1977; DESH & NUTTING, 1977; HALLAS, 1982; LINDQUIST, 1986; AKIMOV & GORGOL, 1990; NUZZACI *et al.*, 2002). The stylets' sliding is guided by the cheliceral groove and the labrum (figs 3-10, 20).

The fixed digits, modified to cover only the dorsal distal region of the gnathosoma, are not fused (figs 5, 7-8) as in *T. nodosus* (NUZZACI *et al.*, 2002), nor laminar-like or involved in salivary discharge as in other mites (NUZZACI & DE LILLO, 1989; 1991b, c, d). Actually, morphologically and functionally, the fixed digits remind of the ones described for *P. major* (NUZZACI & DE LILLO, 1991a; DI PALMA, 1995; DE LILLO *et al.*, 2001) even though in *Tydeus* the paraxial walls are appressed to each other but not reciprocally shaped to build one single piece. Anyway, in *Tydeus* the fixed digits seem to be able to adhere to each other (figs 5, 7-8); the hermetic seal of the apical part of the gnathosoma is then assured by the interlocked lateral lips and fixed digits. Thus alimentary fluids can be sucked thanks to the vacuum realized in the pharyngeal chamber by dilator muscles acting on the elastic dorsal wall. The low pressure status is transferred distally through the food channel and the pre-oral groove to reach the apex of the gnathosoma.

The basal segments of the chelicerae even similar to the ones observed in *P. major* (NUZZACI & DE LILLO, 1991a; DI PALMA, 1995; DE LILLO *et al.*, 2001) are never fused to each other nor with the subcapitulum (figs 6, 10-11, 13). In this respect, other described Prostigmata (including *Penthaleus*) present fused basal articles of chelicerae even if at different levels (NUZZACI, 1979a; NUZZACI

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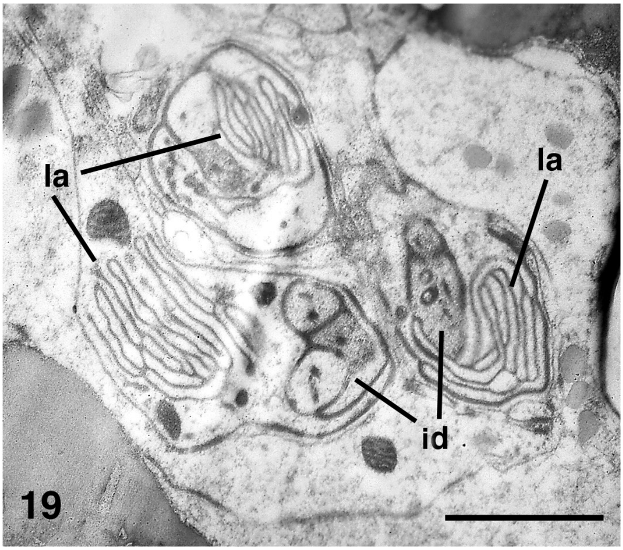

Figs 18-19 - TEM micrographs. 18) Detail of the dendritic segments in the proximal cross section of levers; 19) detail of the labyrinth and the dendritic segments. Abbr.: id, inner dendritic segment; la, labyrinth; lev, lever; od, outer dendritic segment. Scale bar: 2 µm in fig. 18; 1 µm in fig. 19.

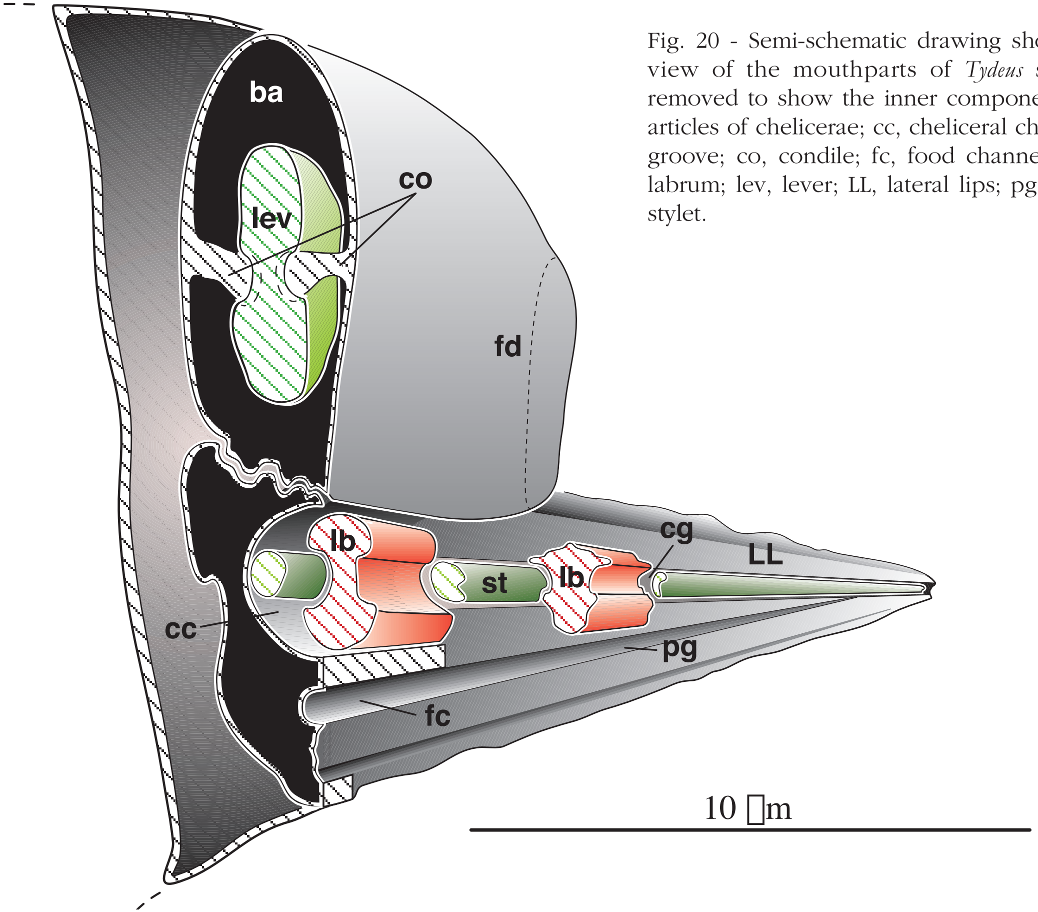

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Fig. 20 - Semi-schematic drawing showing a parasaggital view of the mouthparts of *Tydeus* sp. The left part is removed to show the inner components. Abbr.: ba, basal articles of chelicerae; cc, cheliceral chamber; cg, cheliceral groove; co, condile; fc, food channel; fd, fixed digit; lb, labrum; lev, lever; LL, lateral lips; pg, pre-oral groove; st, stylet.

& de Lillo, 1989; 1991 b, c, d; Nuzzaci & Alberti, 1996; de Lillo *et al.*, 2001).

The subcapitular lips are not fused (figs 2-5, 7), while they are in Tetranychoidea (Blauvelt, 1945; Baker & Connell, 1963; Summers *et al.*, 1973; Hislop & Jeppson, 1976; Akimov & Yastrebtsov, 1981; André & Remacle, 1984; Lindquist, 1985; Alberti & Crooker, 1985; Nuzzaci & de Lillo, 1989; 1991b, d; de Lillo *et al.*, 2001) and Tarsonemidae (Nuzzaci *et al.,* 2002); however they develop an interlocking system (fig. 4) similar to the one described for *P. major* (Nuzzaci & de lillo, 1991a; Di Palma, 1995; de Lillo *et al.*, 2001). Moreover, a mesial furrow accomodates the labrum whose morphology is adapted to seal distally the pre-oral groove (figs 5, 7). The cheliceral chamber (figs 6, 10, 12, 20) housing the stylets and the labrum is homologous to the supralabral cavity described in *P. major* (Nuzzaci & de Lillo, 1991a; de Lillo *et al.*, 2001). In *Tydeus* the cheliceral chamber is completely separated from the food channel; so, the stylet activity evidently is not connected with fluid ingestion realized by the pre-oral groove and the food channel. The morphology of the food channel is peculiar in that it is not closed dorsally by the labrum (as usually in most of other groups) but its dorsal walls are fused instead and the labrum lies on them.

The sensory structures observed in *Tydeus*, are connected to the same components as reported for other prostigmatic mites (Alberti & Crooker, 1985; Nuzzaci & de lillo, 1989; 1991 b, d; Nuzzaci *et al.*, 1992; Nuzzaci & Alberti, 1996; de Lillo *et al.*, 1996; de Lillo *et al.*, 2001). There are mechanoreceptors related to the ventral setae on the lateral lips (figs 6, 9, 12) and a putative proprioceptor connected to the tendon inserted on the pharyngeal dorsal wall (fig. 15). Moreover, chemoreceptors present at the level of the pre-oral groove (figs 5-6, 8-9, 11-12, 16), in the stylets (figs 3-10, 12, 18-19) and in the pharyngeal chamber (fig 17), are involved in food selection.

Finally, according to the previous comparison, the functional morphology of the lateral lips, fixed digits, pre-oral groove and labrum indicate that the mouthparts of *Tydeus* are more similar to the ones of *P. major* compared to the other Prostigmata described. The stylets are shorter than in *P. major* and more similar to *T. nodosus*; so as the presence of a cheliceral groove and a furrow at the level of fusion of lateral lips with the subcapitulum that reminds of the inferior oral commissure, show some homologies with the Tetranychoidea.

Anyway, a detailed comparison among different genera of the Tydeidae family is necessary in order to better understand the evolutionary trend in this group and in other related taxa.

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RIASSUNTO

Studio ultrastrutturale e funzionale delle parti boccali di un acaro appartenente alla famiglia Tydeidae

È stato realizzato uno studio morfologico e funzionale delle parti boccali in un acaro Tideide. Il subcapitulum ed i segmenti chelicerali, pur essendo morfologicamente strutturati per aderire gli uni agli altri, non si presentano fusi a costituire una capsula gnatosomatica; le labbra laterali presentano, lungo la loro superficie adorale, un sistema di solchi e creste che consente loro di coaptarsi.

Il solco perorale si presenta coperto dal labrum solo distalmente; più prossimamente diventa invece un vero canale delimitato dorsalmente da pareti. Pertanto il labrum sembra coinvolto principalmente nella funzione di mantenere in posizione gli stiletti e coprire il solco perorale solo nel tratto distale.

La morfologia esterna dei digiti fissi e dei segmenti basali dei cheliceri consente loro di aderire alle labbra laterali e l'un all'altro nella regione adorale; non si ha la presenza di uno stiloforo. I digiti mobili sono stilettiformi, ciascuno di loro si articola prossimamente ad un lever la cui rotazione consente la protrusione e retrazione degli stiletti stessi con perforazione dei tessuti o del substrato alimentare.

La pompa faringeale, collegata al canale alimentare, consente l'aspirazione dell'alimento.

Infine alcune strutture sensoriali connesse alle parti boccali sono state osservate e descritte.

Parole chiave: stiletti, gnatosoma, digito fisso, lever, labrum, morfologia funzionale.

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