

COMPARATIVE AND FUNCTIONAL MORPHOLOGY OF THE GNATHOSOMA OF *TETRANYCHUS URTICAE* (ACARI : TETRANYCHIDAE)

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TETRANYCHIDAE
GNATHOSOMA
FUNCTIONS
ULTRASTRUCTURE

SUMMARY : The gnathosoma of *Tetranychus urticae* has been studied through light microscopy, S.E.M. and T.E.M. From a functional point of view, the study indicates that the chelicerae are a piercing-sucking structure ; the interlocked stylets are actively protracted but passively retracted. The pathway of food through the gnathosoma is redescribed accordingly. Comparative morphology reveals several new structures unique to Tetranychidae such as the cervical canaliculus and the prelabial and supralabral cavities. Descriptive terminology is standardized with that used for other mites.

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RÉSUMÉ : Le gnathosoma de *Tetranychus urticae* a été étudié en microscopie photonique ainsi qu'en microscopie électronique à balayage et à transmission. D'un point de vue fonctionnel, les chélicères sont des organes piqueurs-suceurs dont les stylets s'emboîtent, se dégagent activement mais se rétractent passivement. Les voies de passage des substances alimentaires au travers du gnathosoma sont redécrites. La morphologie comparée met en évidence de nouvelles structures propres aux tétranyques, comme le canalicule du cervix ou les cavités prélabiale et supralabiale. La terminologie descriptive est standardisée avec celle utilisée pour d'autres acariens.

A. INTRODUCTION

Although *Tetranychus urticae* is a major pest all over the world, the feeding mechanism of this mite is imperfectly understood at the present time. This paradoxical situation is due not only to the difficulty in observing spider mite feeding, but also to the misunderstanding of their morphology. As a result, different hypotheses have been advanced to explain their feeding mechanism and,

particularly, the function performed by the chelicerae. According to JEPPSON *et al.* (1975), scanning electron micrographs indicate that the only function of the chelicerae is to pierce the cell walls of host plants. AKIMOV & BARABANOVA (1977) agree with this hypothesis.

In opposition, SUMMERS *et al.* (1973) state that spider mites ingest through their exerted chelicer-al stylets which function together as a single, interlocked piercing-sucking structure when pro-

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tracted. However, such an attractive hypothesis needs more support. Indeed, it supposes that :

- a. cheliceral stylets fit together **to form a food channel** ;
- b. distally, the food channel **ends in a hole** through which plant cell contents are sucked up ;
- c. proximally, the food channel is **connected with the pharynx** which acts as a pump.

While point a is strongly suspected, points b and c are not yet demonstrated.

Lastly, a third hypothesis relative to stylet function is suggested by HISLOP & JEPPSON (1976) who suspect that salivary secretions might pass through the chelicerae ; this requires, in addition to points a and b above, that the channel formed by the stylets is connected proximally to a gland system.

Misunderstandings relating to cheliceral function are due, it would appear, to lack of comparative morphological data. Despite its apparent simplicity, the gnathosoma of mites represents a highly evolved and specialized body region when compared to the homologous parts of more primitive arachnids, particularly from the standpoint of mouthpart displacement. Lack of a standard interpretation has led to the use of a special terminology peculiar to Tetranychidae and makes any homology with other mites difficult and confused.

The purpose of this paper is twofold : first, to study the functional morphology of the tetranychid gnathosoma and to deduce whether piercing and ingestion occur concomitantly (piercing-sucking function of chelicerae) or alternately (piercing hypothesis) ; second, to approach the comparative morphology of the tetranychid gnathosoma in relation to that of other actinedid mites (especially Tydeidae, Stigmaeidae, Caeculidae...) and to standardize the descriptive terminology with that proposed by HAMMEN (1968, 1976) and COINEAU (1974).

B. MATERIAL AND METHODS

Observations are based on albino (white-eyed) *Tetranychus urticae* adults obtained from the permanent rearing of the animal ecology laboratory.

1. Photon microscopy and transmission electron microscopy.

Some mites were cleared in cold lactic acid and stained with black chlorazol for observation *in toto* as suggested by COINEAU (1974). After section of their posterior part, other mites were fixed into 2.5 % glutaraldehyde in 0.1 M phosphate buffer (pH 7.2) for 1h. After washing in 0.1 M phosphate buffer, they were postfixed for 1h in 1 % osmium tetroxide in the same buffer, and dehydrated through a graded series of ethanol. All steps were performed at room temperature. The tissues were embedded in epoxy resin (Epi-kote). Semi thin sections were stained with toluidine blue (0.5 % in sol. aq. sodium tetraborate 1 %). Ultra thin sections were cut using a Reichert OMU II microtome, equipped with a Diatome diamond knife, and stained with uranyl acetate and lead citrate. The sections were observed in a Jeol JEM 100C electron microscope.

2. Scanning electron microscopy.

After the same fixation procedure as for transmission electron microscopy, the animals were dehydrated through a graded series of acetone, dried in a Balzers critical point drying apparatus, coated in a Balzers metal sputtering apparatus equipped with a gold electrode, and observed in a Jeol JSM-35 electron microscope.

C. RESULT & DISCUSSION

1. Morphology of the cheliceral segment.

Fundamentally, the cheliceral complex comprises a small cheliceral frame with the cheliceral sheath (CX) and the two-segmented chelicerae

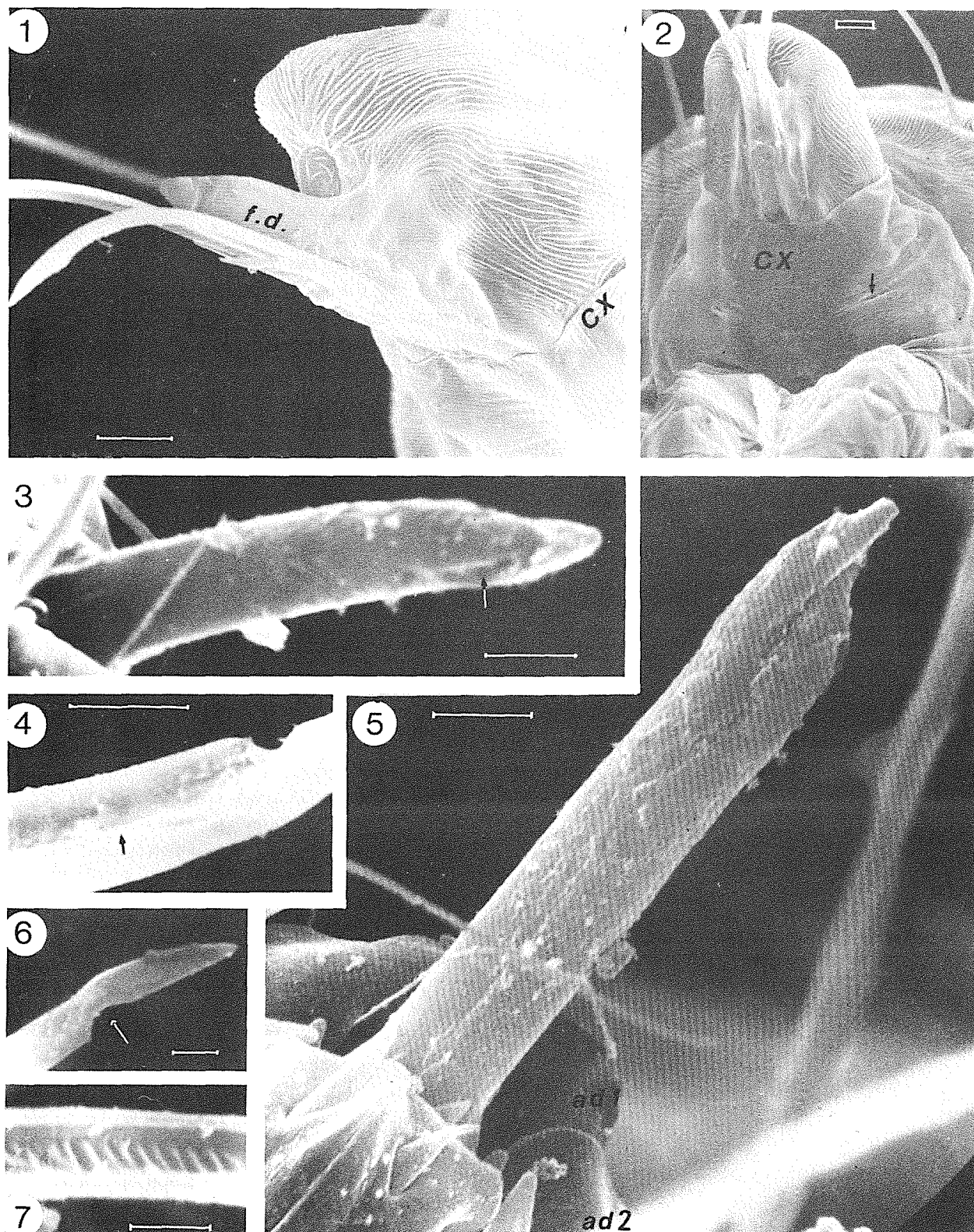


FIG. 1-7 : The gnathosoma of *Tetranychus urticae*.

1 : Lateral view of the cheliceral segment. — 2 : Front view of the cheliceral segment (the arrow indicates a stigma *sti*). — 3 : Interlocked stylets in latero ventral view showing the subterminal opening (indicated by the arrow). — 4 : Stylar notch communicating with the concave face of the stylet (the arrow indicates the matching groove). — 5 : Dorsal view of the stylets interlocked. — 6 : Ventral view of the tip of a stylet with the notch indicated by the arrow. — 7 : Concave face of a stylet (S.E.M. ; bar = 2 μ m, double bar = 10 μ m ; symbols : see appendix).

themselves. The cheliceral bodies — the so-called stylophore — are fused together in great part and only the cheliceral apoteles (*i.e.* the digitus mobilis) and vestiges of the fixed digits (*f.d.*) are free (Figs 1 & 2).

Originally, the respiratory system of Actinedida comprised four stigmata. A pair of slit-like stigmata (*sti*) still open ventrally into the subcheliceral epimeric furrow (Fig. 2). In Tetranychidae, another pair of stigmata (*st π*) opened paraxially between both chelicerae. Following the fusion, tracheal ducts extend by two closed taenidia which initially run up along the paraxial side of the chelicerae and form the vestibulum (*VS*) as in Tydeidae (Figs 13, 24). The vestibulum — the main tracheal trunk of BLAUVELT (1946) — is protected by a chitinous supporting structure, the sigmoid piece (*si.p.*), and terminates in a neostigma sheltered within the cheliceral sheath. Peritremes in Tetranychidae appear to function as extensions of the neostigma.

In addition to the sigmoid piece, the cheliceral body comprises another plate-like chitinous piece, the median septum (*ms*, fig. 13). From the forward part of the median septum two pairs of heavy muscles (the septal retractor muscles of stylophore, *srms*) run back and attach to the sigmoid piece.

The digitus mobilis is composed of the basal part (*b.p.*) and stylets (*ST*) (Fig. 24). The basal part is the vestige of the segment itself. As usual in other actinedid mites, this complex structure displays a bicondylar joint with the median septum and the outer wall of the “stylophore”. But the basal part of Tetranychidae is unique in two points :

- a) it is fused to the median septum through a small process *p* (Fig. 8) ; and
- b) instead of being bidesmotic, it bears only protractor muscles attached to projections from the anterior face (*ts*, figs 10, 11, 12).

The stylets themselves are directed posteriorly from the basal parts, curve sharply downward

and then forward to emerge ventrally from the cheliceral body. Each stylet is protected within a styler pouch (*s.p.* ; fig. 24) formed by an invagination of the outer cuticle. The styler pouch encloses and accommodates closely the entire loop of the stylets and cap their connection with the distal region of the basal parts (Figs 8-10).

The cross-section of stylets is crescent-like with central nerve fibers (*n.f.* ; figs 10, 20-22). The convex surface is oriented inward the loop. The paraxial border of the stylet bears a tongue which fits, at least in the distal region, into a matching groove (Fig. 4) running along the paraxial border of the right stylet. When protracted, both cheliceral stylets are thus tongued distally (Figs 3, 5).

Rigidity of stylets is ensured by transverse “stiffeners” located at the bottom of their concave faces (Fig. 7). The concave face is connected with a subterminal notch (Figs 4, 6). When the stylets are interlocked, the concave faces form a channel opening distiventrally via a subterminal hole delineated by both notches (Fig. 3).

2. Morphology of the infracapitulum.

The infracapitular epimeron bears the 5-segmented palpi ; silk is excreted through the terminal palpal eupathidium (GRANDJEAN 1948, ROBAUX & GUTTIERREZ 1973), which is connected to a silk gland described in detail by ALBERTI & STORCH (1974) and MOTHES & SEITZ (1981).

Ventrally, the infracapitulum bears one pair of subcapitular setae and two pairs of adoral setae, *ad1* and *ad2* (Figs 16, 17) ¹. Lastly an aperture, called the “rostral fossette” by SUMMERS *et al.* (1973), opens behind the adoral setae (Fig. 17) ; it is internally connected to the pharynx (*P*) through a constricted ductule and is nothing other than the inferior oral commissure, *Ji* (Figs 15, 24). However, the lateral lips (*LL*) are fused ventrally and no commissural line is visible anterior to the inferior commissure.

The cervix (*CE* ; figs 16, 18), *i.e.* the dorsal face of the infracapitulum is unique and quite different from the usual pattern found in Tydeidae,

1. The so-called “flaps” or “lobes” ; their setal nature is easy to verify with light microscopy.

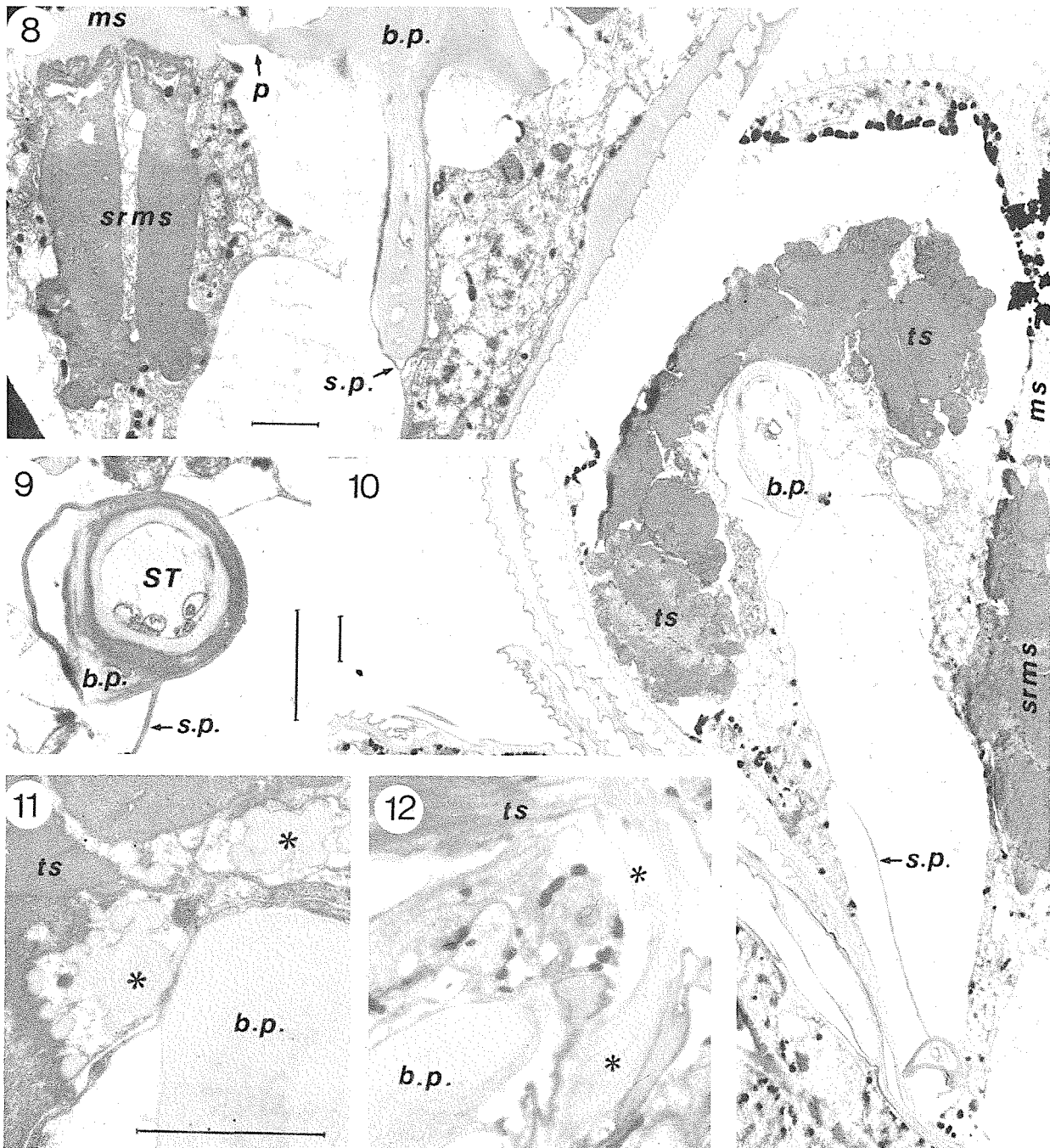


FIG. 8-12 : The gnathosoma of *Tetranychus urticae*.

8 : Cross section through the cheliceral segment. — 9 : Cross section through the connection between the stylet and the basal part. — 10 : Cross section through the cheliceral segment. — 11 : Cross section through the basal part. — 12 : Longitudinal section through the basal part. Asterisks indicate projections of the basal part (T.E.M. ; bar = 2 μ m ; symbols : see appendix).

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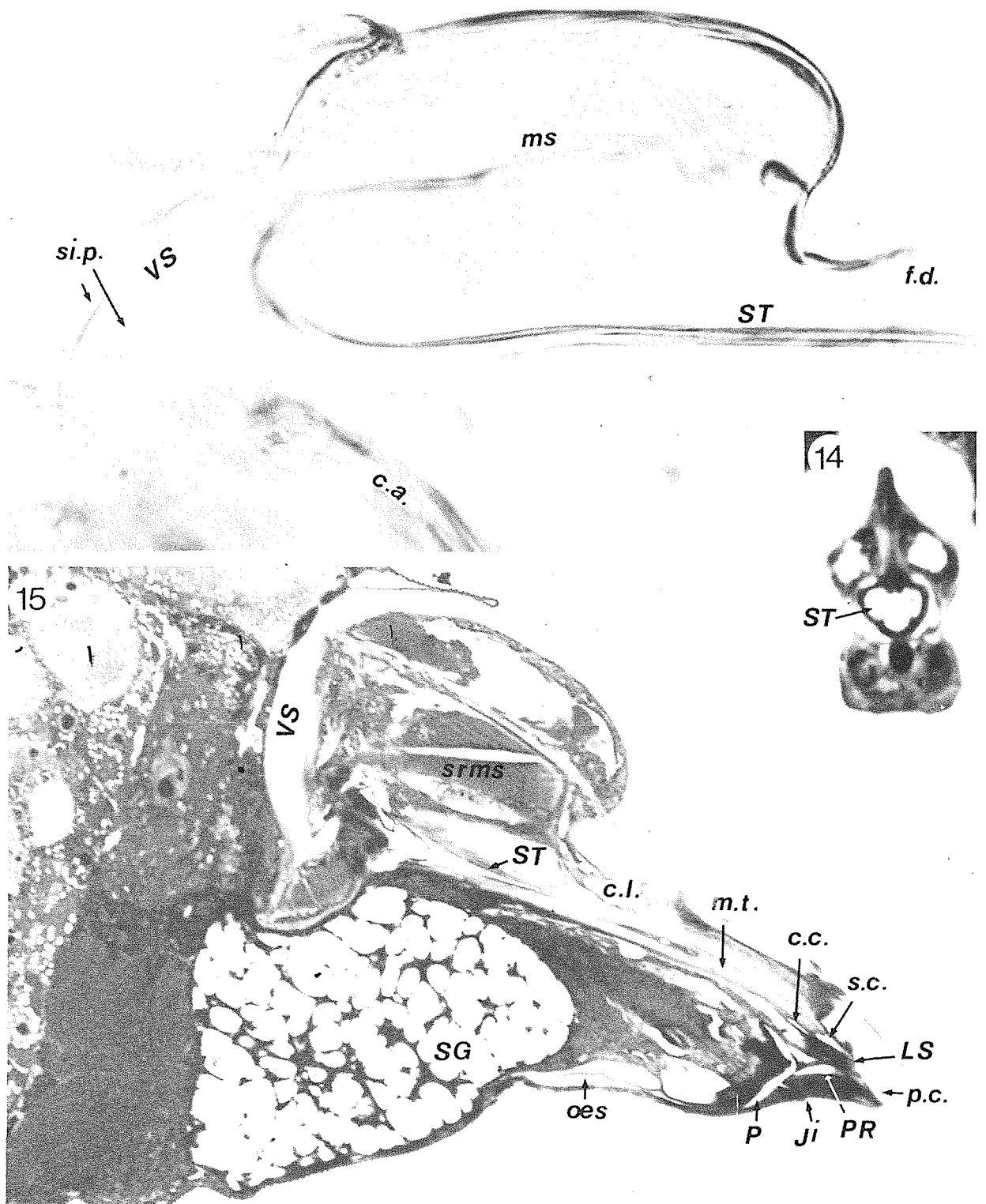


FIG. 13-15 : The gnathosoma of *Tetranychus urticae*.

13 : Cheliceral segment colored with black chlorazol (median plane focused). — 14 : Cross section through the tip of the infracapitulum showing the stylets interlocked in the prelabial cavity. — 15 : Median section through the gnathosoma (Light microscopy ; symbols : see appendix).

Stigmaeidae, and Caeculidae. Usually, the cervix comprises a convex median part, called the capitular saddle, bordered by two longitudinal depressions, the cheliceral grooves, in which the chelicerae rest. In Tetranychidae, the cervix, the labrum and even the mouth are deeply recessed; they are covered by the large lateral ridges of the infracapitulum as if the ridges had expanded upward and inward over the labrum and cervix. As a result, large lateral ridges of the infracapitulum form two elevated lips, the capitular lips (*c.l.*; figs 16, 22), which stand appressed against one another on the median plane over the cervix.

At the bottom of the subcheliceral furrow, both podocephalic canals (*cpc*, fig. 24) run along the line of attachment of the cheliceral frame to the infracapitulum and meet on the median plane. From the junction arises a new median taenidium (*m.t.*)² running down to the labrum base (Figs 18, 20-22); its content seems similar to the fine granular material observed in the podocephalic canals. Parallel to the median taenidium but beginning more distally are two lateral taenidia which serve as a sheath for the stylets (Figs 20-22). These stylar taenidia (*s.t.*) are longer than the median taenidium and extend on each side along the labrum (Fig. 18). The 3 taenidia are closely associated (Fig. 23) and are supported and surrounded by a special apodeme, vertebra-like in cross section, the cervical apodeme (*c.a.*) (Fig. 22).

The mouth, *i.e.* the opening of the pharynx delimited by the 3 commissures, is preceded by a special system formed by the fused lateral lips, the capitular lips and the labrum, and composed of three cavities — the prelabial, supralabral and preoral. The prelabial cavity (*p.c.*) is unique to Tetranychidae; it is anterior to the labrum and formed by the lateral and capitular lips and opens through the prelabial opening, the so-called mouth, bordered by adoral setae. Posterior to the prelabial cavity are two cavities separated horizontally by the labrum (*LS*). The upper one, *i.e.* the supralabral cavity (*s.c.*), corresponds to

the extension of the stylar taenidia, while the lower part is the preoral cavity or propharynx (*PR*). The preoral cavity is the space delimited by the three oral lips and is similar to that described in Tydeidae and Stigmaeidae (Figs 15, 23). This means that the chelicerae do not pass through the real mouth or through the propharynx. The labrum (*LS*) is a complex structure actuated by muscles (*l.m.*) and displays different coaptation systems as the ball-and-socket joint indicated by the asterisk in figure 19. Just behind the base of the labrum and at the end of the median taenidium opens a canaliculus running backward under the median taenidium — the cervical canaliculus (*c.c.*; figs 15, 19, 24).

3. Functional morphology.

The infracapitulum and the cheliceral segment are closely related and must be considered together from a functional point of view.

Functioning of the chelicerae raises some interesting points. The first one concerns the mechanism governing the exertion and retraction of chelicerae. An analogy with a brake cable may help to clarify their movement. As with the cable, chelicerae are encased and slide into a sleeve formed by the stylar pouches, stylar taenidia and lastly the supralabral and prelabial cavities. Rigidity of the sleeves is ensured by “stiffeners” plates (*pl*, fig. 20) and by the cervical apodeme (*c.a.*; figs 20-24), and likely strengthened by the palpi and their calcaria which form a collar around the tip of the infracapitulum (Fig. 17). As with a brake cable, exertion is active while retraction is passive. Exertion is ensured by protractor muscles (*ts*) as in other mites; this exertion may be facilitated by a shortening of the gnathosoma following the contraction of the septal retractor muscles of the stylophore (*srms*; figs 15, 24). Retraction of chelicerae must be passive as no retractor muscles exist; the small process relating the basal part of stylets to the median septum, as well as the chelicerae

2. Sometimes improperly called podocephalic canal. The podocephalic canal is a fundamental feature in most Actinotrichida (Acariformes), but the median taenidium is unique in Tetranychidae.

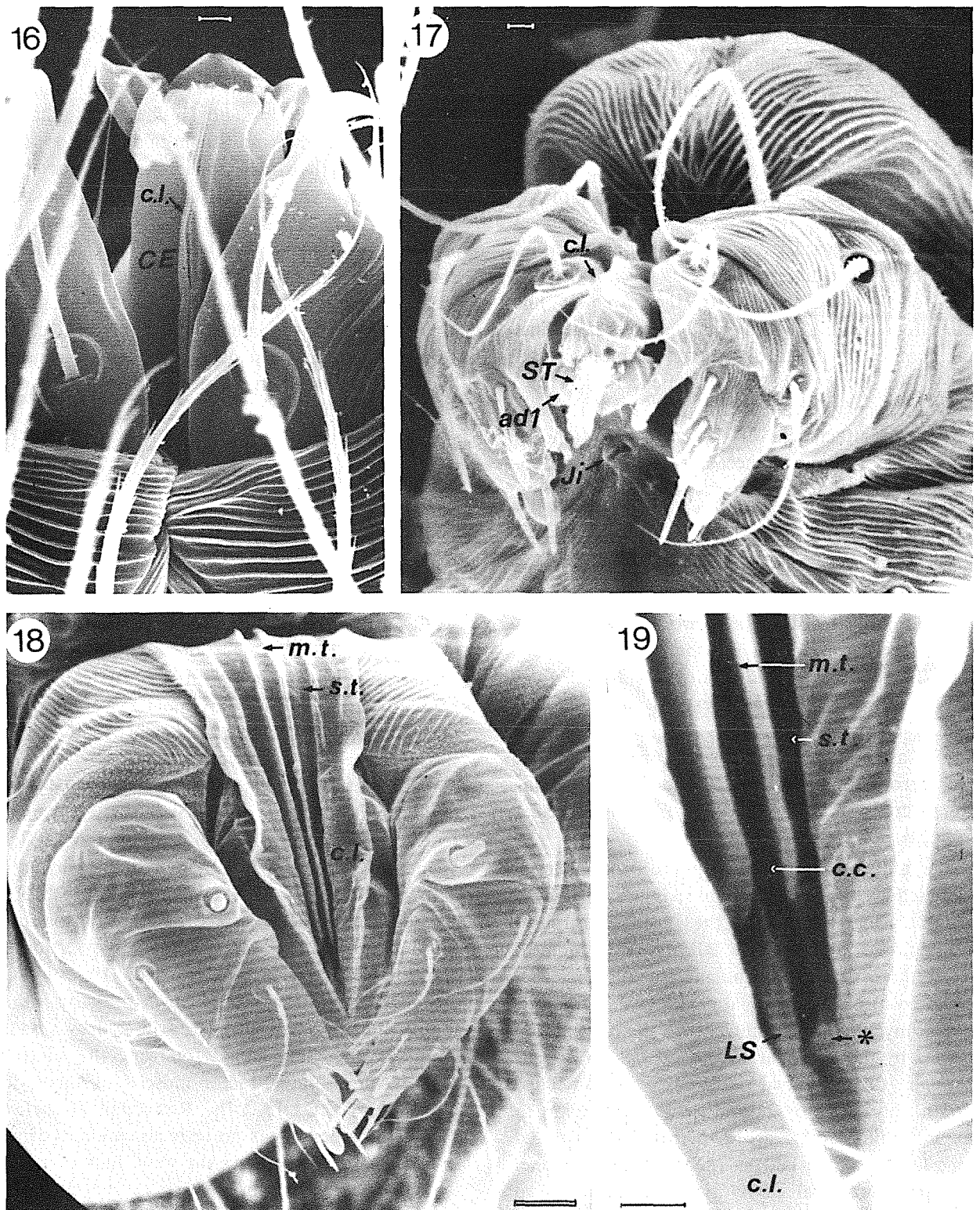


FIG. 16-19 : The gnathosoma of *Tetranychus urticae*.

16 : Tip of the cervix in dorsal view. — 17 : Front view of the gnathosoma. — 18 : Cervix with the capitular lips drawn aside. — 19 : Tip of the cervix and the supralabral cavity with the capitular lips drawn aside (S.E.M. ; bar = 2 μ m, double bar = 10 μ m ; symbols : see appendix).

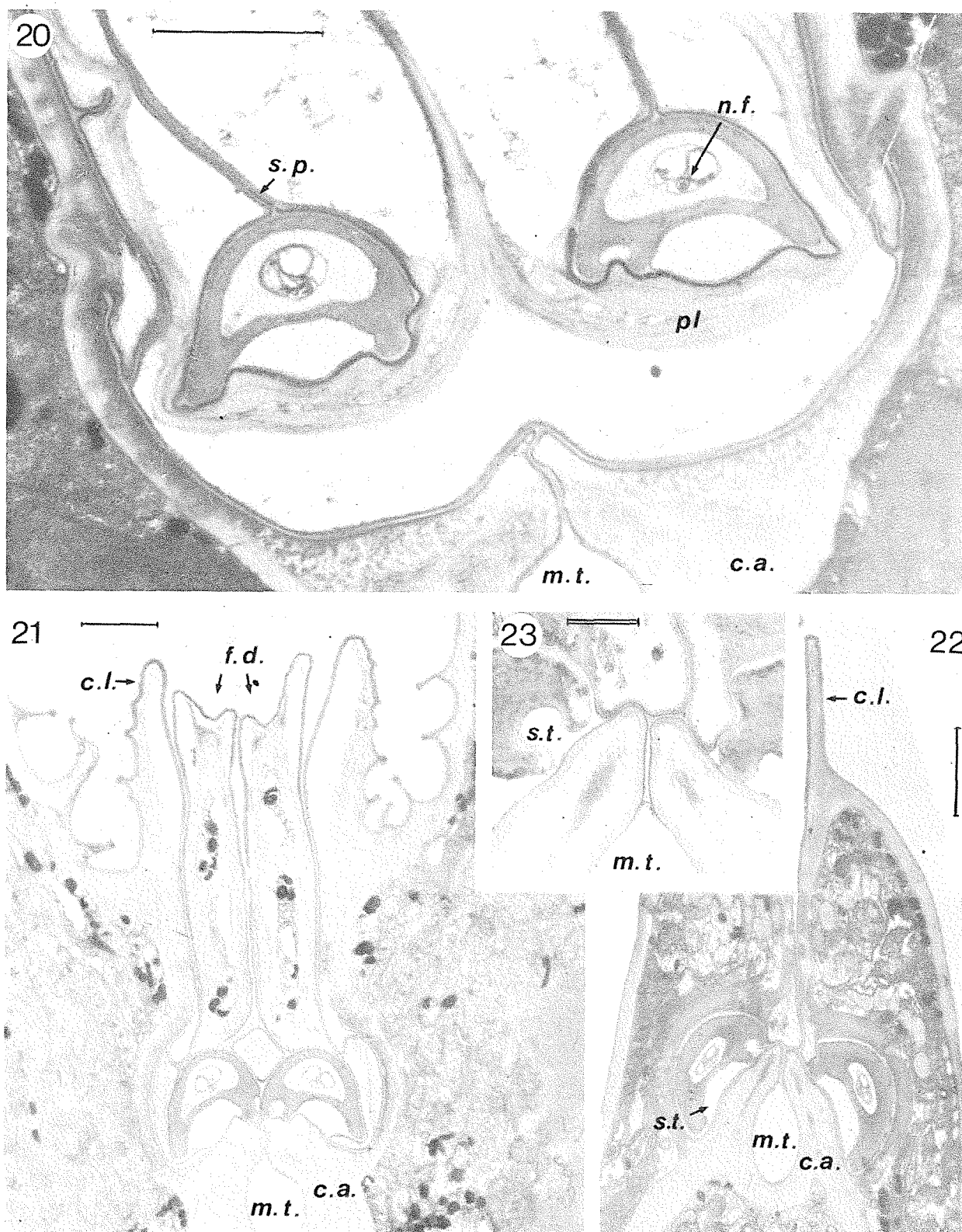


FIG. 20-23 : Cross sections through the gnathosoma displaying the relationships between the cheliceral segment and the infracapitulum. Locations of the successive sections are indicated in figure 24 (T.E.M. ; bar = 2 μ m, double bar = .5 μ m ; symbols : see appendix).

themselves — whose cross section is crescent-like and which are round up at rest —, play the role of a pull-back spring.

The second point concerns the function performed by chelicerae. The presence of cheliceral notches which communicate with the concave stylet faces, and the fact that chelicerae fit together in such a way as to form a channel opening through a subterminal hole, clearly indicate that plant cell contents are sucked up via the cheliceral channel. Thus, the stylets are real piercing-sucking structures.

These findings make possible a description of the pathway of food through the gnathosoma and a definition of the role played by the labrum. Liquids are sucked up via the cheliceral channel to the prelabial cavity where the stylets are no longer interlocked. When the labrum is pressed against the dorsal wall of the supralabral cavity and into the concave face of stylets, cell contents enter the pharynx through the propharynx. In

opposition, when the labrum is pressed down, it obstructs the propharynx but allows the discharge of secretion from the median taenidium to the prelabial cavity. If an up and down movement of the labrum is assumed, then it may give rise to mixing of secretions and cell contents before they are sucked into the pharynx.

D. CONCLUSIONS

This study aimed to highlight some morphological features of the tetranychid gnathosoma, except the gnathosomatic gland system already described in detail by ALBERTI & STORCK (1974) and MOTHES & SEITZ (1981). Particularly, the function performed by the chelicerae has been investigated. The ultrastructure demonstrates the three points advanced in the introduction, *i.e.* that

- a) cheliceral stylets fit together in such a way as to form a food channel ;

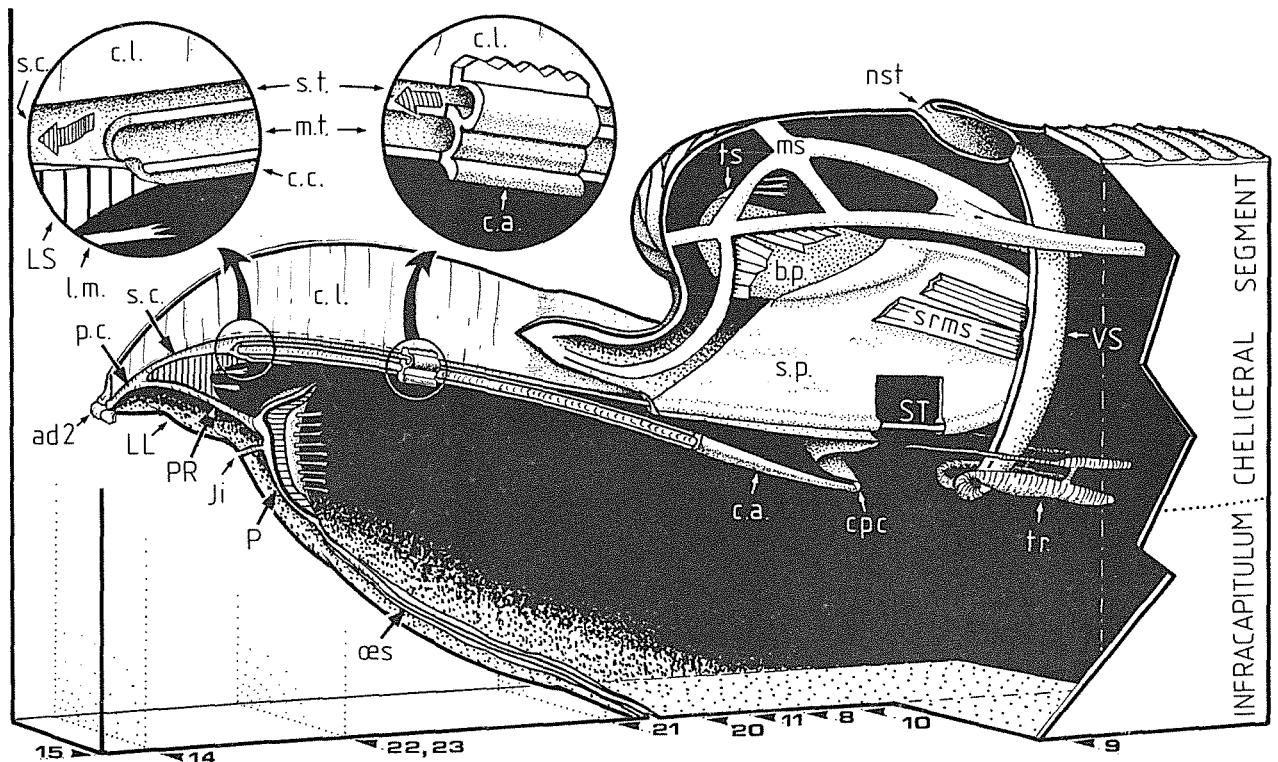


FIG. 24 : Three dimensional scheme drafting the major structures of the gnathosoma. Numerals refer to figures and indicate the location of sections. Arrows in both insets suggest the movement of stylets.

- b) distally, the food channel ends in a hole through which cell contents are sucked up ;
- c) proximally, the food channel is connected with the pharynx which acts as a pump.

This clearly indicates that the chelicerae not only comprise a piercing organ but really form a piercing-sucking structure, the functioning of which is special (active protraction but passive retraction). So far, these three points have not been observed or clearly demonstrated in other mites equipped with stylet-like chelicerae (see e. g. HALLAS 1982, PARAN 1982).

The hypothesis advanced by HISLOP & JEPPSON (1976) that salivary secretions might pass through the chelicerae into the plant leaf is not supported by our observations. In particular, it seems difficult to understand how secretions from the median taenidium could pass into the plant through the cheliceral channel in the absence of a pump analogous to aphids' "salivary pump". In addition, if toxins or any other substances were injected into plant tissues through the chelicerae, viruses might also be injected during feeding ; no experimental evidence of such a transmission is offered (OLDFIELD 1970) ³.

From a comparative point of view, the overall structure described in other mites (Actinedida and Oribatida) can be recognized although considerable modifications have occurred. These modifications entail both the disappearance of some structures (as the retractor muscles of the stylets) and the formation of new structures (as the taenidia on the dorsal face of the cervix, or the capitular lips which delimit in part the supralabial and prelabial cavities), unique to the Tetranychidae. All these modifications are highly apomorphic characters — and not primitive features as suggested by HALLAS (1982) — which entail a special pathway of food and determine the feeding mechanisms.

The function performed by some structures must still be elucidated, as that of the cervical canaliculus and of the inferior commissure. How-

ever, the fundamental feeding mechanism of the spider mites is now well understood. This is a prerequisite to a proper description of the damage caused by Tetranychidae, and to establishing a real understanding of the plant-mite relationship.

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APPENDIX :

List of notations and symbols

ad1, ad2 : adoral setae
b.p. : basal part
c.a. : cervical apodeme
c.c. : cervical canaliculus
CE : cervix
c.l. : capitular lips
cpc : podocephalic canal
CX : cheliceral sheath
f.d. : fixus digitus
Ji : inferior oral commissure
LL : lateral lips
l.m. : labrum muscles
LS : labrum
ms : median septum
m.t. : median taenidium
n.f. : stylet nerve fibers
nst : neostigma
p : small process through which the basal part is fused to the median septum
P : pharynx
p.c. : prelabial cavity
pl : plate
PR : propharynx
s.c. : supralabral cavity
si.p. : sigmoid piece
SG : silk gland
s.p. : stylar pouch
srms : septal retractor muscles of stylophore
ST : stylets

3. This does not mean that the mite stylets could not carry a virus present on the leaf surface into the plant as suggested by THOMAS (1969).

s.t. : stylar taenidia
sti : inferior stigmata
st π : paraxial stigmata
tr : trachea
ts : upper tendons of an apotele and their muscles
VS : vestibulum

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