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Comparative and functional morphology of the mouthparts in larvae of Parasitengona (Acariformes)*

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Abstract

Anatomy and ultrastructural organization of the larval mouthparts in representatives of terrestrial (Trombiculidae parasitizing vertebrates and Microtrombidiidae parasitizing arthropods) as well as aquatic (Pionidae and Hydrodromidae parasitizing arthropods) families from the cohort Parasitengona were studied using whole-mount preparations, semi-thin sections and TEM and SEM methods. In these groups, the organization of the mouth apparatus differs significantly especially with regard to their particular functional specialization and adaptations reflecting evolutionary trends in these groups. In trombiculid larvae, the mouthparts reveal the simplest organization. The gnathosoma is totally free, the infracapitulum and the basal cheliceral segments are short and wide, and the latter are separated from each other. The flexible lateral lips form a temporary sucker, distinguishable when the larva feeds, and the pharynx is totally fused with the bottom of the infracapitulum. In microtrombidiid larvae, the gnathosoma is covered by the arched dorsal shield, the chelicerae are comparatively long and separated, and the lateral lips form a permanent sucker provided with an internal sclerite. Conversely, in water mite larvae, the chelicerae are fused together and either partially (*Piona carnea*) or totally (*Hydrodroma despiciens*) free from the overhanging idiosomal fold. The lateral lips are flexible and organized freely, and the pharynx is totally separated from the bottom of the infracapitulum. In general, water mite larvae show significant variations and specializations but at the same time seem to possess the most plesiomorphic characters in organization of the mouth apparatus. The ancestral parasitengone may have given rise to divergent groups of water mites as such, as well as to trombiculids with the secondary simplification of the mouth apparatus and to microtrombidiids with their particular additional adaptations and specialization in organization of the mouthparts.

Keywords: Actinotrichida, Parasitengona, Trombiculidae, Microtrombidiidae, Pionidae, Hydrodromidae, mouth apparatus, anatomy, TEM and SEM morphology.

Introduction

Larvae of acariform mites are of significant interest in respect to their evolution and particular adaptations in the course of ontogenesis (Mitchell, 1957). Within this group, larvae of the cohort Parasitengona are characterized by strong heteromorphism in comparison with deutonymphs and adults and possess wide biological diversity. They are highly specialized parasites of a wide spectrum of both invertebrates, in particular insects, and vertebrates.

Nevertheless, larval forms of Parasitengona are still poorly investigated in general, and especially with respect to detailed functional morphology of their mouthparts. Larvae of these mites have been studied mostly on light-optical whole-mount preparations (Henking, 1882; Jones, 1950; Wharton, 1946; Vainstein, 1963, 1966, 1976) and rarely on histological sections (Witte, 1978). With the exceptions of trombiculid and microtrombidiid larvae studied by me with SEM (Shatrov, 1981, 2000, 2001a, b), no data are available on the detailed TEM and SEM morphology of larvae of different groups of Parasitengona.

To fill this gap in our knowledge, the anatomy and ultrastructural organization of the mouthparts in larvae of some terrestrial and water mite families were studied in detail with special attention to their probable functions.

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Materials and Methods

Larvae of the following species were used in this study.

Terrestrial mites – (a) Trombiculidae (vertebrate parasites): *Leptotrombidium orientale* (Schluger, 1948), *Leptotrombidium pallidum* (Nagayo, Mitamura & Tamiya, 1916), *Neotrombicula pomeranzevi* (Schluger, 1948), *Hirsutiella zachvatkini* (Schluger, 1948), *Euschoengastia rotundata* (Schluger, 1955), *Kepkatrombicula desaleri* (Methlagl, 1928); (b) Microtrombidiidae (arthropod parasites): *Platytrombidium fasciatum* (C. L. Koch, 1836), *Camerotrombidium pexatum* (C. L. Koch, 1837).

Water mites – (a) Pionidae (arthropod parasites): *Piona carnea* (C. L. Koch, 1836); (b) Hydrodromidae (arthropod parasites): *Hydrodroma despiciens* (Müller, 1776).

Trombiculid larvae were obtained both when feeding on and when crawling off their natural hosts (voles) and mostly from a laboratory colony (first laboratory generation) initiated from fully fed larvae dropped off their natural hosts captured in different regions of the Russian Federation. Unfed larvae of *L. pallidum* were kindly sent to me by Dr. M. Takahashi (Kawagoe Senior High School 2-6 Kuruwa-machi Kawagoe-shi, Saitama, 350-0053 Japan) and larvae of *K. desaleri* feeding on their natural host, chamois [*Rupicapra r. rupicapra* (L.)], were kindly sent by Dr. S. Rehbein (Merial GmbH, Kathrinenhof Research Center, Rohrdorf, Germany).

Microtrombidiid larvae were obtained from females collected from the soil surface in Leningrad Province in spring-summer period from 1996 to 2003. Approximately two weeks after capture, females began to lay eggs, from which active larvae hatched around two weeks later. Identification of adult mites was kindly done by Dr. J. Mąkol (Institute of Biology, Wrocław University of Environmental and Life Sciences, Poland).

Egg masses of the water mite species studied were obtained from females by Dr. P.V. Tuzovskiy (Institute of Biology of the Internal Waters RAS, Borok, Russia); these were collected in Yaroslavl Province in spring period from 2000 to 2004. Egg masses and hatched larvae were then kindly sent to me for investigation.

For preliminary and general observations, semi-thin sections were stained with toluidine blue and methylene blue and investigated and photographed in Amplival and Leica DM LS-2 light optical microscopes. Whole larvae were also embedded in Hoyer-Berlese solution and examined with light-optical microscope using phase-contrast method.

For SEM study, larvae were washed in alcohol series and cleaned in ultrasonic cleaner for 3–4 min. Larvae were then dried at the critical point of carbonic acid in a Hitachi HCP-2 vacuum evaporator, or were treated with hexamethyldisilazane (HMDS) for 5–10 min as an alternative method to critical point drying for maintaining the natural shape and size of the mite's body. Immediately after these procedures, larvae were covered with a platinum layer in an Eiko IB-5 apparatus and examined with SEM Hitachi S-570 and Hitachi TM-1000 at 20 and 15 kV respectively.

For TEM examinations, larvae were initially fixed in 2–2.5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.2–7.4) for 2–6 h or more. After immersion of mites into the fixative fluid, their integument was carefully pierced through with tiny insect pins for a better penetration of the fixative, but some larvae were left intact. Mites were then washed in several changes of 0.2 M phosphate buffer, postfixed in 2% osmium tetroxide in 0.1 M phosphate buffer for 6 h to overnight, dehydrated in ethanol and acetone series, and finally embedded in an araldite mixture. Serial ultra-thin sections both in transverse and longitudinal planes were made on a LKB-III and Leica UC-6 ultramicrotomes. After staining with uranyl acetate and lead citrate, the sections were examined and photographed with Tesla BS-500 and LEO-900 transmission electron microscopes at 60–80 kV.

Results and Discussion

Significant contributions to our knowledge of the mouthparts organization in arachnids and, particularly, in Acari were published by Snodgrass (1948), van der Hammen (1980) and Alberti & Coons (1999). Terminology used for the description of the mouthparts in other studies is mostly based on these works. In the present study, I strongly follow the terminology proposed in the review of Alberti & Coons (1999).

Trombiculidae (Fig. 1A–G)

In trombiculid larvae, the mouthparts have the simplest organization. The gnathosoma is totally free from both the dorsal and the ventral aspects and is not inserted into the idiosomal body fold. The dorsal plate, scutum, is small and placed on the idiosoma. The infracapitulum and the basal cheliceral segments are short and wide, and the latter are totally separated from each other. The lateral portions of the malapophyses envelop the distal portion of the chelicerae, and, turning back, the lateral lips form mostly a temporary structure resembling a kind of sucker, which is apparently applied to the host epidermis when the larva is feeding, helping it in sucking the liquid food. Such an organization of the lateral lips was found, for instance, in *N. pomeranzevi*, *H. zachvatkini* and *L. orientale*. The movable digits are protruded and hooked upward in active condition and retracted and hidden within the stretched forward sleeve-like lateral lips when the larva is not feeding.

In contrast to the above mentioned species, in *K. desaleri*, which feeds on large animals including humans, the lateral lips are found to form a soft permanent sucker disk with a median vertical slit through which the movable digits protrude. The application of the sucker disk to the stratum corneum of the host epidermis (chamois) and thus isolation of the preoral cavity from surrounding air that allows for a more secure vacuum is thought to provide an additional pumping effect for engorgement of the liquid food through the long stylostome that may extend deep into the dermis.

However, both temporary and permanent sucker disks are not complex structures, although the latter may be classified as an apparent evolutionary acquisition among trombiculids. It should be noted however that each of these types of 'suckers' is a passive structure without any additional rigid or contractive elements, and the clinging effect is expected to be a result of: (1) tight application of this structure to any surface and (2) removal of air from underneath it. Close application of this structure to the skin surface can be the result of the pressure in the adjacent haemocoelic space, turning the sucker rigid, while removal of the air between the surface of the sucker and the surface of the host can be done by the action of the pharyngeal pump.

The labrum is a thick but weakly sclerotized cuticular 'rod' that protrudes into the preoral cavity. It is quite characteristic that in *L. pallidum* a cuticular 'bridge' overhanging the bottom of the preoral cavity and connecting the internal walls of the lateral lips is found beneath the labrum. This structure fusing with the basal portion of the labrum forms the mouth—the entrance into the pharynx. The pharynx is totally fused with the bottom of the infracapitulum. For the most part, the cervix is a thin weakly sclerotized cuticular plate with a median thickened rod, becoming thick and sclerotized only at its base beneath the basal portions of the chelicerae. The pharyngeal dilator muscles originate on the sclerotized basal portion of the cervix and on the capitular apodemes. The pharynx possesses not only dilators but also small muscles, the constrictors (flexors) of the pharynx.

The short and stout sigmoid pieces serve for the origin of the powerful levators of chelicerae, muscles that insert onto the obliquely inclined posterior wall of the basal cheliceral segments. Retraction of the chelicerae and the gnathosoma is mediated by retractors originating on the posterior portions of the scutum and inserting on the posterior parts of the posterior walls of the basal segments and on the capitular apodemes.

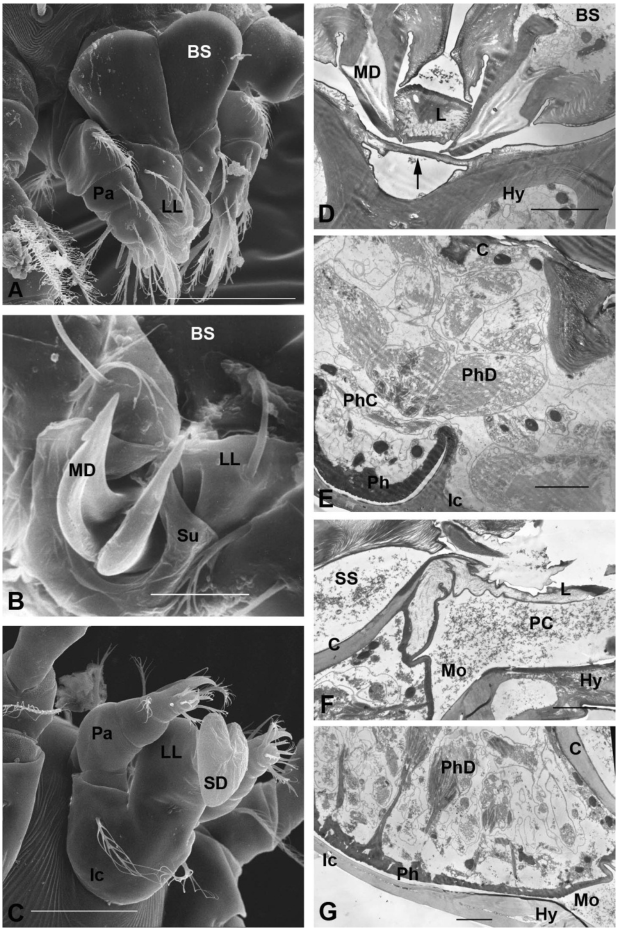

FIGURE 1 (A-G). Organization of the mouthparts in larvae of Trombiculidae. (A) Dorsal view of gnathosoma of *Hirsutiella zachvatkini*. SEM. Scale bar: 43 μm; (B) Frontal view of gnathosoma of *Neotrombicula pomeranzevi* with protruded movable digits and formation of a temporary sucker by the lateral lips. SEM. Scale bar: 20 μm; (C) Lateral view of gnathosoma of *Kepkatrombicula desaleri* showing the sucker disk. SEM. Scale bar: 38 μm; (D) Transverse section of gnathosoma of *Leptotrombidium pallidum* on the level of the basal portion of the labrum showing the movable digits and the lamina (arrow) between the internal walls of the malapophyses (hypostome). TEM. Scale bar: 5 μm; (E) Transverse section of gnathosoma of *L. pallidum* on the level of the middle portion of the pharynx. TEM. Scale bar: 5 μm; (F) Longitudinal section of gnathosoma of *L. pallidum* on the level of the labrum and the lateral thickened portion of the cervix. TEM. Scale bar: 5 μm; (G) Longitudinal section of gnathosoma of *L. pallidum* on the level of the pharynx. TEM. Scale bar: 5 μm.
BS—basal cheliceral segment; C—cervix; Hy—hypostome; Ic—infracapitulum; L—labrum; LL—lateral lips; MD—movable digit; Mo—mouth; Pa—palp; PC—preoral cavity; Ph—pharynx; PhC—pharyngeal constrictors; PhD—pharyngeal dilators; SD—sucker disk; SS—subcheliceral space; Su—temporary sucker.

Microtrombidiidae (Fig. 2A–G)

The gnathosoma is covered from above by a large arched dorsal shield, scutum (stolascutum, see Wohltmann *et al*., 2003), and mostly free from the ventral side. The lateral lips form a quite characteristic permanent apomorphic sucker (stephanostome, see Wohltmann *et al*., 2003; Gabryś *et al*., 2005) provided with an internal separate circular sclerite, lyre-like on longitudinal sections (Shatrov, 2011). This sucker possesses internal (smaller) and outer (larger) rings that are both provided with

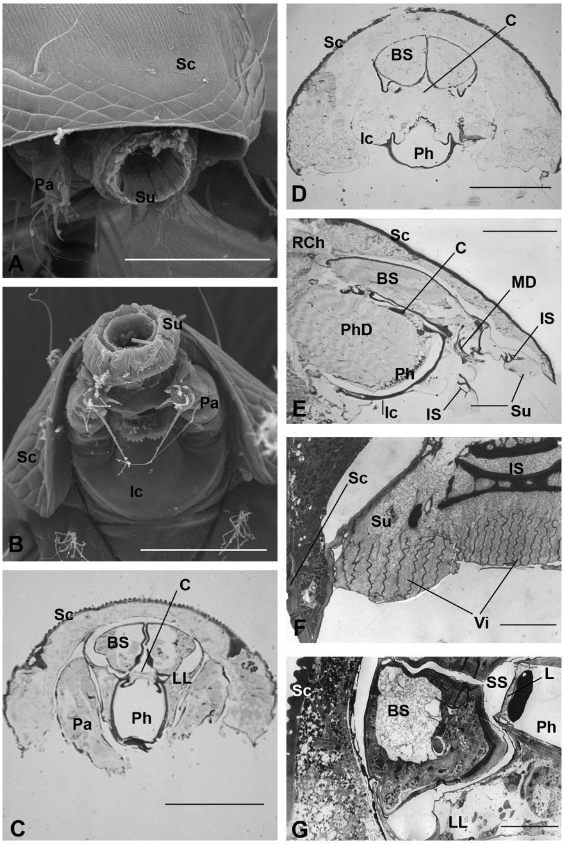

FIGURE 2 **(A-G).** Organization of the mouthparts in larvae of Microtrombidiidae. (A) Frontal and dorsal view on the frontal part of the body of *Camerotrombidium pexatum*, showing the large scutum and the sucker. SEM. Scale bar: 50 μm; (B) Ventral view of gnathosoma of *Platytrombidium fasciatum*. SEM. Scale bar: 50 μm; (C) Transverse section of gnathosoma of *P. fasciatum* on the level of the beginning of the pharynx. Semi-thin toluidine blue stained section. Scale bar: 30 μm; (D) Transverse section of gnathosoma of *C. pexatum* on the level of the middle portion of the pharynx. Semi-thin toluidine blue stained section. Scale bar: 30 μm; (E) Longitudinal section of gnathosoma of *C. pexatum* on the level of one of the chelicerae, showing movable digit. Semi-thin toluidine blue stained section. Scale bar: 30 μm; (F) Longitudinal section through the sucker of *C. pexatum*. TEM. Scale bar: 5 μm; (G) Transverse section of the gnathosoma of *P. fasciatum* on the level of the beginning of the pharynx. TEM. Scale bar: 5 μm.
C — cervix; BS — basal cheliceral segment; Ic — infracapitulum; IS — internal sclerite; L — labrum; MD — movable digit; Pa — palp; Ph — pharynx; PhD — pharyngeal dilators; RCh — retractors of chelicerae; Sc — scutum; SS — subcheliceral space; Su — sucker; Vi — villi.

finger-like projections on the external surface tightly opposed to each other. These structures are thought to help in tight adherence to the host epidermis and were not previously described on histological and TEM sections (Wohltmann *et al*., 2003; Gabryś *et al*., 2005).

The basal cheliceral segments are comparatively long and, as in trombiculid larvae, separated from each other. The movable digits of the chelicerae (cheliceral claws) are hook-shaped with the tips turned upward and always hidden within the malapophyses. The movable digits form an entrance into the preoral cavity by their inner groove. The labrum and the cervix delimit the pharynx and the subcheliceral space with the mouth located at the base of the labrum. For the most part, the labrum and the cervix are slender and weakly sclerotized cuticular plates and, as in trombiculid larvae, do not have own muscles.

The pharynx is extremely wide and, as in trombiculids, totally fused with the bottom of the infracapitulum. The pharyngeal dilators originate on the posterior sclerotized portions of the cervix and on the capitular apodemes and, in contrast to trombiculids, run nearly parallel to the cervix to their insertion onto the dorsal pharyngeal wall. Pharyngeal constrictors are lacking. Comparatively short, but longer than in trombiculids, sigmoid pieces serve as a place of origin of the levator cheliceral muscles inserting on the posterior wall of the basal cheliceral segments.

There are two sets of extrinsic gnathosomal muscles originating on the posterior portion of the scutum: retractors of the chelicerae, inserting on the posterior portions of the basal cheliceral segments, and retractors of the gnathosoma, inserting on the very posterior portions of the capitular apodemes.

Pionidae (Fig. 3A–H)

In larvae of *P. carnea*, the gnathosoma forms an angle of up to 90º with the long axis of the body, being inserted into the idiosoma by its basal portion. The basal cheliceral segments are long and, in contrast to trombiculid and microtrombidiid larvae, totally fused to each other. They are bent ventrad and widen at their bases. The basal cheliceral segments form a structure not seen in any of the other species examined in this study, totally fused flexible anterior projection, which protrudes forward between the movable digits. This projection is thought to be the fixed digits that are usually totally reduced in other groups of the Parasitengona (Witte, 1991; Alberti & Coons, 1999). The movable digits are always found in protruded position, with their tips strongly curved upward; each of them has an inner groove.

The flexible lateral lips do not form a sucker but are organized as a 'sleeve' composed of a folded flexible cuticle provided with several probably rigid teeth faced posterad. These lateral lips envelop the protruded movable digits and thus form an entrance into the preoral cavity. This portion of the mouth apparatus, looking like a real hypostome, is quite narrow, squeezed between the extremely large palps and provided with a characteristic ventral cuticular fork of unknown functions. The palps face downward and backward, and bear the large curved palpal claws on the tibia, turned laterad in opposite directions. The palp tarsus is small and hidden under the overhanging palp genu. The palp femur bears ventrally a characteristically wide spade-like projection opposite to the palpal claw. The projection appears to be provided with the own muscles originating on the dorsal wall of the femur.

Whereas the labrum is represented by a thick cuticular arrow-like structure protruding forward, the cervix is a thin weakly sclerotized plate and only at its base, just posterior to the bases of the basal cheliceral segments, becomes thick and sclerotized. The mouth apparatus of *P. carnea* is provided with a particular labral valve, projecting from the dorsal basis of the labrum forward into the preoral cavity. Besides this and in contrast with trombiculid and microtrombidiid larvae, the labrum is provided by characteristic small labral muscles originating on the particular cervical apodemes and running parallel to the cervix to the insertion onto the widened posterior portion of the labrum.

In contrast with trombiculid and microtrombidiid larvae, the pharynx in *P. carnea* is totally separated from the ventral wall of the infracapitulum but devoid of ventral dilators. Like the entire

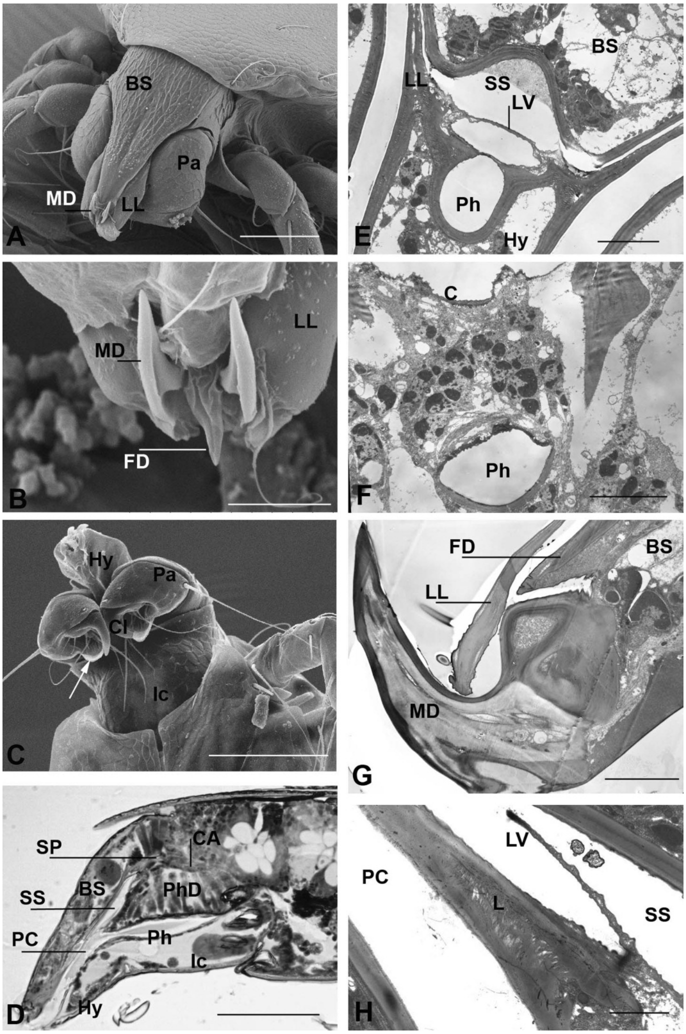

FIGURE 3 (A–H). Organization of the mouthparts in larvae *Piona carnea* (Pionidae). (A) Dorsal view of gnathosoma. SEM. Scale bar: 50 μm; (B) Dorsal and frontal view of the anterior portion of gnathosoma showing movable and fix digits. SEM. Scale bar: 10 μm; (C) Ventral view of gnathosoma showing palps and spade-like projections. SEM. Scale bar: 60 μm; (D) Longitudinal section of gnathosoma on the level of one of the chelicerae. Semi-thin toluidine blue stained section. Scale bar: 50 μm; (E) Transverse section of the gnathosoma on the level of the beginning of the pharynx. TEM. Scale bar: 5 μm; (F) Transverse section of gnathosoma on the level of the middle portion of the pharynx and the cervix. TEM. Scale bar: 5 μm; (G) Longitudinal section through the movable and fix digits. TEM. Scale bar: 5 μm; H—Longitudinal section through the labrum and the labral valve. TEM. Scale bar: 3 μm.

BS—basal cheliceral segment; C—cervix; CA—capitular apodeme; Cl—palpal claw; FD—fixed digit; Hy—hypostome; Ic—infracapitulum; L—labrum; LL—lateral lip; L—labral valve; MD—movable digit; Pa—palp; PC—preoral cavity; Ph—pharynx; PhD—pharyngeal dilators; SP—sigmoid piece; SS—subcheliceral space.

gnathosoma, the pharynx is also greatly inclined in relation to the axis of the body running to the posterior margin of the infracapitulum at large angle. The dorsal pharyngeal dilators originate on the short, thick and sclerotized basal portion of the cervix and, posteriorly, on the weakly represented capitular apodemes combined with ducts of the salivary glands. Due to the overall composition of the mouth apparatus and in contrast with trombiculid and, especially, microtrombidiid larvae, the pharyngeal dilators run not forward but straight downward and even backward from their origin on the cervix and capitular apodemes. Besides the pharyngeal dilators, the pharynx possesses ventral and lateral suspensions of connective tissue fibers.

The short sigmoid pieces serve for origin of the short powerful levator cheliceral muscles. Retraction of the chelicerae and retraction and inclination of the gnathosoma are mediated by several sets of powerful muscles—retractors of the chelicerae and retractors of the gnathosoma. All these muscles have their origin on different parts of the dorsal body wall and insert onto the posterior portion of the infracapitulum, the capitular apodemes and the basal cheliceral segments.

Joint actions of these muscles result in different inclination of the gnathosoma in relation to the long axis of the body.

Hydrodromidae

Larvae of *H. despiciens* were studied only by TEM methods. The gnathosoma is free and not inserted into the idiosoma by its base. Externally, the chelicerae are totally separated from each other and the apical portions of the lateral lips are only slightly bent laterad without forming a sucker. The palps are large, direct forward and with the long tarsus and the large palpal claw (the "thumb-claw" complex) bent ventrad against the distal portion of the hypostome, protecting it anteriorly.

Conclusion and Perspectives

Representatives of Erythraeoidea, Calyptostomoidea and Trombidiidae are not included in my study but I would like to think that the mites already examined represent a wide enough spectrum of the larval organization. Several possible transformation trends of Parasitengona larval mouthparts may be proposed depending on the starting point and taking into consideration that the groups studied share both primitive and derived characters. In general, water mite larvae show a significant variation and specialization of the mouth apparatus (Mitchell, 1957), but also seem to possess the most generalized plesiomorphic mouthparts (the presence of the fixed digit, the pharynx separated from the bottom of the infracapitulum), except for the fusion of the basal cheliceral segment in *P. carnea*. It seems likely that the ancestral parasitengone gave rise to divergent groups of water mites as such, as well as to trombiculids, with the secondary simplification of the mouth apparatus, and to higher microtrombidiids, with their particular additional adaptations and specialization in organization of the mouthparts such as permanent sucker.

However, several position concerning larval constitution and, in particular, mouth apparatus remain to be discussed, with special consideration to the following aspects:

1. Are larval forms primarily primitive and have evolutionarily developed afterwards into the more and more complicated recent mature organism, or, on the contrary, are larvae secondarily reduced (simplified), acquiring additional adaptations?
2. Are the mouthparts of trombiculid larvae secondarily reduced (simplified) and specialized, taking into consideration their highly specialized deutonymphs and adult forms, which live deep in the soil, or they are more primitive?
3. Which characters in the larval mouthpart organization should be considered as generalized and primitive and which should be considered derived and specialized?

4. In which way has the transformation of the mouthparts and other organs progressed in larvae and from larva to adult? What is the evolutionary distance between the recent larvae and adults in the same and in different groups? What are the ecological reasons for that?

The answers on these questions may be resolved with the use of modern experimental and phylogenetic methods combined with detailed traditional morphological approaches.

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