

DESCRIPTION OF MOUTHPARTS IN ADULT MITES OF *PLATYTROMBIDIUM FASCIATUM* (C.L. KOCH, 1836) (ACARIFORMES: MICROTROMBIDIIDAE) WITH A COMPARISON OF THOSE OF THE LARVAE

ОРГАНИЗАЦИЯ РОТОВОГО АППАРАТА ВЗРОСЛЫХ КЛЕЩЕЙ *PLATYTROMBIDIUM FASCIATUM* (C.L. KOCH, 1836) (ACARIFORMES: MICROTROMBIDIIDAE) И ЕГО СРАВНИТЕЛЬНЫЙ АНАЛИЗ С ЛИЧИНОЧНЫМИ ФОРМАМИ

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ABSTRACT

The mouthparts of adult mites of *Platytrombidium fasciatum* (C.L. Koch, 1836) (Acariformes: Microtrombidiidae) were examined using both light optical (mounted mites, toluidine blue stained semi-thin sections) and electron microscope (TEM, SEM) methods. The gnathosoma is formed ventrally by the wide gnathocoxal plate, extending forward as the cone-shaped hypostome without a conspicuous sucker, and dorsally by two-segmented chelicerae, each with a blade-like cheliceral claw (movable digit). The proximal portion of the gnathosoma is inserted into a camerostomal fold formed of the body wall. The voluminous subcheliceral space terminates posteriorly by the proximal chamber with characteristic sclerotization of its walls. Membranous bottom of the subcheliceral space bears the labrum anteriorly and the weakly expressed epistome posteriorly. The proximal chamber serves as a saliva reservoir. The labrum and the inner walls of the hypostome form the mouth leading to a crescent pharynx. The latter possesses dorsal dilators originating on the floor of the subcheliceral space and mostly on the lateral walls of the gnathocoxal plate and constrictors. The ventral pharyngeal wall is conspicuously separated from the gnathosomal bottom and has no ventral dilators. The main tracheal trunks are S-shaped in longitudinal sections and are connected with the proximal chamber through narrow channels. Posterior portions of the tracheal trunks have sclerotized walls and serve for origination of the extrinsic cheliceral muscles. The cheliceral apodemes are therefore expressed twice as the sclerotized elements behind the inner walls of the basal cheliceral segments and as the particular

sclerotization of the tracheal trunks. Laterally, the gnathosoma bears large 5-segmented palps. On the dorsal aspect of the tibia, there are two sclerotized claws. Such an organization of the mouthparts of adult microtrombidiid mites seems to be closely responded to the actinedid prototype and appears to be more generalized than the specialized mouthparts of the larvae.

РЕЗЮМЕ

Ротовой аппарат взрослых клещей *Platytrombidium fasciatum* (C.L. Koch, 1836) (Acariformes: Microtrombidiidae) был изучен с использованием как светооптических (целые заключенные клещи, полутонкие срезы), так и электронно-микроскопических (ТЭМ и СЭМ) методов. Гнатосома, несущая ротовой аппарат, образована снизу широкой гнатококсовой пластинкой, продолжающейся вперед в виде конического гипостома без оформленной присоски, а дорсально несет двучлениковые хелицеры с кинжаловидным когтем в качестве подвижного пальца. Проксимальные части гнатосомы заключены в складку покровов — камеростом. Тонкое дно объемного субхелицерального пространства несет лабрум спереди и слабо выраженный эпистом позади, и заканчивается сзади так называемой проксимальной камерой со склеротизированными стенками. Проксимальная камера служит в качестве резервуара для слюны. Лабрум и внутренние стенки гипостома образуют ротовое отверстие, ведущее в полулунную глотку, снабженную верхними дилататорами, начинающимися на дне субхелицерального прост-

ранства, но главным образом на боковых стенках гнатококкальной пластинки, а также констрикторами. Нижняя стенка глотки явственно отделена от дна гнатосомы, однако нижние дилаторы не выражены. Главные трахейные стволы имеют S-образную форму на продольных срезах и соединены с проксимальной камерой посредством узких каналов. Задние части трахейных стволов имеют склеротизированные стенки, служащие для крепления внешних мышц хелицер. Хелицеральные аподемы, следовательно, выражены двояко — как склеротизированные элементы позади внутренних стенок базальных члеников хелицер, и как особая склеротизация трахейных стволов. Латерально гнатосома несет крупные 5-члениковые пальпы, вооруженные двумя склеротизированными когтями на верхней части голени. Подобная организация ротового аппарата взрослых клещей микротромбидид хорошо соответствует актинидидному прототипу и выглядит более генерализованной, чем специализированный ротовой аппарат личинок, обнаруживающий некоторые черты недоразвития и вторичного упрощения.

INTRODUCTION

The basic characteristic of the feeding organs of arachnids is given by Snodgrass [1948] in his excellent work. Since that time a number of accurate studies on the mouthparts structure and functions have been made for the Acariformes [see, for example, Hughes, 1953; Lange, 1962; Hammen, 1968; Summers, Witt, 1971; Hislop, Jeppson, 1976; Nuzzaci, 1979; Hallas, 1982; Paran 1982; Desch, 1988; Akimov, Gorgol, 1990; Desch et al., 1991; Yastrebtsov, Gorgol, 1991; Akimov, Badanin, 1999; Badanin, 2000; Akimov et al., 2002; etc.]. Besides specialized studies, data on the organization of mouthparts in acariform mites are scattered in extensive literature of morphological and systematic value, and are partly summarized by Evans [1992] and Alberti and Coons [1999] along with other organ systems.

Nevertheless, among trombidiform mites (suborder Actinedida), detailed morphological investigations of the mouthparts and other organs using histological methods are relatively scarce and mostly deal with the specialized taxa such as the Tetranychidae [Becker, 1935; Blauvelt, 1945; Baker, Connell, 1963; Summers et al., 1973; Akimov, Barabanova, 1977; Akimov, Yastrebtsov, 1981; Akimov, Gorgol, 1984; Andre, Remale, 1984; Alberti, Crooker, 1985; Nuzzaci, Lillo de, 1991] and the Para-

sitengona. In the latter group, members of the families Erythraeidae [Witte, 1978], Smarididae [Witte, 1998], Trombidiidae *sensu lato* [Pagenstecher, 1860; Henking, 1882; Moss, 1962; Mathur, LeRoux, 1965; Shatrov, 2001a, b], Trombiculidae [Jones, 1950; Brown, 1952; Wharton, 1954; Mitchell, 1962a; Shatrov, 1981, 1985, 2000] and water mites [Croneberg, 1878; Schmidt, 1935; Mitchell, 1955, 1962b, 1972; Davids, 1973; Zhavoronkova, 1990a, b, 1992; 1993; 1999] have been examined in respect with the structure and function of the mouthparts. It is important to note that within the Parasitengona, in a number of cases, the feeding organs of the larvae were also studied [Jones, 1950; Wharton, 1954; Witte, 1978; Shatrov, 1981, 2001a, b] and a particular physiological and functional evaluation concerning feeding mechanisms of both parasitic larvae and adult mites has been suggested [Jones, 1950; Wharton, 1954; Mathur, LeRoux, 1965; Davids, 1973; Baker, 1982; Smith, 1988, Shatrov, 2000]. Finally, phylogenetic relationships within the Parasitengona, mostly based on mouthparts organization, have been proposed [Witte, 1991].

From the references listed above, it is obvious that the latest work on mouthparts of adult trombidid mites, the group embraced at present at least several families, is 40 years old [Mathur, LeRoux, 1965] and is not entirely satisfactorily. It is especially important that investigations of the mouthparts using TEM methods have not been previously carried out for the Parasitengona.

Based on these reasons, I undertake a morphological investigation of the mouthparts in adults of the microtrombidid mite *Platytrombidium fasciatum* (C.L. Koch, 1836) (Acariformes: Microtrombidiidae) using both light-optical and electron microscopy. A comparative analysis of adult and larval mouthparts is also the purpose of this study.

MATERIALS AND METHODS

Adult mites of *P. fasciatum* were collected from the soil surface in Leningrad district (Russia) during spring-summer of 1996–2005. Mites were initially placed into small plastic jars with soil particles as a substrate, then some of these mites were taken for fixation approximately 5–7 days after capture, and the others were mounted on slides for identification. Before fixation, mites were active being previously *ad libitum*-fed in natural conditions.

For the light-optical microscopy, whole mites were mounted on slides in Hoyer-Berlese medium after clearing in Nesbitt solution for about a month.

The animals were then investigated under an Amplival light-optical microscope either in bright-field or in phase-contrast.

For scanning electron microscopy (SEM), mites after the alcohol fixation and alcohol and acetone treatment were dried at the critical point of carbonic acid in a Hitachi HCP-2 vacuum evaporator, covered with a platinum layer in an Eiko IB-5 apparatus, and examined with a Hitachi S-570 electron microscope at 20 kV.

For transmission electron microscopy (TEM), adult mites were initially fixed in 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.2–7.4) for 2–4 h. The mites were then washed in several changes of 0.2 M phosphate buffer, postfixed in 2% osmium tetroxide in phosphate buffer containing 8.56% sucrose for 1–6 h to overnight, dehydrated in ethanol and acetone series, and finally embedded in an araldite mixture. Serial ultra-thin sections both in transverse and in longitudinal planes were made on an LKB-III ultramicrotome and, after staining with uranyl acetate and lead citrate, were examined with Tesla BS-500 and LEO-900 transmission electron microscopes at 80 kV.

For general and light-optical observations of sectioned specimens, serial semi-thin sections were stained with toluidine blue and studied and photographed with an Amplival light optical microscope.

List of abbreviations used in the Figures:

BS — basal cheliceral segment; Ca — cam-erostome; ChA — cheliceral apodeme; ChE — cheliceral elevators; ChP — cheliceral protractors; ChR — cheliceral retractors; Cr — crista metopica; DChW — dorsal cheliceral wall; DESS — dorsal extension of subcheliceral space; DP — dorsal projection; DPhW — dorsal pharyngeal wall; EGM — extrinsic gnathosomal muscles; Ep — epistome; EPM — extrinsic palp muscles; Ey — eye; FSS — floor of subcheliceral space; GnB — gnathosomal bottom; GnP — gnathocoxal plate; GnPr — gnathosomal protractors; GnR — gnathosomal retractors; GS — gnathosoma; He — haemocyte; HS — haemocoelic space; Hy — hypostome; IChM — intrinsic cheliceral muscles; IHW — inner hypostomal wall; La — labrum; LCl — larger claw; LI — leg I; LII — leg II; LL — lateral lip; MD — movable digit; MDP — movable digit protractors; MDR — movable digit retractors; Mo — mouth; NS — nude seta; OHW — outer hypostomal wall; Pa — palp; PC — proximal chamber; PCl — palp claw; PD — palp depressors; PE — palp elevators; PF — palp femur; PG — palp genu; Ph — pharynx; PhC —

pharyngeal constrictors; PhD — pharyngeal dilators; PrC — preoral cavity; PT — palp tarsus; PTi — palp tibia; PTr — palp trochanter; SA — sensillary area; SCl — smaller claw; SG — salivary glands; SS — subcheliceral space; St — stigma; To — tooth; TPhD — tendons of pharyngeal dilators; Tr — main tracheal trunk; VPhW — ventral pharyngeal wall.

RESULTS

The mouthparts are a complex functional inter-segmented unit of the frontal part of the body providing the food ingestion and its initial processing by the organism. In respect with the Acari, this head unit is frequently called gnathosoma [Evans, 1992], capitulum [Alberti, Coons, 1999], or gnathema [Lange, 1962]. The latter term implies that the gnathosoma is a pseudotagma. In the Trombidioidea and particularly in the Parasitengona, the mouthparts are shown to be highly specialized for sucking liquid food, either from the host's or from the victim's tissues, after piercing them with the claw-like digits of the chelicerae [Alberti, Coons, 1999].

As in other arachnids [Snodgrass, 1948], the mouthparts in *P. fasciatum* are generally composed of the first two segments and of their appendages — the chelicerae and the pedipalps. Internal sclerites of these segments (apodemes) as well as remnants of the embryonic head lobe are also integrated in the feeding organs. A heavily sclerotized apodema — the so-called crista metopica with a specialized sensillary area — occupies a mid-dorsal position above the mouthparts. The crista metopica is functionally associated with the mouthparts as a muscle attachment site but belongs to the prodorsum (Figs. 1–3). Such a combination of the skeleton elements constitutes the frame for numerous muscles providing the movements and functioning of the gnathosoma.

Light microscopic observations of slide mounted specimens

The gnathocoxal plate at the base of the gnathosoma has strongly bent lateral walls and a posterior indentation of its bottom (Fig. 4). Large five segmented palps are joined to the gnathocoxal plate laterally by means of the trochanters. The palps show an elbow bend of the massive femur and are provided with numerous setae (Figs. 4, 5, 7). On the tip of the palp tibia there are two strongly sclerotized and slightly ventrally bent claws. Relatively long tarsus is placed of the opposite side to the claws, on the ventral aspect of the tibia (Figs. 5, 7). This combination of the claws and the tarsus consti-

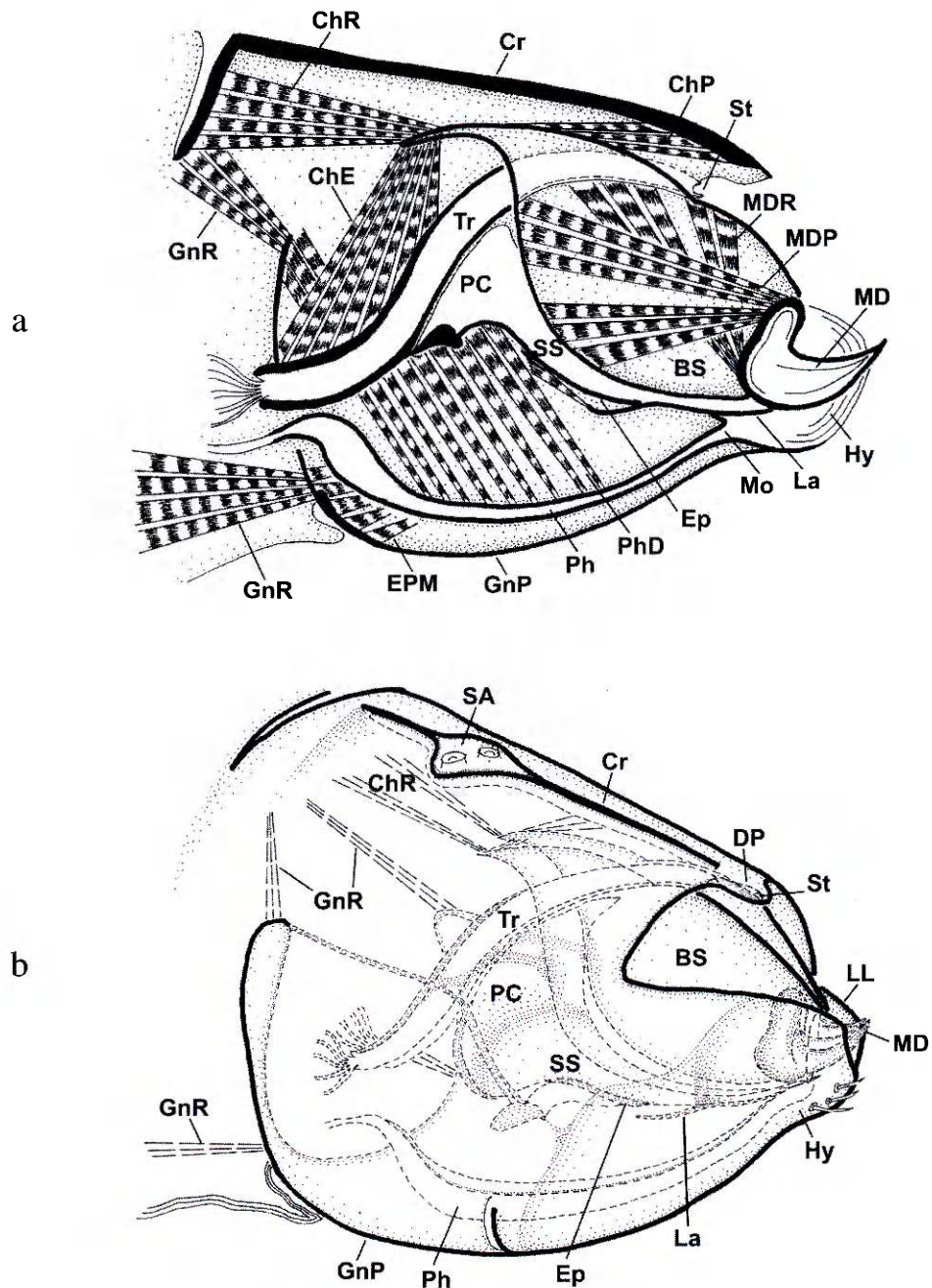


Fig. 1. a — Schematic drawing of sagittal section of mouthparts of adult mites *P. fasciatum*. Elements of only one side of the body are demonstrated. b — Schematic drawing showing spatial organization of cuticular elements of mouthparts of adult mites *P. fasciatum*.

Рис. 1. а — Схема продольного разреза гнатосомы *P. fasciatum*. Показаны структуры только одной половины тела. б — Схема пространственной организации кутикулярных элементов ротового аппарата *P. fasciatum*.

tute the thumb-claw complex, characteristic for the Actinedida and especially for the Parasitengona [Alberti, Coons, 1999]. The bodies of the chelicerae are weakly visible, but the blade-like and well sclerotized movable digits (digiti mobili), or claws of the chelicerae, are conspicuous elements of the mouthparts (Figs. 6, 7). They possess a massive basal portion providing an unicondylar articulation

with the basal segment. This joint is seen located at the dorsal aspect of the basal portion of the digit. A blade-like distal part of the claws bends nearly at a right angle to the basal portion of the movable digit and is armed with a sharp cutting edge and a pointed tip (Figs. 6, 7). The blade-like claws appear to have a groove on their inner side apparently elaborated for the current of a liquid food and the saliva when

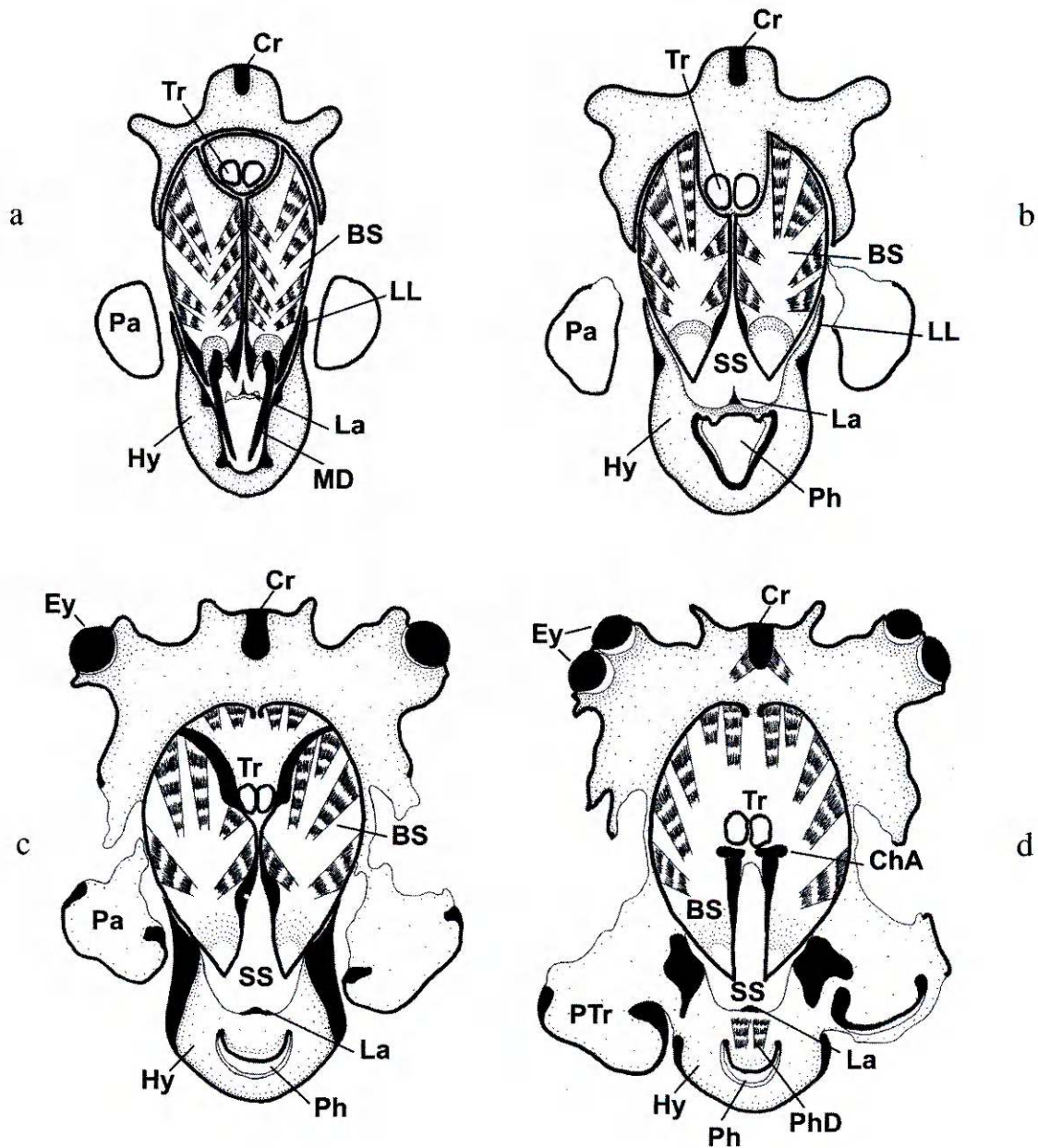


Fig. 2. Schematic drawings of transverse sections of gnathosoma of adult mites *P. fasciatum* on the level of: a — bases of movable digits; b — formation of pharynx; c — back third of hypostome; d — hypostomal base.

Рис. 2. Схемы поперечных разрезов гнатосомы *P. fasciatum* на уровне: а — оснований режущих пальцев хелицер; б — формирования глотки; с — задней трети гипостома; d — основания гипостома.

the digits are adjoined to each other during the feeding process.

SEM observations

From the external view by SEM, the gnathosoma, in comparison with the remaining part of the body, looks relatively small and is partly hidden between the palps, as they are usually tightly adjoined to each other from the dorsal-anterior position, and extended far beyond the tip of the gnath-

osoma (Figs. 8–10). From the posterior, the basal portion of the gnathosoma is covered by the integumental fold, which is frequently termed as the camerostome — a characteristic feature for the Acariformes [Snodgrass, 1948; Lange, 1962] (Fig. 11). Like in other mites studied [Snodgrass, 1948; Alberti, Coons, 1999], including the closely related family Trombiculidae [Shatrov, 1985, 2000], the base of the gnathosoma in *P. fasciatum* is formed by a wide and stout sclerotized plate, posterior and

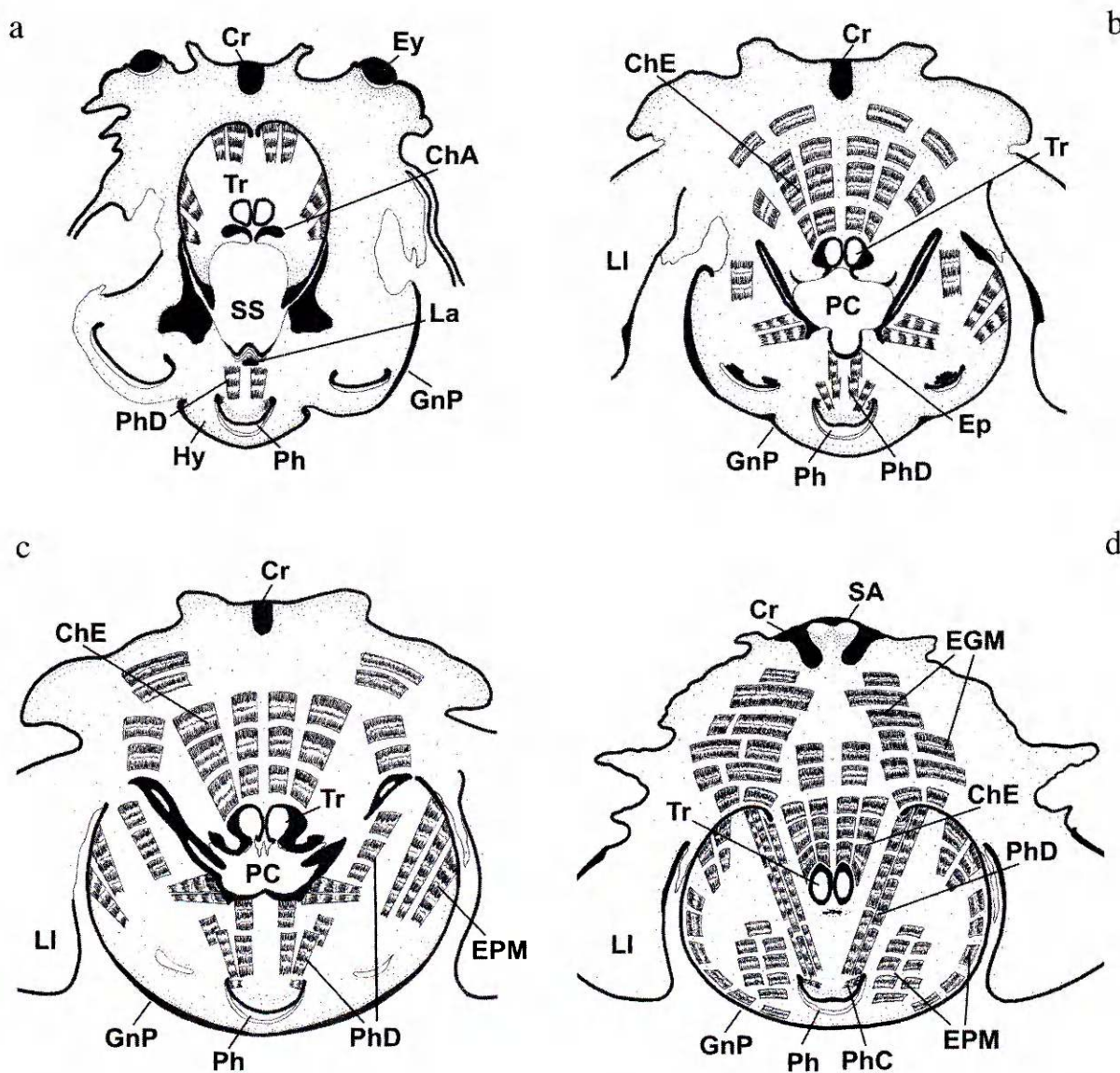
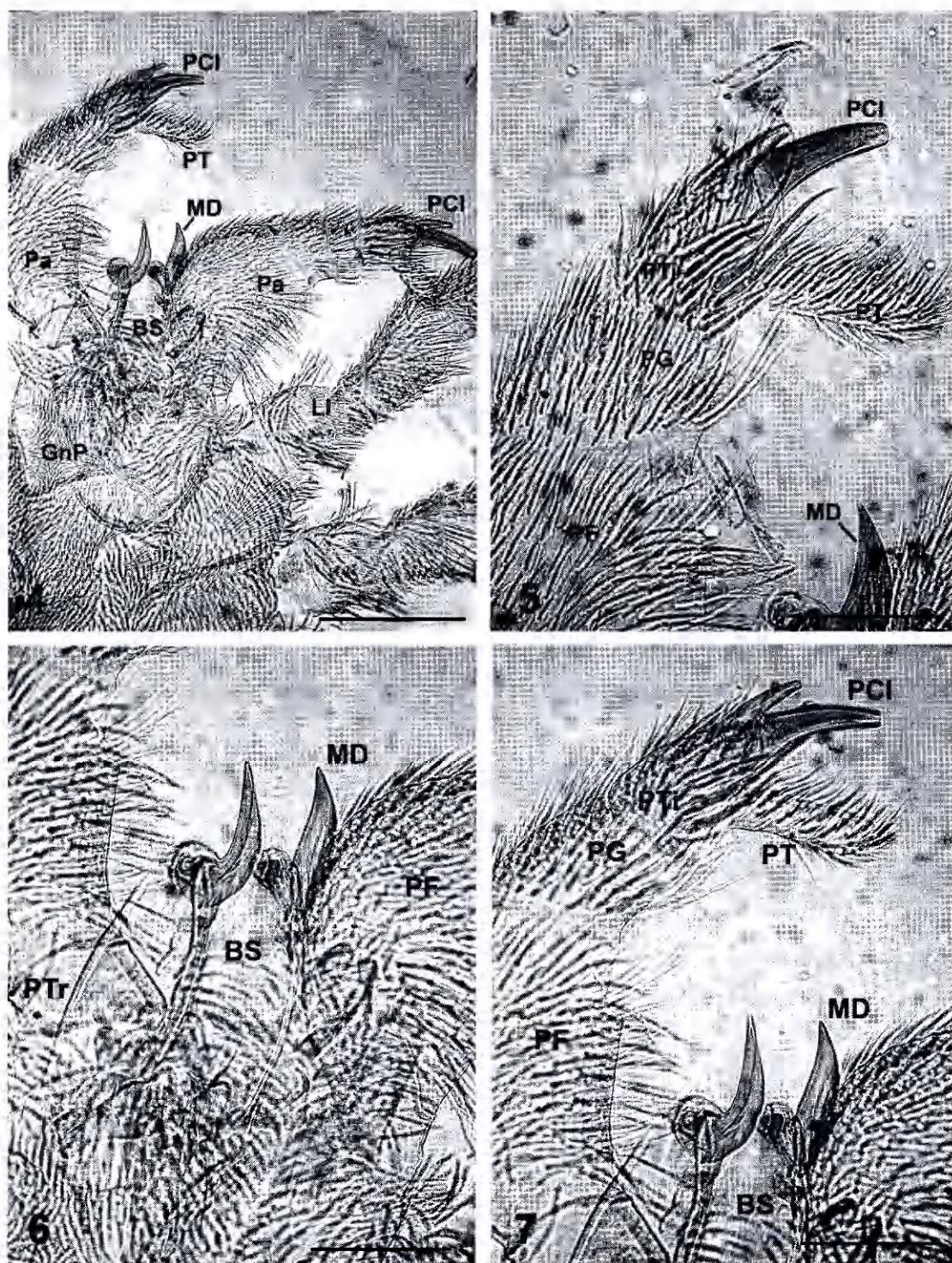


Fig. 3. Schematic drawings of transverse sections of gnathosoma of adult mites *Pl. fasciatum* on the level of: a — bases of basal cheliceral segments; b — epistome; c — base of proximal chamber; d — base of gnathosoma and sensillary area.

Рис. 3. Схемы поперечных разрезов гнатосомы *Pl. fasciatum* на уровне: а — основания базальных члеников хелицер; б — эпистома; с — основания проксимальной камеры; д — основания гнатосомы.

lateral edges of which are bent dorsad and hidden partly beneath the integumental fold of the ventral body wall and partly beneath the coxae of first legs (Fig. 12). As is generally assumed [Snodgrass, 1948; Evans, 1992; Alberti, Coons, 1999; etc.], this plate is derived from the fused palp coxae and thus, may be termed as the gnathobase, gnathocoxa, or, at last, infracapitulum [Alberti, Coons, 1999]. In *P. fasciatum*, this gnathocoxal plate bears numerous irregularly arranged, uniform mechanoreceptive setae. There is a narrow, free of setae, strip along the axis of the plate (the line of the supposed fusion) (Fig. 12). From the level of the palps' attachment, the coxal plate is narrowed to form the hypostome

[Snodgrass, 1948], which is cone-shaped from below (Fig. 12). Both the gnathocoxal plate and the hypostome form a ventral wall (bottom) of the gnathosoma. Lateral portions of the hypostome, frequently termed as the lateral lips [Alberti, Coons, 1999], are bent upward to envelop the distal parts of the chelicerae (Figs. 11, 13). Thickened distal parts of the lateral lips form the terminal opening of the hypostome (Fig. 13). Several nude setae probably serve also as mechanoreceptors surround the terminal opening. Tips of the cheliceral claws with tiny denticulate upper cutting edges may be seen protruding from this terminal opening (Figs. 13, 14). In contrast to the larvae of this species [Shatrov,



Figs. 4–7. Light microscopic views of gnathosoma of slide mounted adult mites *P. fasciatum*. 4 — ventral view of gnathosoma showing chelicerae with movable digits and large palps bearing two apical claws on the tibia, scale — 200 μm ; 5 — distal portion of a palp with a thumb-like complex, scale — 100 μm ; 6 — chelicerae with movable digits from ventral aspect, scale — 100 μm ; 7 — positional relationship of the chelicerae and palps, scale — 100 μm .

Рис. 4–7. Гнатосома на плоскостных светооптических препаратах взрослых клещей *P. fasciatum*.

2001], and some adult water mites [Zavoronkova, 1990b, 1992; Alberti, Coons, 1999; etc.], the apical portion of the hypostome does not seem to form an obvious permanent sucker, although the first steps in this direction may be traced in its

particular configuration (Figs. 13, 14). The lateral lips in their upper sides are formed by a soft cuticle and do not tightly contact each other above the chelicerae (Fig. 13) that permits the chelicerae to move in a certain way.

Figs. 8–13. SEM views of adult mites *P. fasciatum* and details of their mouthparts. 8 — mite from somewhat frontal and ventral aspect; tightly adjoined palps are clearly seen in frontal position of the mite body, scale — 1 mm; 9 — lateral and somewhat dorsal view of anterior portion of the mite body; note crista metopica taking a mid-dorsal locality and palps protecting gnathosoma from above and from the front, scale — 100 μm ; 10 — anterior portion of the mite body from somewhat dorsal and frontal aspect; the same disposition of palps as in the previous figure; note eyes on the sides of crista metopica; arrow points to an integumental “groove” behind crista, scale — 300 μm ; 11 — dorsal view of gnathosoma; arrow indicates dorsal projection of the integumental body wall covering stigmata, scale — 100 μm ; 12 — ventral view of the wide gnathocoxal plate and narrowing hypostome, from the apical orifice of which movable cheliceral digits are seen protruding; note that the palps are artificially moved apart, scale — 100 μm ; 13 — frontal view of the gnathosomal apex; note movable digits protruding between the apical thickened parts of the lateral lips, scale — 10 μm .

Рис. 8 — 13. Взрослые клещи *P. fasciatum* и их ротовой аппарат в сканирующем электронном микроскопе (СЭМ).

Figs. 14–19. SEM views of details of the mouthparts of adult mites *P. fasciatum*. 14 — apical portion of hypostome from somewhat dorsal and lateral aspect with tips of lateral lips turned back; note movable digits with an indented cutting edge protruding between the lips; arrow indicates presumed rudiments of fix digits, scale — 10 μm ; 15 — distal portion of a palp with tarsus faced ventrad and two apical claws; inner side of the left palp, scale — 50 μm ; 16 — apical portion of the right palp from the front; note large nude setae located on the outside surface of the tibia, scale — 50 μm ; 17 — right palp from the frontal and somewhat inner aspect; note that the bases of the claws are oriented in perpendicular planes, scale — 50 μm ; 18 — sensillary area with trichobotriae, scale — 5 μm ; 19 — double eye under the united cuticular cornea, scale — 20 μm .

Рис. 14–19. Детали строения ротового аппарата взрослых клещей *P. fasciatum*. СЭМ.

Figs. 20–27. Sequential transverse semi-thin sections of the mouthparts of adult mite *P. fasciatum* from the front to back up to the level of epistome. Toluidine blue. Scale — 100 μm (20–23, 26) and 50 μm (24, 25, 27). See text for details.

Рис. 20–27. Поперечные полутонкие срезы ротового аппарата взрослого клеща *P. fasciatum* спереди назад до уровня эпистома. Толуидиновый синий.

Figs. 28–33. Sequential transverse semi-thin sections of the mouthparts of adult mite *P. fasciatum* from the level of the base of the epistome back up to the level of posterior termination of the tracheal trunks. Toluidine blue. Scale — 100 μm (28, 29) and 50 μm (30–33). See text for details.

Рис. 28–33. Поперечные полутонкие срезы ротового аппарата взрослого клеща *P. fasciatum* спереди назад от уровня основания эпистома до уровня окончания главных трахейных стволов. Толуидиновый синий.

Figs. 34–39. Sequential sagittal semi-thin sections through the mouthparts of adult mite *P. fasciatum* indicating a disposition of the main tracheal trunks, cheliceral elevator muscles, proximal chamber and pharynx (34–38), and of a palp (39). Note dorsal integumental fold with crista metopica in the middle position covering proximal parts of the gnathosoma. Toluidine blue. Scale — 100 μm everywhere. See text for more details.

Рис. 34–39. Сагитальные полутонкие срезы ротового аппарата взрослого клеща *P. fasciatum*, показывающие взаимное расположение главных трахейных стволов, элеваторов хелицер, проксимальной камеры и глотки (34–38), а также пальпы (39). Толуидиновый синий.

Figs. 40–44. TEM views of ultra-thin transverse sections showing details of the mouthparts of adult mites *P. fasciatum*. 40 — labrum and attachment of movable digit to the basal cheliceral segment, scale — 5 μm ; 41 — labrum composed of a cuticle of two types — electron-dense with pore canals in the dorsal part and electron-light with loosely packed fibrils in the ventral part, scale — 3 μm ; 42 — large cuticular mass of irregular outlines of the floor of subcheliceral space, scale — 5 μm ; 43 — epistome and posterior portion of labrum deepened under the floor of subcheliceral space, scale — 10 μm ; 44 — epistome with deep ventral curvature, scale — 10 μm .

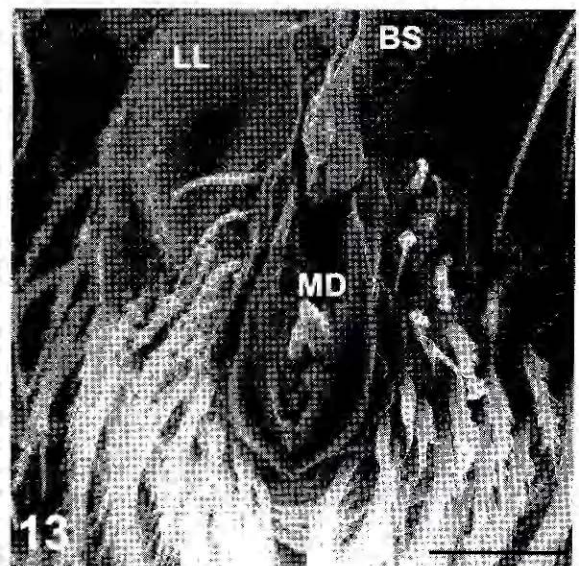
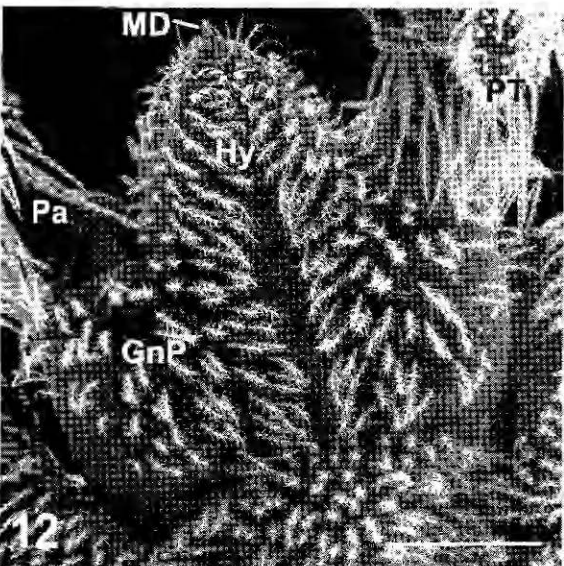
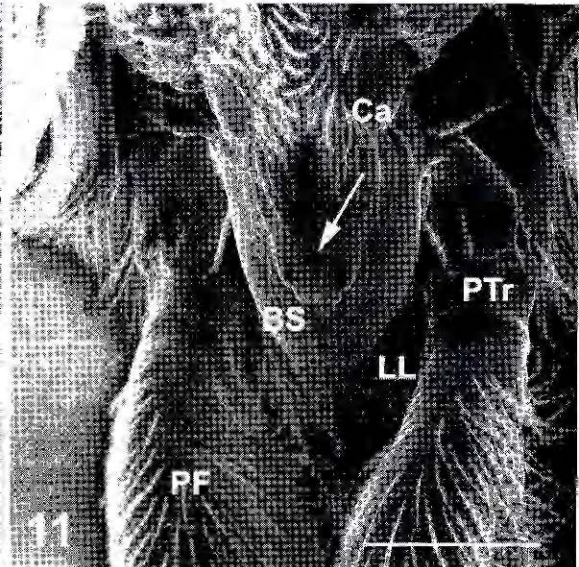
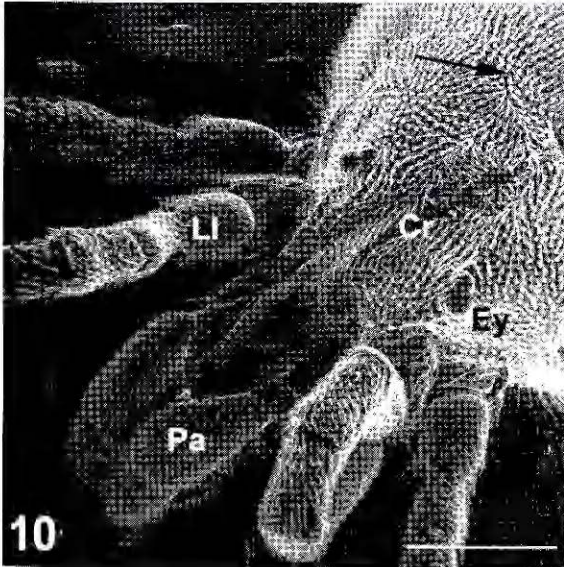
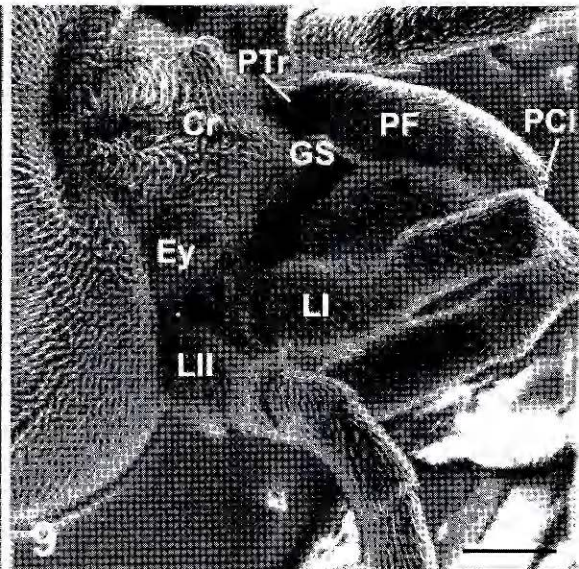
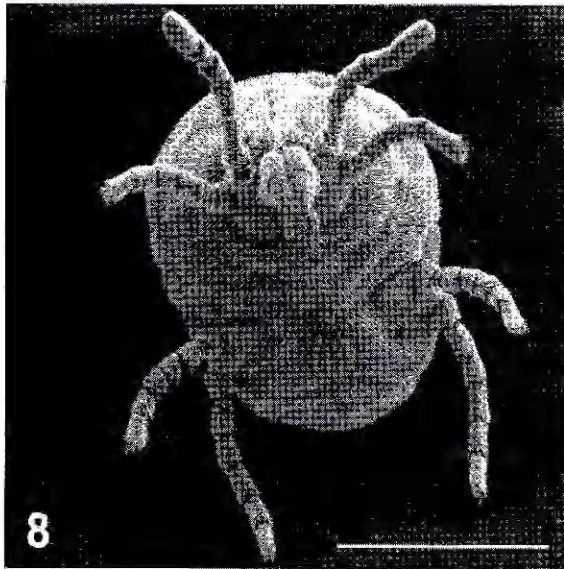
Рис. 40–44. Ультраструктура деталей ротового аппарата взрослых клещей *P. fasciatum*. ТЭМ.

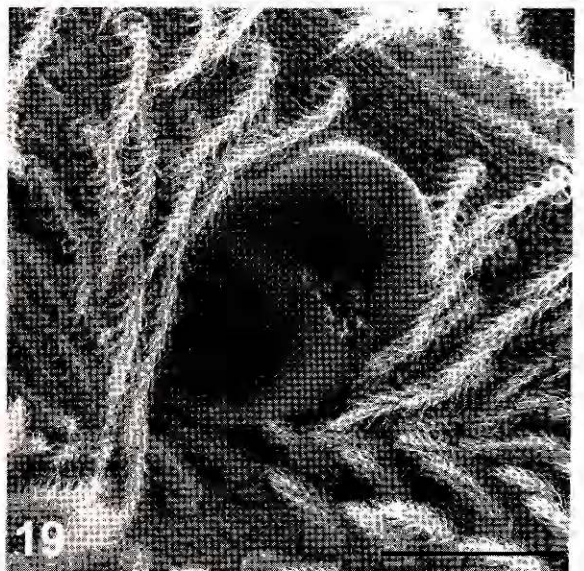
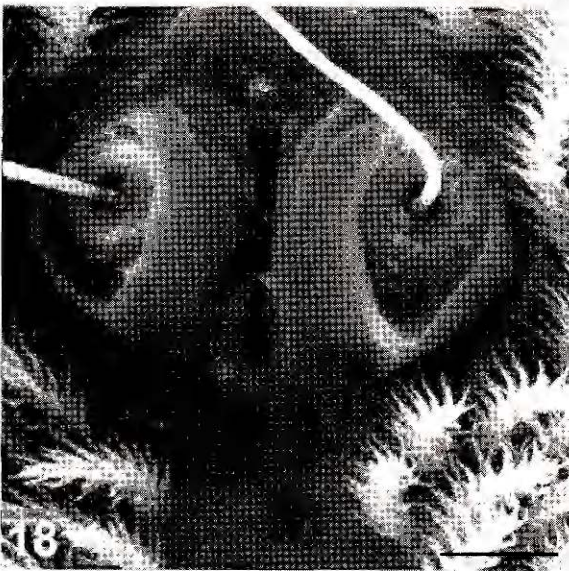
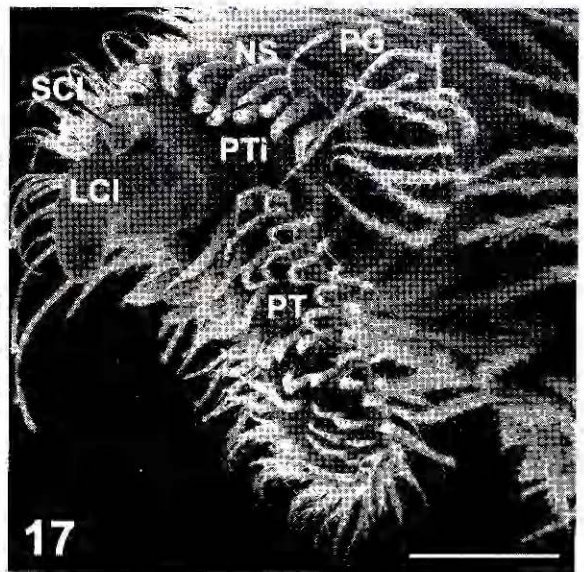
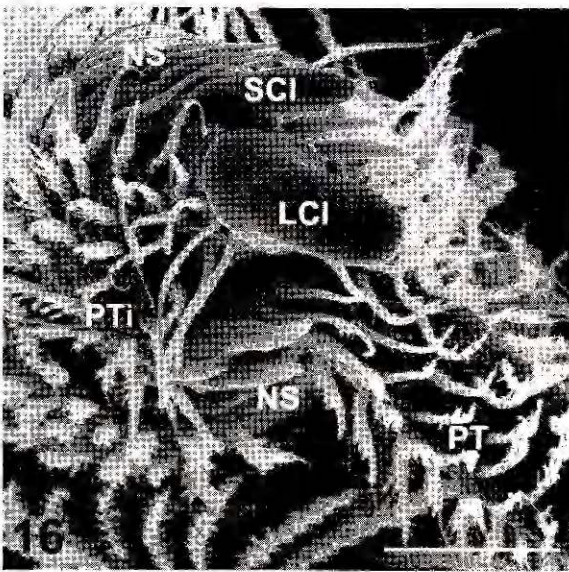
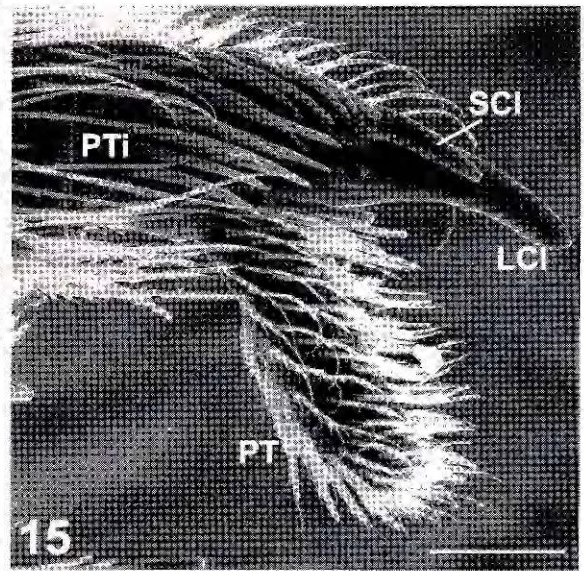
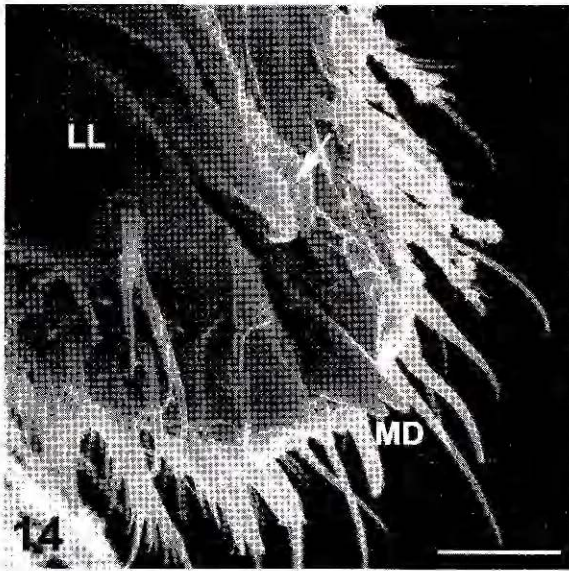
Figs. 45–48. TEM views of ultra-thin transverse sections showing details of the mouthparts of adult mites *P. fasciatum*. 45 — character of space between the inner and the outer hypostomal walls anterior to the formation of pharynx containing loosely packed connective and fat tissues as well as some haemocytetes, scale — 5 μm ; 46 — movable digits lying in the preoral cavity; small arrows indicate dense vesicles in the hypostomal cuticle, large arrow points to cuticular bulge; see text for details, scale — 5 μm ; 47 — character of attachment of movable digit to basal cheliceral segment; arrow indicates arthroal membrane, scale — 5 μm ; 48 — middle part of the pharynx, distinctly separated from the gnathosomal bottom, scale — 5 μm .

Рис. 45–48. Ультраструктура деталей ротового аппарата взрослых клещей *P. fasciatum*. ТЭМ.

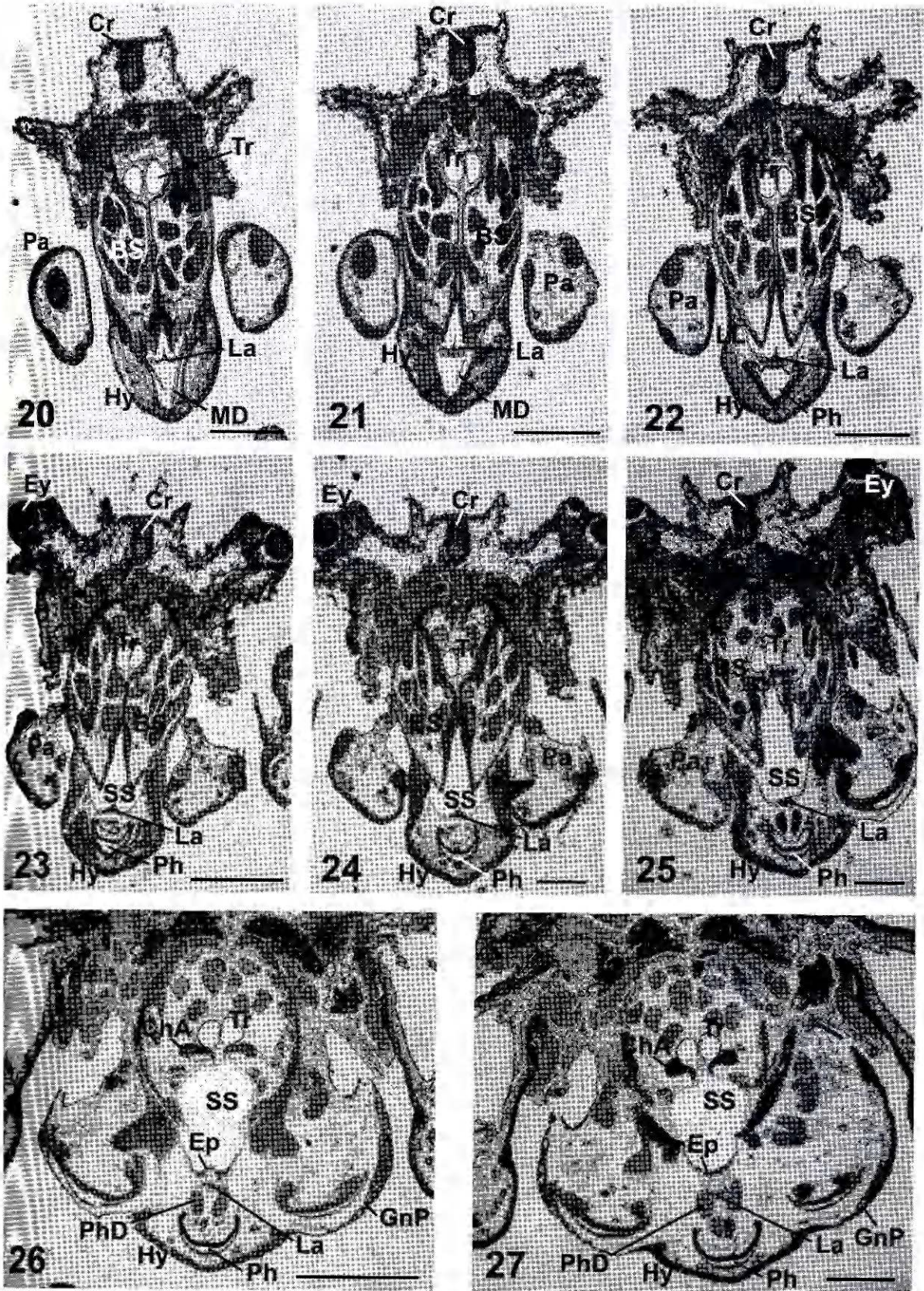
Figs. 49–51. TEM views of ultra-thin transverse sections showing details of the mouthparts of adult mites *P. fasciatum*. 49 — main tracheal trunks lying within the particular body fold separated from the dorsal cheliceral walls, scale — 5 μm ; 50 — dorsal extension of the subcheliceral space coming close to the main tracheal trunks, scale — 5 μm ; 51 — combined picture showing relationship of the main tracheal trunks, cheliceral apodemes and proximal chamber; arrows indicate channels connecting tracheal trunks and proximal chamber, scale — 10 μm .

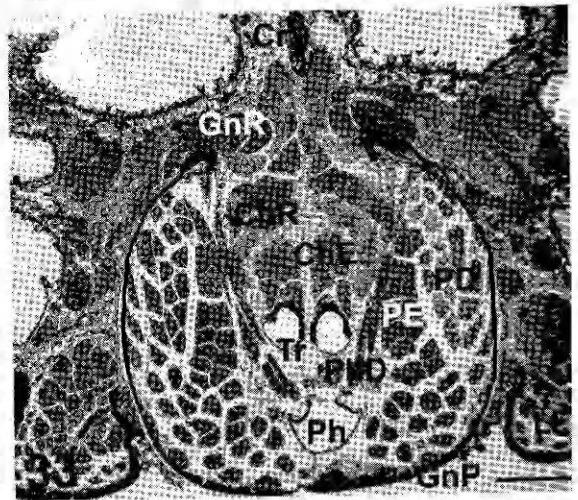
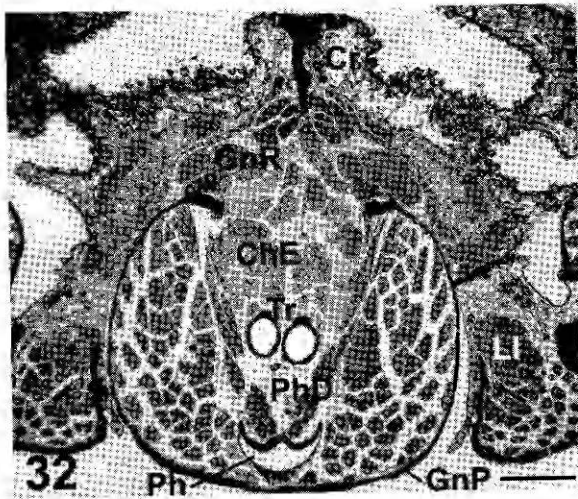
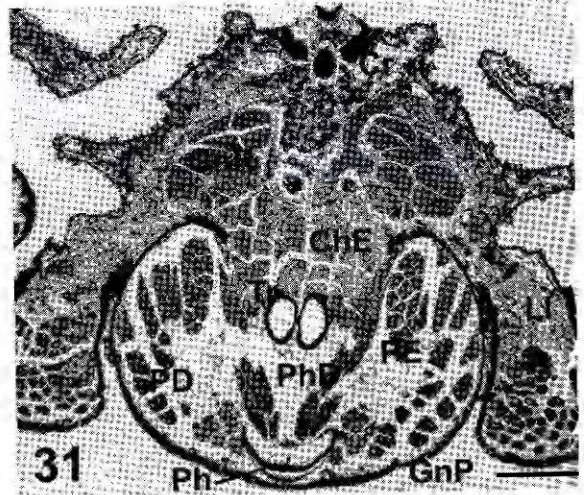
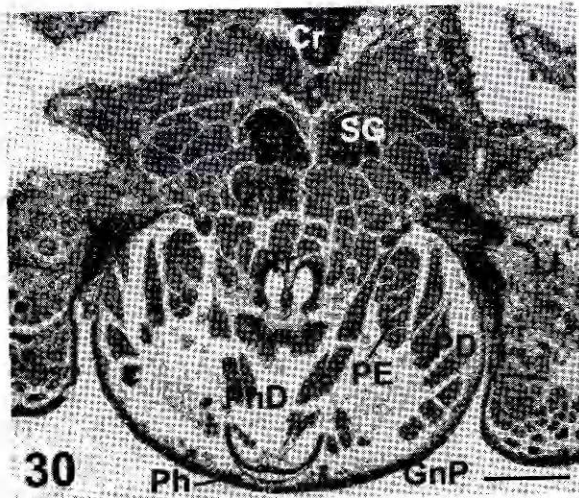
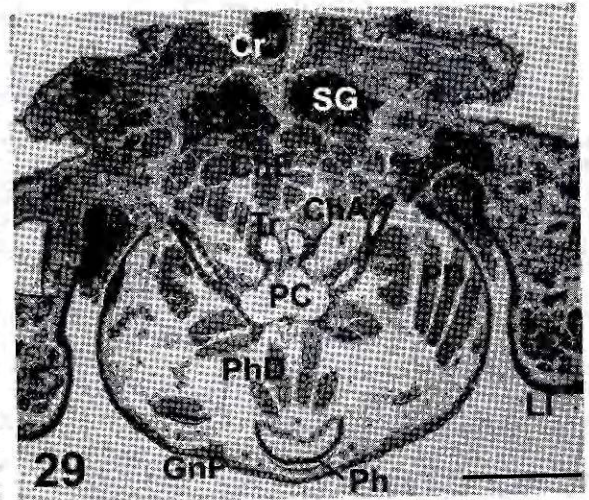
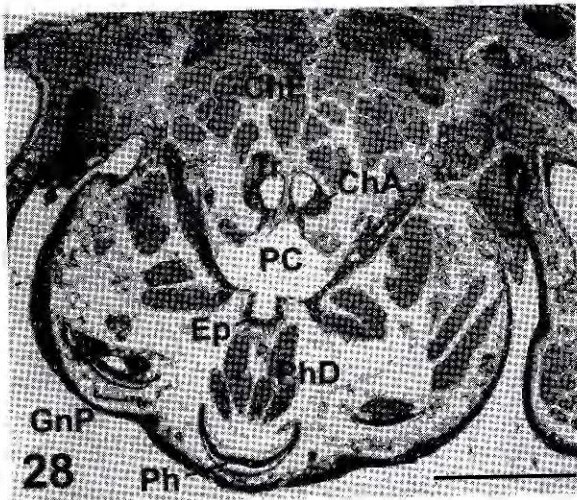
Рис. 49 — 51. Ультраструктура деталей ротового аппарата взрослых клещей *P. fasciatum*. ТЭМ.



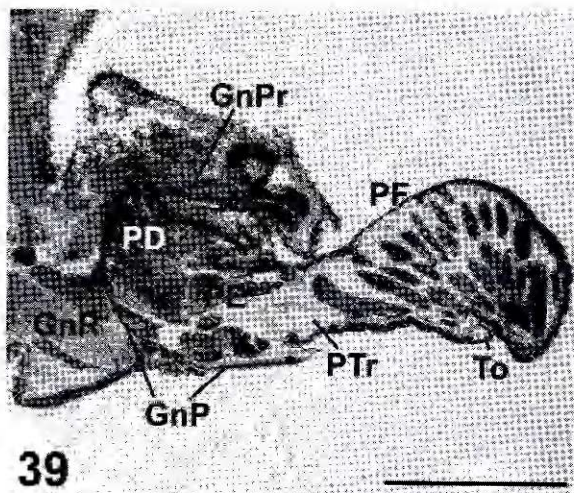
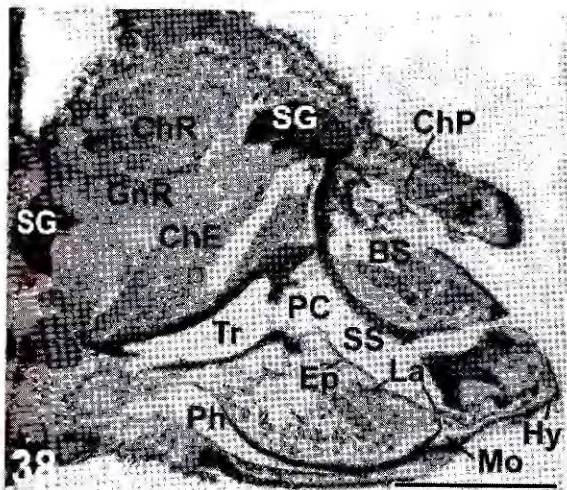
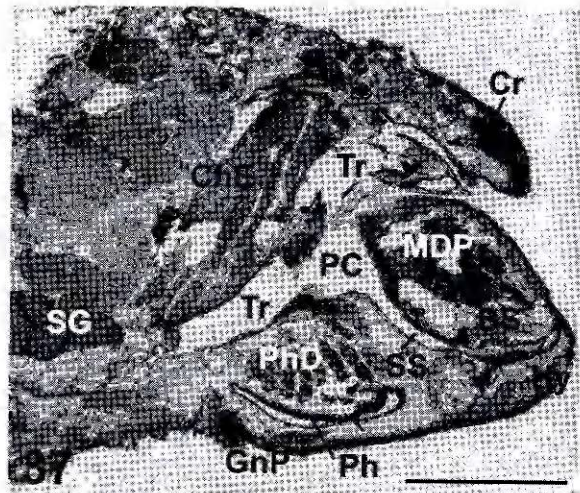
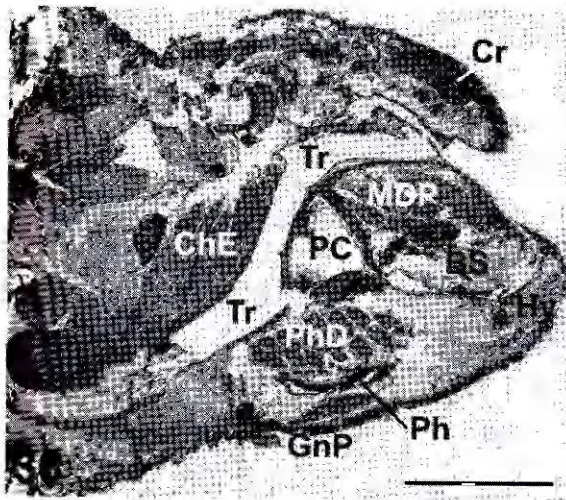
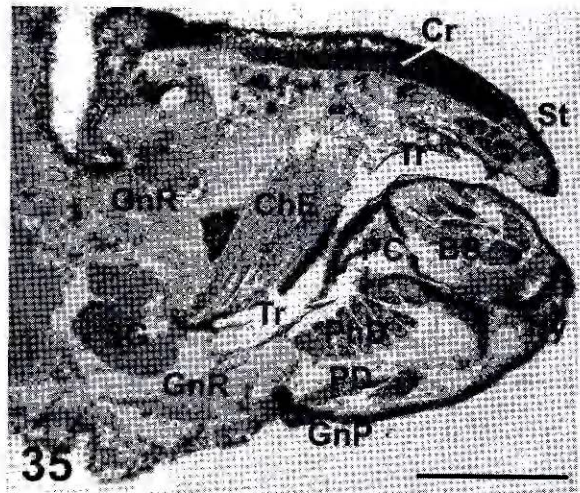
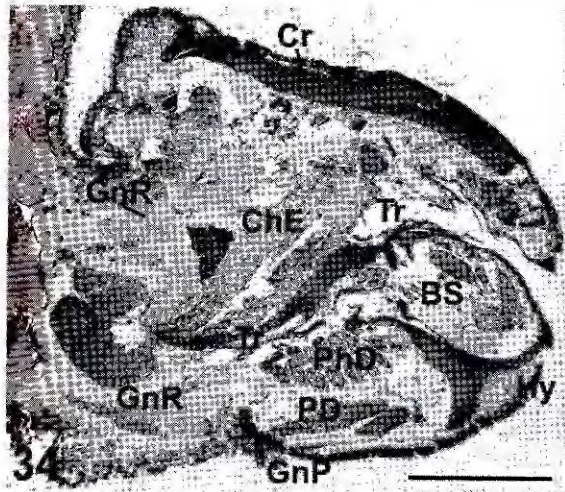


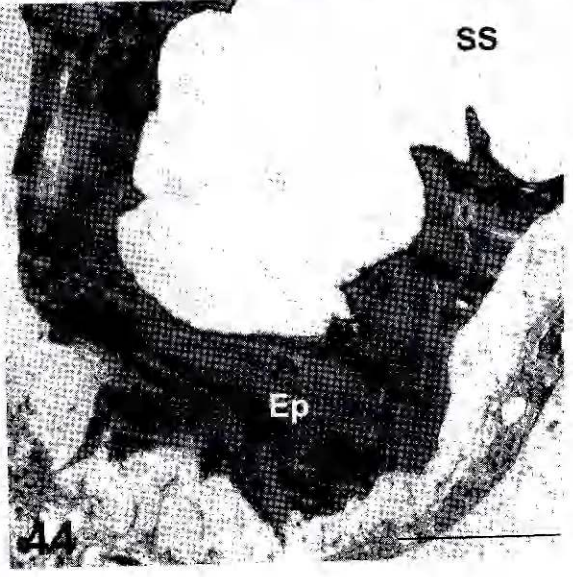
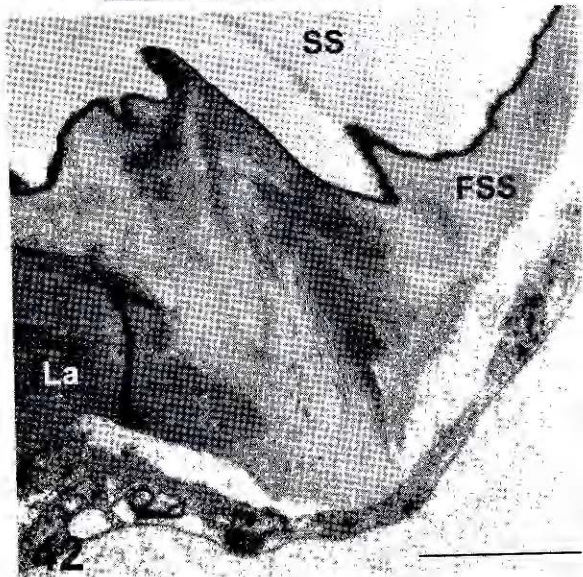
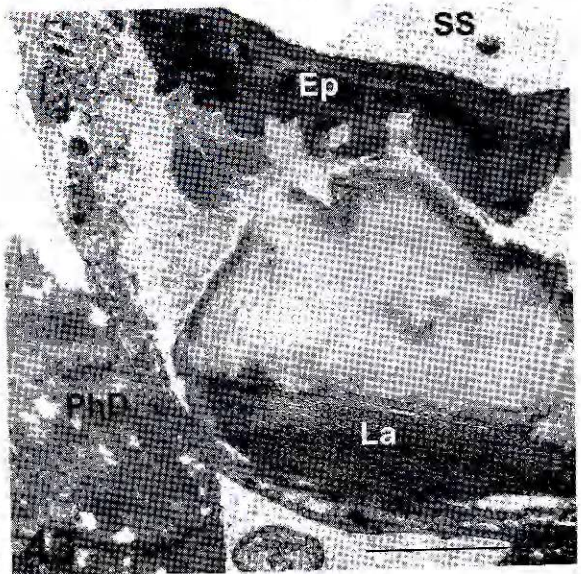
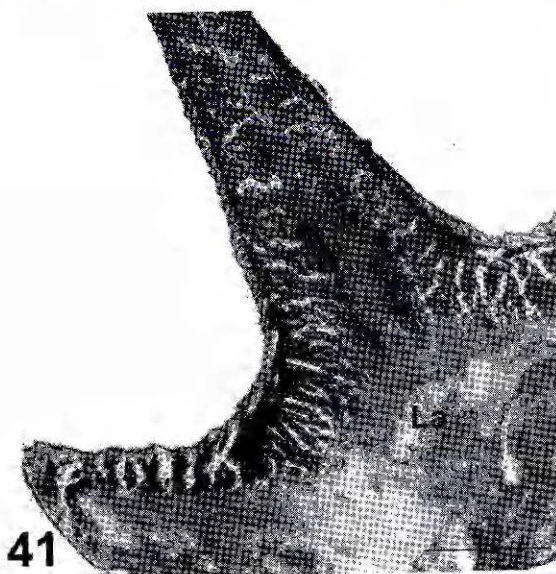
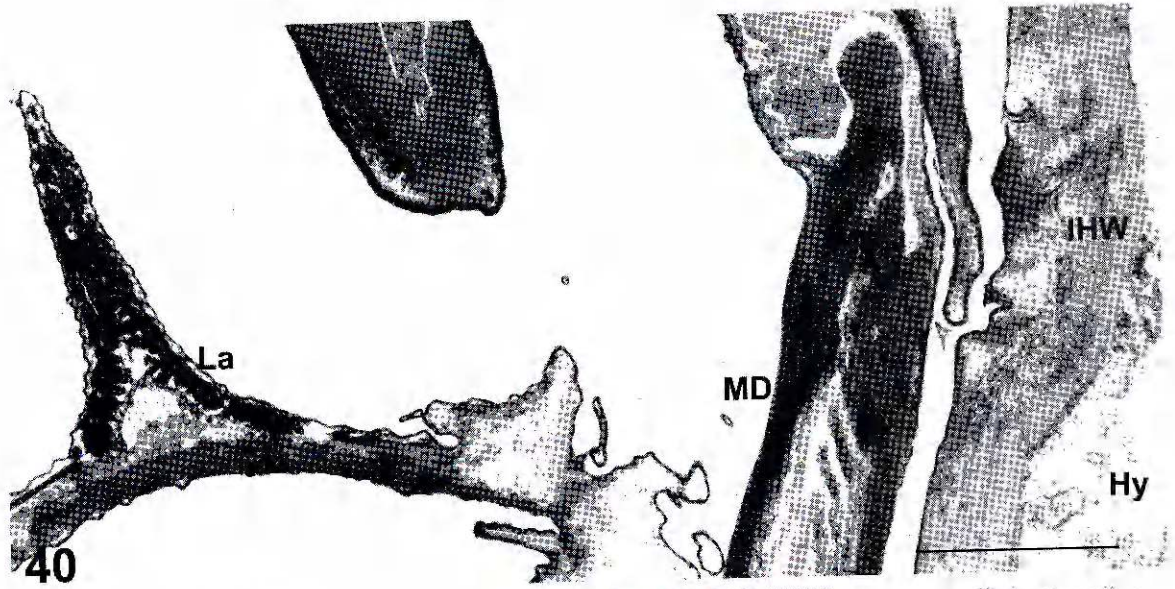
Description of mouthparts in adult mites of *Platytrombidium fasciatum*

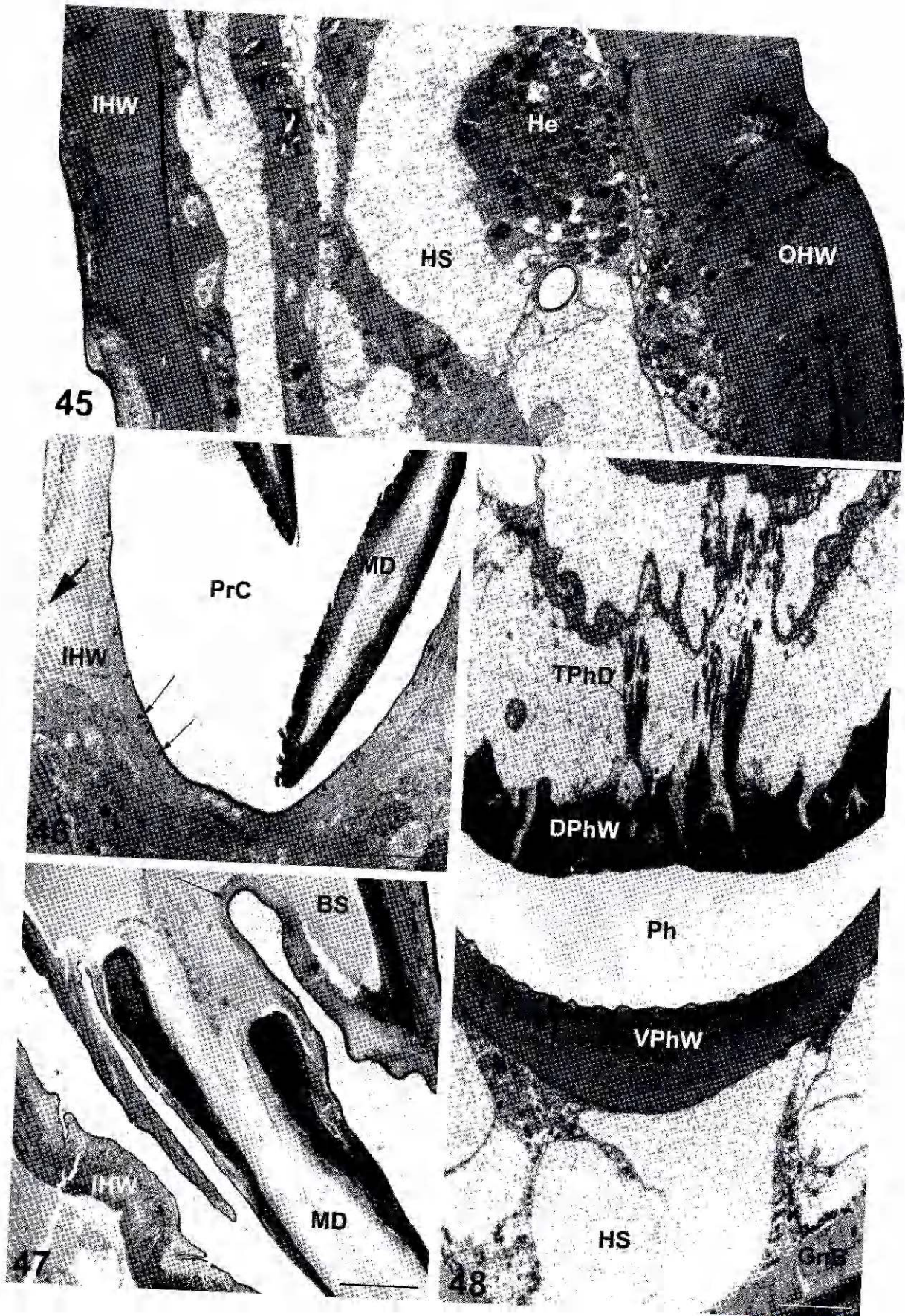


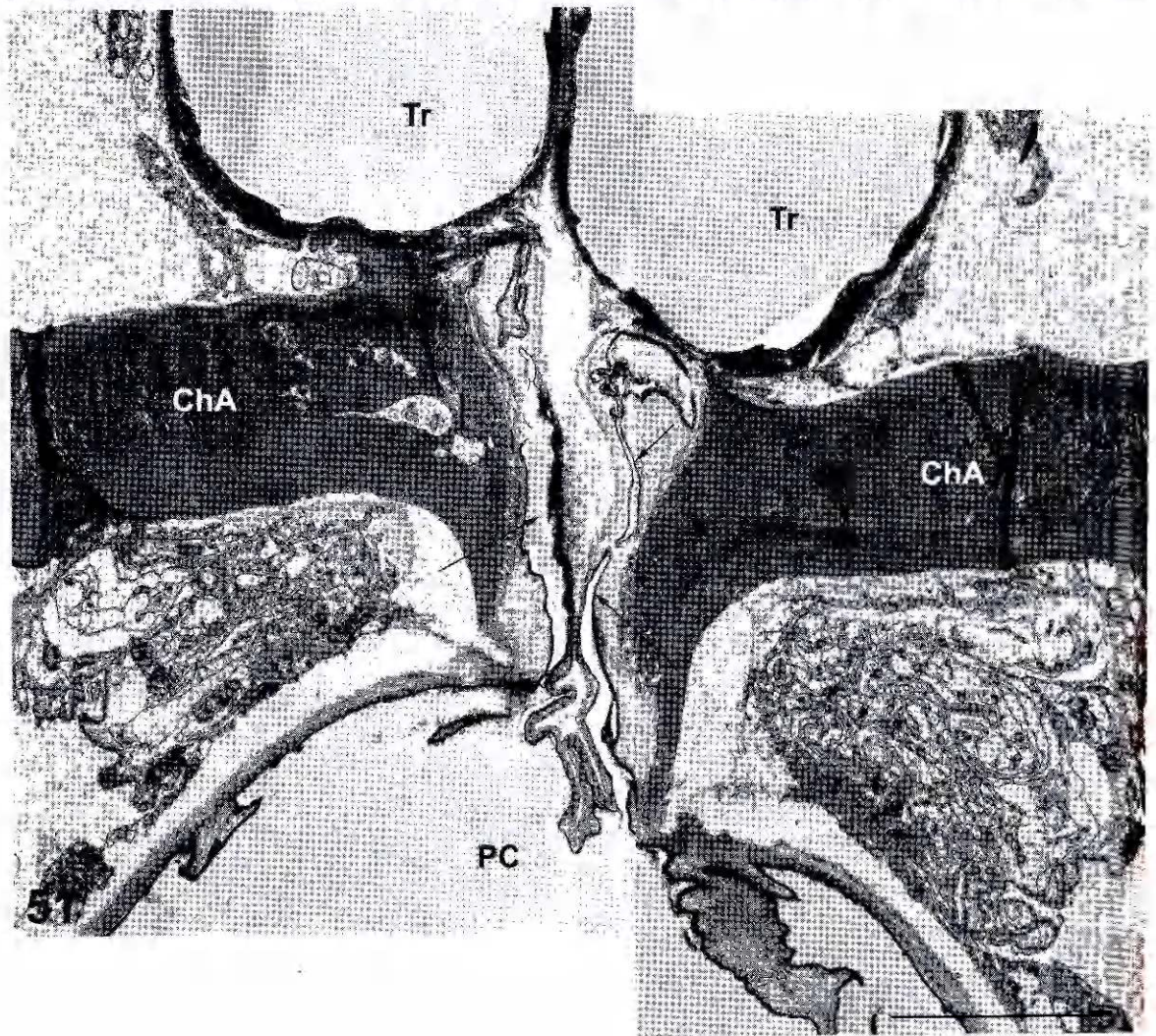
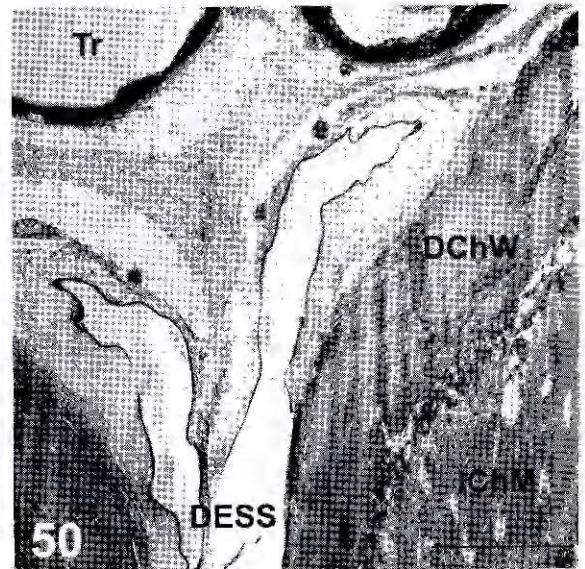
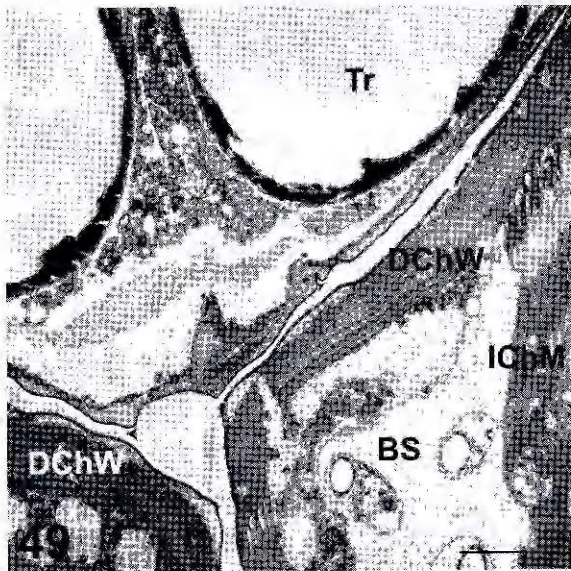


Description of mouthparts in adult mites of *Platytrombidium fasciatum*









From the dorsal aspect, the gnathosoma is armed with stout, tightly adjoined bodies of the chelicerae, i.e. principal [Alberti, Coons, 1999], or basal segments of the chelicerae devoid of any setae on the opened surface (Fig. 13). Their proximal portions are inserted into the integumental fold, the camerostom, bearing from above the crista metopica (Fig. 10). This integumental fold forms a particular dorsal projection anteriorly, which apparently serves as a cover for stigmata (Fig. 11). Nevertheless, such a dorsal projection can doubtfully be identified as a separate tectum, the supposed derivate of the embryonic head lobe [Snodgrass, 1948]. The latter, conversely, is observed in adults of trombiculid mites [Shatrov, 1985, 2000], but seems to be reduced in *Pl. fasciatum* and other trombiculids *sensulato* [Henking, 1882, Mathur, LeRoux, 1965]. Laterally, the integumental fold is joined with the dorsally extended basal angles of the hypostomal edges by thin membranous folds (see below) to form a characteristic continuous frame surrounding the gnathosoma, known as the basis capituli [Snodgrass, 1948]. From their upper sides, distal edges of the basal cheliceral segments bear characteristic membranous folds (Fig. 14), which are probably rudiments of the fixed digits, totally reduced in the Actinedida [Alberti, Coons, 1999].

Laterally, the gnathosoma bears the vertically oriented palps consisting of five free segments: small trochanter, massive femur bent ventrally, genu, tibia armed with two claws on its apical tip, and tarsus. The relatively long and uniformly wide tarsus is situated on the ventral surface of the tibia and directed downward (Figs. 9, 15). Except for the trochanter, all these segments bear irregularly arranged, uniform, tiny-branched setae looking forward. Besides these branched setae, there are also large and stout nude setae situated obliquely in three-five rows along the inner side and partly along the upper ridge of the tibia (Figs. 15, 17). Up to five very large stout nude setae directed straight forward are also placed on the outer surface of the tibia at its ventral aspect (Fig. 16). All these large, nude setae accompany the palp claws, which are thought to have historically originated from such setae [Snodgrass, 1948; Alberti, Coons, 1999].

The palp claws have wide bases and blunt apices, are slightly curved and oriented in perpendicular planes to each other so that the terminal larger claw takes a nearly vertical plane and the smaller inner claw takes a nearly horizontal plane (Figs. 15, 17). The larger claw is around 110 μm long, whereas the smaller one is around 80 μm . The

palp tarsus, about 130 μm long, being approximately of the same width through its length, is densely covered by uniform branched setae and is supposedly used as mechanoreceptors when the mite walks in the soil searching for food. The combination of the claws and the palp tarsus is thought to constitute a claw-thumb complex in the Actinedida [Alberti, Coons, 1999] that functions in the reception and grasping of potential food. As was mentioned above, in natural conditions, the palps are tightly adjoined together and appear to protect the apical tip of the hypostome from accidental damages, when the mites are dwelling in the soil or on its surface.

The crista metopica is around 300 μm long and devoid of setae. It occupies a mid-dorsal position on the prodorsum. Approximately at its posterior quarter, the crista metopica has a widened, so-called sensillary, area [see Moss, 1962] where trichobotriae, organs of spatial orientation [Alberti, Coons, 1999], are located (Fig. 18). A pair of double eyes is situated on the sides of the crista approximately at its middle level. Externally, each eye is composed of the paired hemispheres under a united cuticular cornea (Fig. 19). The eye hemispheres have a slightly diagonal orientation with the larger one taking a more external and frontal position (Figs. 10, 19). A detailed consideration of the eye organization is beyond the scope of this work.

Light-optical observations of semi-thin sections

Serial semi-thin sections made both in transverse and in the sagittal planes seem to provide essential information about the internal organization of the gnathosoma (see Figs. 1–3).

An apical portion of the gnathosoma, flattened from the lateral sides, is composed of the basal cheliceral segments, tightly opposed to each other, and of the semi-circled double-walled hypostome enveloping the chelicerae from below (Figs. 20–25) (see below). Movable digits are articulated to the basal segments of the chelicerae in the frontal-ventral position (Figs. 20, 21). The basal segments possess sclerotized walls having a flat inner side without any locking structures through their length, and a nearly semi-rounded outer side (Figs. 20–23). From a dorsal aspect, the basal segments have indentations on their inner sides facing to each other. This pattern is especially developed at the distal portions of the segments, where the main tracheal trunks lie. In the most apical portions, the trunks are enclosed within a separate body projection situated over the chelicerae like a tongue-like

structure (Figs. 11, 20, 34–36). Posteriorly, still above the chelicerae, this structure is united with the camerostomal fold covering the chelicerae from dorsal and posterior aspects (Figs. 21, 22). In the posterior direction, the tracheal trunks are gradually running down, remaining between or even partly inside the basal cheliceral segments. In their course associated with the chelicerae, the tracheal trunks have thin, non-sclerotized walls, but never show collapsed cavities and always have a clear inner space (Figs. 21–23). In the posterior portion of the basal cheliceral segments, the indentations of the inner walls, where the tracheal trunks lie, become deeper. Rounded outer walls continue upwards far beyond the point of the fusion with the inner walls. They are directed towards each other forming here the dorsal walls of the basal segments, which end freely being separated by a narrow space (Figs. 23–24). The inner walls of the basal segments in their most posterior portions, in contrast to all other sides, are thick and strongly sclerotized (Fig. 24). The ventral parts of the basal segments look sharp, and end freely within the subcheliceral space (Fig. 25) (see below). The basal cheliceral segments contain well developed muscles: elevators and depressors of the movable digits (cheliceral claws) originate mostly on the outer and also on the inner walls of the basal segments (Figs. 36–38). The largest width of the basal cheliceral segments is around 60–70 μm .

Dorsally, the chelicerae, together with the tracheal trunks, are covered by a frontal projection of the prodorsum, which is filled with loosely organized intermediate, connective and fat tissues (Figs. 34–38). On its dorsal aspect, this body fold bears a heavily sclerotized medial crista metopica that is deeply inserted into the body cavity (Figs. 20–25, 30–33, 34–36). Cheliceral protractor muscles originate on the sides of the anterior portions of the crista and are also present within this frontal projection (Fig. 38). In the posterior, lateral sides of this dorsal projection are going down along the lateral cheliceral faces to fuse with the dorsally extended basal angles of the hypostomal sides by thin membranous folds, thus completing the formation of the camerostomal ring, into which the basal portions of the gnathosoma are inserted (Figs. 23–25). More posteriorly, bicondylar articulations of the gnathosomal base with palp trochanters, inserted into the latter, are observed (Figs. 23–25). On the dorsum of the body, approximately at this level, the eyes are situated on the folds of the body wall (Figs. 2, 3, 23–25).

The hypostome is situated ventrally, in close association with the chelicerae. It constitutes the gnathosomal apex from a ventral aspect (Fig. 20). Apical portions of the hypostome have semi-circular outlines on transverse sections and double cuticular walls, between which the body cavity is filled with elements of loosely organized fat tissue. This construction is supposedly elaborated for protecting the slender movable digits from accidental damages when the latter are retracted in non-functional conditions. The lateral hypostomal sides are therefore thickened leaving a relatively narrow space where the movable digits are enclosed and rest (Figs. 20–21). The cuticular walls of the hypostome are thick showing characteristic bulges on the inner walls. The bulges are directed to the inside of the space between the hypostomal walls and probably serve to protect the inner and outer walls from collapsing (see Fig. 21). The lateral sides of the hypostome are extended upwards, becoming thinner and partly enveloping the distal portions of the chelicerae. The width of the hypostome is around 120 μm .

In the narrow space between the bases of the movable digits, a fine and slender apex of the labrum may be distinguished. The apex of the labrum is armed by a middle vertical ridge (Figs. 20–21). Posteriorly, the labrum becomes larger and wider, and behind the basal termination of the movable digits, the labrum fuses its lateral sides with the inner walls of the hypostome, where the latter are essentially thick (Fig. 22). The terminal opening into the pharynx, formed by the joining of the labrum and the inner hypostomal walls, is a mouth (see Fig. 38) [Snadgrass, 1948]. The space anterior to the mouth, between the hypostomal sides, may be anatomically defined as the preoral cavity. Posteriorly from the mouth, the pharynx becomes a morphologically separated organ. Its anterior portion is triangular on transverse sections, with rather thick lateral walls derived from the inner walls of the hypostome. Further posteriorly, the pharynx is passing through the hypostomal space being however separated from the ventral wall of the hypostome, i.e. the gnathosomal bottom (Figs. 23–25). Posterior to the formation of the pharynx, the upper concave wall, or the roof of the hypostome, apart from the labrum, which is lacking here the median ridge, is formed by a thin membranous cuticle constituting the floor of the subcheliceral space (Fig. 25). At this level, the lateral walls of the hypostome are thicker, especially at their dorsal portions. They probably support the basal

segments of the chelicerae (Figs. 24–25). In the posterior direction, the ventral wall of the hypostome becomes more flat and the lateral walls disappear, leaving two large cuticular masses flanking the voluminous subcuticular space from the lateral sides (Figs. 25, 26). The hypostomal plate gradually transforms into the wide and rather bent gnathocoxal plate. Lateral sides of the latter appear to be formed by a thin membranous cuticle in their frontal portions (Figs. 26, 27). These lateral walls are bent dorsally in the form of a wide cup and further posteriorly they are sclerotized (see Figs. 28–33).

The pharynx has a crescent form with a darkly-stained dorsal wall and a less stained ventral wall. Both walls are thick and appear to be sclerotized (Figs. 23–25). No muscles are attached to the pharyngeal walls within the hypostomal space. At the level of the base of the hypostome, tendons of the dorsal dilator muscles are inserted to the upper concave pharyngeal wall (Fig. 25). During the course of the pharynx, up to ten paired sets of dorsal dilators are attached to the dorsal pharyngeal wall (Figs. 26–33). The dilators originate on the epistome and mostly on the upper parts of the lateral walls of the gnathocoxal plate that is deeply inserted into the body. In contrast to adult trombiculid mites [Shatrov, 1985, 2000], no ventral pharyngeal dilators were observed in adults of *P. fasciatum*. The pharynx, however, remains distinctly separated from the bottom of the gnathosoma. Conversely, the pharyngeal constrictors are present. They connect the angles of the pharynx between sets of the dilators nearer to the base of the gnathosoma (see Fig. 30). The pharyngeal lumen remains narrow except for its posterior portions, where pharyngeal walls become thinner losing their sclerotization and the lumen is rounded when the pharynx merges into the esophagus (Fig. 33). The maximum width of the pharynx is about 70–80 μm , whereas its length is up to 200 μm . Besides the pharyngeal dilators, no other muscles are present within the hypostomal space, and regions on the sides of the pharynx are filled with elements of intermediate and fat tissues.

Approximately at the level of the formation of the united gnathocoxal plate, the proximal termination of the basal cheliceral segments is observed. The inner (paraxial) walls of the basal segments terminate more anteriorly than the outer ones and leave sclerotized apodemes situated immediately beneath the tracheal trunks. These apodemes may be termed as the cheliceral apodemes because they are in close contact if are not derived from the inner

cheliceral walls. At this place, the tracheal trunks are going down to be situated at the base of the chelicerae (Figs. 25, 26). The outer (antiaxial) walls of the chelicerae terminate more posteriorly, and their dorsal portions serve for attachment of a group of muscles: elevators, retractors and protractors of the chelicerae (Fig. 1, 30–38). From these muscles, the elevators are well developed and originate on the dorsal aspect of the tracheal trunks (see below) and are directed obliquely forward and dorsad to the dorsal cheliceral walls (Figs. 30–38). The retractors and protractors of the chelicerae take their origin on the opposite sides of the crista metopica (Fig. 1). Posteriorly, the cheliceral apodemes, are slightly flattened in a dorsal-ventral plane, fused with ventral and lateral walls of the tracheal trunks and where they take a tear-shaped form (Figs. 26, 27). Posteriorly, this fusion spreads over the whole lateral and then dorsal sides of the tracheal trunks serving here as a place of muscle attachment. Apparently, the tracheal trunks play the main role in air passage. Because of the fusion with the cheliceral apodemes, the tracheal trunks in the posterior half also serve as the site of attachment of the extrinsic cheliceral muscles. In general, on their course from the stigmas to the posterior, the tracheal trunks appear as an inclined “S”-shaped figure that is seen on sagittal sections (Figs. 35, 36). Approximately at the posterior end of the pharynx and, correspondingly, at the posterior termination of the ventral gnathocoxal wall, the tracheal trunks are divided into numerous tracheal branches spreading throughout the organism (Figs. 35, 36).

The most interesting and distinct feature of the gnathosoma in adults of *P. fasciatum* is the morphological character of the bottom of the subcheliceral space, particularly the labrum and the epistome.

Posteriorly to the formation of the pharynx, the lateral walls of the hypostome are connected to each other via a thin membranous wall. This wall has a large, directed downwards bending (Figs. 24–26). There is a large cavity between this dorsal wall of the hypostome and the chelicerae known as the subcheliceral space (Figs. 23–27). Thus, the roof of the hypostome is the bottom of the subcheliceral space. Posteriorly to the chelicerae, the subcheliceral space is situated at the center of the gnathosoma. The bottom of the subcheliceral space, curved ventrally, connects the inner cuticular elements of the gnathobase (see below). The roof of the subcheliceral space is formed by membranous walls that are the posterior continuation of the ventral portions of the inner cheliceral walls and has a large

dorsal flexure (Figs. 26, 27). In contrast to classical conceptions [see Snodgrass, 1948; Evans, 1992; Alberti, Coons, 1999, etc.], the subcheliceral space expands posteriorly far beyond the basal cheliceral segments and the bodies of the chelicerae do not lie on or move upon the epistome.

It is interesting that the labrum loses the medial ridge in its posterior part and deepens under the membranous dorsal wall of the hypostome (Figs. 26, 27, 38). The labrum extends in this position approximately up to the level of the posterior end of the chelicerae. Here it is enclosed by a cuticular mass situated beneath the dorsal hypostomal wall. This cuticular mass is formed by loosely organized electron-light fibrils and cannot be classified as an apodeme. Conversely, the membranous dorsal wall of the hypostome soon acquires characteristic sclerotization and in this form may be conventionally classified as the epistome (subcheliceral plate, cervix) [Alberti, Coons, 1999]. The epistome connects the internal gnathocoxal elements (Figs. 26–28, 38). Further posteriorly, the epistome shows a ventral bend, lateral walls of which are gradually fused, and this structure is finally terminated far behind the posterior end of the labrum (Figs. 28, 29). It is important to note that the posterior portions of such a weakly developed epistome serve, nevertheless, for the attachment of the labral muscles. These muscles lead to the caudal end of the labrum nearly in a horizontal plane. In the space between the epistome and the pharynx, fibers of the obliquely arranged pharyngeal dilator muscles are present. They originate, however, not on the epistome, but on the ventral wall of the proximal chamber (see below) and on the upper portions of the deeply immersed lateral walls of the gnathocoxal plate.

It is clearly seen from this consideration that the cheliceral-epistomal complex in the microtrombidiid mite *Pl. fasciatum* has a rather atypical expression that is also observed in the organization of the proximal chamber of the subcheliceral space.

The proximal chamber is a widened proximal portion of the subcheliceral space and is situated in the center of the gnathosomal base. In this place, there are neither the chelicerae nor the epistome are present (Figs. 28–29, 36–38). Anteriorly, this chamber is flanked by two large sclerites derived from the thick dorsal portions of the hypostomal walls. These sclerites give rise to 1) the conspicuous apodemes extended obliquely in a dorsal and posterior direction to the lateral walls of the gnathocoxal plate (Figs. 28, 29) and, 2) a characteristic

sclerotized armament of the posterior end of the chamber with the most expression on the ventral and posterior walls of the later (Figs. 30, 36). This chamber receives the ducts of the salivary glands [Shatrov, 2005] and has well developed muscles. Two or three paired sets of muscles originating on the ventral wall of the chamber behind the epistome are the pharynx dilators (Figs. 29, 30, 37, 38). Several sets of well-developed muscles attach to the lateral walls of the chamber. The muscles are directed obliquely downwards to the lateral walls of the gnathocoxal plate (Figs. 28, 29). These muscles, together with the pharyngeal ones, serve for dilating the chamber providing the intake of the saliva to the chamber from the salivary ducts and, through the action of the pharyngeal dilators (the pharyngeal pump), ingestion of liquid food to the pharynx.

The proximal chamber is situated just beneath the tracheal trunks. Narrow curved channels connect the space of the proximal chamber and the tracheal trunks and may be observed in ultra-thin sections (Fig. 51). These unusual channels, however, could supposedly evolve to compensate for the air pressure in the space of the chamber. The width of the proximal chamber is about 80 μm . From the anatomical point of view, the posterior wall of this chamber appears to be the most posterior part of a frontal body wall [Snodgrass, 1948] deeply inserted into the gnathosoma. On the whole, the frontal body (cephalic) wall is going on the line from the apical termination of the dorsal body fold covering the chelicerae back to the basal parts of the basal cheliceral segments and from the posterior termination of the medial walls of the basal segments again back to the end of the subcheliceral space. In the latter case, this membranous wall is rather extensive and devoid of sclerotization.

The posterior portion of the gnathosoma is typical for most of the Parasitengona, except for the centrally located tracheal trunks. The gnathocoxal plate is strongly bent so that in transverse sections it is semicircular with a small span between the dorsal edges of its lateral walls (Figs. 31–33). The space within the gnathobase is mostly filled with various muscles: 1) the pharyngeal dilators, 2) palp depressors and elevators originating on the lateral gnathocoxal walls and invaded all the volume on the sides of the dilators (Figs. 30–33), and, 3) elevators or protractors of the chelicerae, which are originated on the dorsal aspect of the tracheal trunks and terminate on the ventral aspect of the dorsal walls of the basal cheliceral segments (Fig.

31–33). The ventral wall of the gnathocoxal plate is slightly extended inside the body. The lateral walls of the gnathocoxal plate extend far posteriorly in the body, and in their most caudal parts are abruptly curved mediad and forward. The width of the gnathosoma at its base is around 330 μm .

A body cavity situated dorsally of the gnathobase contains extrinsic muscles of the gnathosoma, i.e., dorsal retractors of the gnathosoma originating on the lateral surfaces of the deeply inserted sclerotized part of the crista, running forward and terminating on the upper sides of the lateral walls of the gnathocoxal plate (Fig. 31–35). The extrinsic muscles of the chelicerae — retractors of the chelicerae, are also present, which originate on the crista and are inserted into the most posterior portions of the dorsal cheliceral walls (Fig. 33). Besides these muscles, the powerful extrinsic muscles, ventral retractors of the gnathosoma are attached to the ventral-lateral angles of the gnathocoxal plate (Figs. 34, 35, 39). The presence of these muscles, originating on the ventral body wall, as well as the dorsal retractors, indicates that the gnathosoma is capable of moving along the axis of the body and inclining to this axis. It is interesting to note that the first leg coxae are attached to the body approximately at the level of the top of the gnathosoma. At the same time, the coxae of the first legs are also shifted anteriorly so that the gnathosoma, especially at its base, is almost completely surrounded by the leg segments. It is also worth noting that in a zone of the sensillary area, the rod of the crista is divided onto two elements, which seem to protect the sensillary (trichobotria) bases (Fig. 31). Behind the sensillary area, they are fused together again into a prominent vertical apodema, from which the extrinsic cheliceral and gnathosomal muscles originate (Fig. 32).

On sagittal sections, some features of the gnathosomal organization are seen more clearly. First of all, they are seen in respect to the proportions of the gnathosoma and its parts. At the base of the chelicerae, the proximal chamber is well presented showing close contact with the tracheal trunks in their middle parts (Figs. 37, 38). The apical termination of the tracheal trunks (stigmas) together with the bases of the basal cheliceral segments is covered from above by the integumental fold (camerostomal fold) bearing dorsally the heavy sclerotized crista (Figs. 34–36). The anterior termination of this fold, that is seen on SEM figures as a particular tongue-like structure (Fig. 11), does not look as a separate anatomical part in sections and, therefore, can hardly be classified as the tectum

typically present in trombiculid mites [Shatrov, 2000]. Most likely, this structure functionally serves for protection of the stigmas terminating over the chelicerae and has elaborated apart from the totally reduced tectum. On longitudinal sections, characteristic muscles going from the frontal parts of the crista back to the dorsal portions of the basal cheliceral segments may be found. Taking into account the apparent rigidity of the crista, these muscles may be identified as protractors of the chelicerae or gnathosoma (Fig. 38). The palps are provided with the powerful elevators and depressors inserted alternatively on the dorsal and ventral aspects of the trochanter walls, at their bicondylar articulations with the gnathosomal base (Fig. 39). The trochanter contains only depressors of the femur originating on its dorsal wall and inserted by their tendons to the ventral wall of the femur (Fig. 39). There are only depressors in the remaining palp segments. The strengthening of the palps is thought to be accomplished by hydrostatic pressure of the body [Snodgrass, 1948; Alberti, Coons, 1999]. It is interesting to note that the palp femur bears on its ventral aspect a characteristic, directed forward tooth that presumably prevents exceeding depression of the palps (Fig. 39). The whole length of the gnathosoma from the tip of the hypostome to the posterior end of the gnathocoxal plate is around 400 μm ; the length of the crista is 300 μm ; the length of the pharynx is only 200 μm ; and the length of the chelicerae is around 250 μm .

TEM observations of ultra-thin sections

TEM observations help to clarify some essential characteristic features of the organization of the mouthparts.

The labrum generally situated between and behind the movable digits, is a complicated irregularly outlined cuticular structure, which gives a vertical medial ridge with a sharpened tip extending between the chelicerae from below (Fig. 40). The labrum is composed of a cuticle variously developed in its different parts. The lateral portions of the labrum consist of electron-light and loosely arranged cuticular filaments. Its medial ridge is mostly built up from patches of uniform, electron-dense material (Fig. 40), which further posteriorly occupies the whole medial part of the labrum and has curved pore canals (Fig. 41). This material and its morphological structure closely resemble the electron-dense cuticular component of the salivary ducts walls produced at their bases [Shatrov, 2005]. Ventral and partly lateral portions of the labrum are

formed by the common fibrillar and predominantly electron-light cuticle (Fig. 41). From the outside, the labrum is enveloped by a thin electron-dense epicuticle (Figs. 40, 41). From this examination, it is obvious that the labrum is not heavily sclerotized and probably retains flexibility in its distal parts. After the insertion beneath the bottom of the subcheliceral space, the labrum loses its morphological integrity, but can be nevertheless identified by higher electron density than the surrounding cuticular mass (Figs. 42, 43).

The cuticle at the distal parts of the inner and outer hypostomal walls is extremely thick (up to 4 μm and 6 μm for the inner and outer walls respectively), electron-light and partly sclerotized from its inner portions (endocuticle) with masked fibrils (Fig. 45). It is interesting to note that the exocuticle at the bottom of the preoral cavity, where the movable digits lie, is electron-light, formed by rather loosely packed fibrils. Electron-dense vesicles are seen scattered throughout this cuticular layer (Fig. 46). They may be detached from or, conversely, attached to the outer electron-dense layer, supposedly the epicuticle (Fig. 46). At the ventro-lateral angles of the inner hypostomal wall, the sclerotized endocuticle shows large bulges extending into the space between the walls and supposedly preventing collapse of the walls and occasional damage of the digits (Fig. 46). More detailed consideration of the cuticle organization is beyond the scope of this paper. The space between the hypostomal walls contains loosely organized elements of the epithelial, connective, and fat tissues, as well as some amount of haemocytes, which tend to be placed in the proximity of the outer wall (Fig. 45).

The movable digits, despite their heavy sclerotization, are seen as rather slender segments composed nevertheless of thick sclerotized walls with an electron-dense outer and an electron-light inner portion. There is a very narrow space between the walls of the movable digits (Figs. 40, 47). These walls are connected with the distal parts of the basal segments by a folded cuticular arthrodistal membrane that permits movements of the digits (Fig. 47). The dorsal portions of the basal articulation of the digits are surrounded by a fine granular substance of a moderate electron density of still unknown function (Fig. 40).

The crescent-like pharynx, in particular its ventral convex wall, is derived from the inner wall of the hypostome and composed of a thick lamellar cuticle of moderate electron density (Fig. 48). Con-

versely, its dorsal concave wall is built from an electron-dense material with irregularly outlined basal portions and provided with conspicuous pore canals (Fig. 48). Cuticular lamellae may be rarely distinguished in the dorsal pharyngeal wall. The tendons of the dorsal pharyngeal dilators are immediately attached to this substance (Fig. 48).

In the posterior direction, the labrum as a distinct morphological structure loses its medial ridge and sinks into the prominent cuticular mass evolved in the middle part of the ventral wall (floor) of the subcheliceral space (Figs. 42, 43). This irregularly outlined cuticular mass is formed of non-sclerotized, loosely packed, and electron-light cuticular lamellae running in different directions. It may contain an internal cavity and in most posterior part loses immediate contact with the ventral wall of the subcheliceral space (Fig. 43). It is impossible to give this separate cuticular structure any clear anatomical definition, except that it contains posterior portions of the labrum. The ventral wall of the subcheliceral space, being already separated from the cuticular labral mass, especially its medial portion, acquires a particular thickness and electron density just like the dorsal pharyngeal wall (Fig. 43). Going posteriorly, this sclerite shows a ventral flexure (Fig. 44). The lateral walls of this flexure gradually close up to form a vertically oriented internal electron-dense ridge, which finally disappears. This sclerite is identified here as the epistome (see above).

The tracheal trunks in their upper halves possess only thin electron-dense cuticular walls like any other tracheae and are not provided with an additional cuticular structures or muscles (Figs. 49, 50). In the most frontal and dorsal portions, the tracheal trunks are enclosed into a particulate body fold obviously separated from the dorsal cheliceral walls (Fig. 49). Further posteriorly, ventral walls of the tracheal trunks face the narrow dorsal extension of the subcheliceral space, which spreads between the inner walls of the basal cheliceral segments and is surrounded by a thin cuticle (Fig. 50). Behind the posterior end of the chelicerae, in the area of the anterior portions of the cheliceral apodemes, the proximal dilation of the subcheliceral space, i.e. the proximal chamber, forms two curved narrow channels leading to the tracheal trunks and occupying a position between the cheliceral apodemes (Fig. 51). Rounded chambers may be seen on the course of these channels immediately beneath the tracheal trunks (Fig. 51). This construction supposedly serves for regulation of the air pressure mostly in the

proximal chamber, when the volume of the latter increases through the action of the lateral muscles (see above) and of the pharyngeal dilators.

Comparison with the larval mouthparts

The structure and composition of the larval mouthparts [Shatrov, 2001a, b] substantially differ from that of adult mites.

The larval gnathosoma is completely covered dorsally by a large dorsal shield, a derivate of the dorsal body wall. The apical parts of the hypostome form a constant terminal sucker with a particular internal armature. Small four-segmented palps face downwards by their tips, do not reach the apex of the gnathosoma and lack a large claw on their tibiae. The larval palps look functionally poorly developed, with the only supposed actions of touching the covers of the host by the small sensory tarsus. In contrast to the adult mites, the wide gnathocoxal plate of larvae has only one pair of tritorostral [Moss, 1962] or subcapitular setae of quite unusual structure [Shatrov, 2001a].

The larval gnathosoma seem to show a more generalized constitution in comparison with adults and much less derived from the hypothetical prototype, thus closely resembling the mouthparts of trombiculid mites [Shatrov, 2000]. The basal cheliceral segments are relatively longer and narrower, with a nearly flat ventral side and, in contrast to adult mites, occupy a horizontal position beneath the dorsal shield, being attached to the membranous body wall at their bases. Thus, the chelicerae are not deeply inserted into the body, but only covered dorsally by an integumental fold with the shield on its dorsal aspect. The tectum is completely reduced. Thus the chelicerae immediately lie on the epistomal plate of a quite complex structure. In contrast to the adult mites, microtrombidiid larvae are totally lacking the tracheal system and possess conspicuous cheliceral apodemes. These characters are shared with trombiculids. The cheliceral apodemes are in a form of relatively short sclerotized rods with small cavity inside, they run parallel to each other from the posterior ends of the ventral cheliceral walls obliquely downwards and posteriorly. The cheliceral apodeme serve for attachment of the cheliceral elevator muscles, which are directed upwards and towards the posterior wall of the basal cheliceral segments. The chelicerae also possess retractors originating on the posterior portions of the dorsal shield and directed to the caudal ends of the dorsal cheliceral walls. Protractors of the chelicerae are lacking in the larvae.

The slightly curved subcheliceral plate of various thicknesses and sclerotization leaves a relatively narrow subcheliceral space above it and beneath the basal cheliceral segments and the large lacunas at the lateral sides of the basal segments. These lacunas apparently serve as saliva reservoirs. This feature is not present in adults. Anteriorly, the subcheliceral plate continues to the narrow, electron-light labrum, that does not have any particular sclerotization. In the posterior direction, the subcheliceral plate (epistome) extends as separate epistomal apodemes mostly serving for attachment of the pharyngeal dilators. It is important to note that, because the labrum joins with the dorsal hypostomal walls far behind the posterior ends of the cheliceral claws, the anatomical mouth in the larvae is situated very deeply within the gnathosoma. Both the preoral cavity and the pharynx in its anterior portion are extremely large. Unlike the adults, the ventral wall of the pharynx is attached to the bottom of the hypostome and the gnathobase. In this part, the dorsal wall of the pharynx shows an abrupt dorsal flexure, although it is devoid of the pharyngeal dilators. The latter are only developed at the posterior portions of the subcheliceral plate. On the whole, the pharyngeal dilators are nearly horizontally orientated because the frontal parts of the pharynx and, correspondingly, the bottom of the gnathosoma have a nearly vertical orientation in respect with the long axis of the mite. In the posterior portion of the gnathosoma, the pharynx loses its close connection with the bottom of the gnathosoma, although does not display the ventral dilators. From the ventral position, the integumental fold of the ventral body wall covers the posterior portion of the gnathosoma, as in the adult mites.

DISCUSSION

As seen from this investigation, the organization of the mouthparts in adult mites of *P. fasciatum* does not show any strong specialization both in composition and in proportions of the gnathosoma, and generally corresponds to the acarine model proposed by Shodgrass [1948]. Nevertheless, the studied mouth organs reveal some particular differences from this model especially in respect with the organization of the epistome and subcheliceral space. In contrast to adults of trombiculid mites [Brown, 1952; Mitchell, 1962; Shatrov, 1985, 2000], the tectum and the ventral pharyngeal dilators are totally reduced in the composition of the gnathosoma in *P. fasciatum*.

Among three works dealing with morphology of trombiculid mites *sensu lato* [Henking, 1882; Moss, 1962; Mathur, LeRoux, 1965], only the latter contains a detail description of the mouthparts. At the same time, the work of these authors contains many contradictions between description and bad drawing figures, some of which may be ascribed to difficulties in interpretation of sections by the authors. A comparison of mouthparts of *P. fasciatum* and *Allothrombium lerouxi* Moss [Mathur, LeRoux, 1965] reveals several differences in the organization of the gnathosoma between the two species. The gnathosoma of *A. lerouxi* is somewhat larger than that of *P. fasciatum* and only partially covered by the dorsal integumental fold. Mathur, LeRoux [1965] report the subcheliceral sclerite lying beneath the chelicerae, but do not figure it in transverse sections. The epistome, as a particular sclerite, is shown at the base of the chelicerae, where, however, no any sclerotized element on the floor of the subcheliceral space is situated in *Pl. fasciatum*. The so called epipharynx cannot be identified in *P. fasciatum* as a separate morphological structure as well. After the formation of the pharyngeal lumen, the membrane derived from the ventral labral portion immediately transforms into the dorsal pharyngeal wall and cannot be interpreted as a roof of the preoral cavity. In contrast to *A. lerouxi*, the tracheal trunks (sigmoid pieces) of *P. fasciatum*, do not attach to the epistomal apodeme (absent in this species), and acquire sclerotization only at their posterior halves after joining with a sclerite that can be interpreted as the cheliceral apodeme. Mathur and LeRoux [1965] indicate that the floor of the pharynx is firmly attached to the ventral wall of the gnathosoma, although their figures state otherwise. However, the obvious differences in the organization of the gnathosoma between these two species do not appear to be so dramatic, and the main characteristics of the mouthparts are expected to be similar. Henking [1882] has reported a quite similar organization of the gnathosoma of *Trombidium fuliginosum* Herm. to that found in this study. However, he depicts the ventral pharyngeal wall detached from the gnathosomal bottom in its posterior half, and the ventral dilators in this place are shown.

A comparison of the mouthparts of adult forms of the closely related family Trombiculidae [Wharton, 1946; Brown, 1952; Mitchell, 1962; Shatrov, 1985, 2000] indicates that representatives of this quite specialized family show at the same time more generalized characteristics in the organiza-

tion of the gnathosoma than *P. fasciatum*. First, adults of trombiculids retain the ancient tectum, the derivate of the embryonic head lobe. Second, they also retain, at least *Hirsutiella zachvatkini* (Schluger) [Shatrov, 1985, 2000], the ventral pharyngeal dilators. Because trombiculids are lacking the tracheal system, the tracheal trunks are also absent in this group, whereas the large cheliceral apodemes (sigmoid pieces) are present and play a role in axial motion of the basal cheliceral segments [Brown, 1952; Mitchell, 1962; Shatrov, 1985, 2000]. Conversely, this function, together with separate powerful cheliceral apodemes, is apparently reduced in *P. fasciatum*. In this species, the cheliceral apodemes are developed as doubled structures, as the sclerotized elements behind the inner cheliceral walls and as a particular sclerotization of the walls of the tracheal trunks serving at their posterior portions for origination of the cheliceral elevator muscles. It is important to note that in trombiculids, inside the cheliceral apodemes there are cavities corresponding to reduced tracheal trunks.

The question of the origin of the cheliceral apodemes is discussed in the literature [Mitchell, 1962; Mathur, LeRoux, 1965]. Within the Parasitengona, these sclerites are also present in water mites [Mitchell, 1955, 1962; Zhavoronkova, 1990a, b, 1992, 1993; etc.]. Apart from the Parasitengona, they were found in the Tetranychidae [Blauvelt, 1945; Andre, Remacle, 1984], Anystidae, and Halacaridae [Witte, 1991], and in all cases seem to be associated with the tracheal trunks. Such a location of the cheliceral apodemes led Mathur and LeRoux [1965] to a conclusion, after Mitchell [1962], that “the sigmoid piece is an elaborate sclerotization of the tracheal wall that secondarily assumes a role in cheliceral movement” (p. 44). Nevertheless, the situation in *P. fasciatum* indicates that the cheliceral apodemes, at least in their anterior portions, may evolve independently of the tracheal trunks obeying the functional necessity. For example, in the specialized mouthparts of adults of the Erythraeidae, tracheae do not have any additional skeleton or muscle elements and, correspondingly, do not have any additional functional properties [Witte, 1978], whereas their larvae possess the capitular apophyses, a presumed homologue of the sigmoid piece. In the Actinedida (=Prostigmata), in general, the anterior end of the tracheae predetermines the appearance of the particular sclerotization around their proximal portions and frequently serve for attachment of the extrinsic cheliceral muscles. Thus, such a sclerotization, better developed in trombiculids

and water mites, may be considered as a synapomorphy of this group. It is interesting to note that in water mites, an obvious secondary specialization is occurred. Particular skin transpiration has evolved with termination of the tracheae within the cuticle just beneath the epicuticle [Mitchell, 1972] that apparently led to dysfunction of the tracheal trunks. In these cases, the sigmoid pieces function only as cuticular or cheliceral apodemes.

Although heteromorphic six-legged parasitic larvae of the Parasitengona are expected to be more specialized in comparison with adults, they appear to have a more reductive type of mouthparts, except for the particular sucking armature of the hypostome [Wharton, 1946; Jones, 1952; Witte, 1978; Shatrov, 1981]. Larvae of trombidids and trombiculids lack tracheae and the sigmoid pieces are reduced to relatively short cuticular rods named the cheliceral apodemes, which retain the cavities remaining from the lost tracheal ways. Also, larvae are lacking the tectum and the ventral pharyngeal muscles. Moreover, in most cases, their ventral pharyngeal wall seems to be fused with the hypostomal bottom to strengthen the action of the dorsal pharyngeal dilators. The latter, in contrast to adult mites, has nearly an axial orientation within the gnathosoma.

Larvae of the Parasitengona do not recapitulate the possible phylogenetic prototype but demonstrate a particular regression or, most likely, a sort of underdevelopment of some features that are normally present in adults of this lineage of the Acariformes. Simultaneously, such a reduction or underdevelopment, influenced by des-embryonization of the larval stage, leads to a progressive specialization and may be regarded as a synapomorphy. As a result, the larvae reveal more simple and progressive morphology than more generalized adults, and in a hypothetical case of progenesis could give rise a principally new branch of the Acariformes.

In spite of the fact that the active postlarval instars of trombiculid mites show some specialization and apparent secondary simplification owing to the soil dwelling (the absence of eyes and pigmentation) and extra-oral digestion (closing of the midgut), the manifestation of some morphological characteristics of their mouthparts (the presence of the tectum and the ventral dilators) apparently shows that they appear to be a more basal lineage than trombidids.

The sucking of trombidid and trombiculid adults, is accomplished by the combined action of

the saliva-pharyngeal pump [Mathur, LeRoux, 1962; Shatrov, 1981, 2000]. As a consequence of the structure of the subcheliceral space, labrum, and anterior origination of the pharyngeal dilators on the epistome, in deutonymphs and adults of trombiculid mites, one can expect a coordinated action of the saliva-pharyngeal pump. However in *P. fasciatum*, the main role for saliva pumping is probably belonged to the proximal chamber and its powerful lateral muscles, whereas the bottom of the subcheliceral space (epistome) is a quite flexible and labile structure lacking any powerful muscles and obviously it cannot play an important role in a saliva discharge. The pharyngeal pump presumably acts independently from the saliva stream through the action of the dorsal pharyngeal dilators originating on the dorso-lateral edges of the lateral walls of the gnathocoxal plate.

Mechanism of suction was examined in some trombidid larvae parasitizing insects [Wharton, 1946] and on both larvae and adults of the water mite *Hydrachna conjecta* Koenike [Davids, 1973]. The feeding mechanism was also observed in various species of water mites [Zhavoronkova, 1990a, b, 1992, 1993, 1999]. Wharton [1946] reported that before injection into a wound, saliva flows into the preoral cavity and the pharynx and then is forced into the host tissue by the action of the pharyngeal pump. Davids [1973] observed that fixation of *H. conjecta* on the host is mediated by the palp claws hooking the host integument facilitating thereby the piercing of the host cuticle by the chelicerae from the other side. Other species of water mites either stick to the victim (larvae of chironomids) by the sucker and then pierce its integument through the action of the chelicerae (*Limnochara aquatica* (L.) and *Eylais* spp.) [Zhavoronkova, 1990b, 1992], or hold the food by the palps that helps to pierce the integument of the victim by the chelicera from the opposite direction (*Limnesia maculata* (Müller) and *Terrenticola amplexa* (Koenike)) [Zhavoronkova, 1993, 1999] just like it was described by Davids [1973]. Besides that, water mites may use their legs and palps for catching and grasping the victim (host) [Davids, 1973]. Adults of trombiculid mites feeding on insect eggs, after touching the potential food by their palp tarsus, clasp the egg by the palps armed with claws from above whereas the hypostome and chelicerae act from the opposite direction piercing the egg [Shatrov, 2000]. Unfortunately, the exact mode of feeding is still unknown in trombidid adults. Nevertheless, it may be supposed that the feeding behavior is similar to that

found for trombiculids, as their long palps are nearly identical to that of trombiculids and act for grasp and hold the victim while the cheliceral claws pierce its integument. Conversely, adult mites of *Leptus* sp. (Erythraeidae) penetrate strongly sclerotized cuticle of hosts only with their long and slender chelicerae, apparently without any help from the palps [Baker, 1982].

Water mites demonstrate a wide variety of morphological organization of the mouthparts within the general principles described and discussed here for the Parasitengona [Schmidt, 1935; Mitchell, 1955, 1962b; Zhavoronkova, 1990a, b, 1992, 1993, 1999]. It is interesting to note that among water mites one ecological group shows an exceeding development of the sucker formed by the distal portion of the hypostome, like in trombidiid larvae, whereas another group demonstrates long chelicerae and a cone-shaped hypostome without the sucking disk [see Mitchell, 1962b for discussion].

Other actinedid groups, such as Tetranychidae [Becker, 1935; Blauvelt, 1945; Baker, Connell, 1963; Summers et al., 1973; Akimov, Yastrebtsov, 1981; André, Remacle, 1984; Alberti, Crooker, 1985; Nuzzaci, Lillo de, 1991], Cheyletidae [Summers, Witt, 1971; Hallas, 1982; Akimov, Gorgol, 1984, 1990], Anystidae [Yastrebtsov, Gorgol, 1991; Akimov, Badanin, 1999], Ereynetidae [Badanin, 2000], Myobiidae [Paran, 1982] and some others [Nuzzaci 1979; Akimov et al., 2002] display various specializations in the structure of their gnathosoma more or less differed from the type of the mouthparts generally specified for the Parasitengona. A detailed discussion is available in works of Lange [1962], Evans [1992], Alberti and Coons [1999], and Akimov et al. [2002]. It is important, however, that the general course of evolution of the mouth organs within the Actinedida is directed, on the one hand, to a somewhat simplification (for instance, to the reduction of the subbasal (third) segment of the chelicerae (which is found in the Anystidae) and their movable digits) and, on the other hand, to the elaboration of the special fixation and piercing mechanism. The latter is mostly expressed in the development of characteristic stylets (Tetranychidae and Cheyletidae) and the sucking apparatus variously developed in the Parasitengona, especially in water mites. In particular, water mites display the course of specialization from the cone-shaped mouthparts, with long piercing chelicerae to a rather specialized gnathosoma provided with variously developed sucking disks and biting cheliceral claws [see Mitchell, 1962b].

Thus, in general, the evolution of mouthparts, at least within the Parasitengona, is thought to have led from the cone-shaped slender gnathosoma armed with long chelicerae and relatively small movable digits to the short and wide gnathosoma bearing stout basal cheliceral segments movably articulated with the powerful blade-like cheliceral claws. Simultaneously, such an organization of the gnathosoma is influenced the development of a wide pharynx provided with the powerful pharyngeal sucking pump. Besides that, the palps appear to become shorter, apparently losing many of their original sensory functions as well as functions in catching of prey. Larvae of the Parasitengona seem to display most of these characters, and the organization of their mouthparts may be considered as progressive.

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