

**SOME ASPECTS OF TROPHIC SPECIALIZATION IN BOTH FREE-LIVING AND PARASITIC PROSTIGMATID MITES (ACARI: ACTINOTRICHIDA) FROM THE MORPHO-FUNCTIONAL VIEWPOINT**

**НЕКОТОРЫЕ АСПЕКТЫ ТРОФИЧЕСКОЙ СПЕЦИАЛИЗАЦИИ СВОБОДНОЖИВУЩИХ И ПАРАЗИТИЧЕСКИХ КЛЕЩЕЙ-ПРОСТИГМАТ (ACARI: ACTINOTRICHIDA) С МОРФО-ФУНКЦИОНАЛЬНОЙ ТОЧКИ ЗРЕНИЯ**

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**ABSTRACT**

Some functional characteristics of the suctorial type of gnathosoma in various prostigmatid mites are analyzed. The activity of the labrum including its possible role in the hermetization of the preoral cavity is considered. The oligomerization processes of the muscular complexes of the gnathosoma as well as the functional substitution of its structures are discussed. As a whole, the trophic specialization of mite species studied is characterized by the various morphological adaptations of their mouthparts. These structural transformations of the gnathosoma are more flexible if compared with its muscular system being rather more conservative.

**РЕЗЮМЕ**

Анализируются некоторые функциональные особенности гнатосомы сосущего типа у различных клещей-простигмат. Рассматриваются функции лабрума, включая его возможную роль в герметизации предротовой полости. Обсуждаются процессы олигомеризации мышечных комплексов гнатосомы, а также функциональная субституция ее структур. В целом, трофическая специализация изученных видов клещей характеризуется разнообразными морфологическими адаптациями их ротовых органов. Подобные структурные преобразования гнатосомы являются более лабильными в сравнении с ее довольно консервативной мышечной системой.

**INTRODUCTION**

Numerous adaptations of the mouthparts to various nutritional patterns in the representatives of Acarina are comparable to the great diversity of the trophic specialization found in insects [Alberti & Coons, 1999]. Prostigmatid mites are characterized by the greatest variety of the mouthparts among other mite groups. Possibly it resulted from their evolutionary success in the exploitation of the wide range of food resources in various habitats. However, only structural changes in the gnathosoma were studied for many mite taxa while the characters of its functional anatomy were often unknown, especially in the free-living forms. Thus, the aim of this work was to analyze the functional characteristics of some gnathosomal structures in the representatives of Prostigmata, mainly predatory forms and parasites of animals.

**MATERIALS AND METHODS**

The following prostigmatid mites were studied:

— Anystidae: *Chaussieria venustissima* Berlese, 1882; *Tarsotomus* sp.;

— Bdellidae: *Bdella iconica* Berlese, 1923; *Biscirus silvaticus* Kramer, 1881;

— Ereyenetidae: *Riccardoella oudemansi* Thor, 1904.

The laboratory culture of *R. oudemansi* were reared on slugs *Deroceras reticulatum* (Agriolimacidae), *Limax maximus* (Limacidae) and *Arion subfuscus* (Arionidae).

Standard anatomical and histological methods were used for the preparation of slides for light microscopy. The whole specimens were fixed in the Dubosque-Brazil modification of Bouin's fixative mainly for 5–6 d (except for *R. oudemansi*, 3 d), embedded in paraffin wax (melting point 56°C), sectioned at 4 to 8 µm and stained in haematoxylin and eosin. The mites were embedded also in Epon-812, then sectioned at 1 µm on LKB-III ultramicrotome and stained with 1% methylene blue (1:1 with 1% borax solution). For general observation, the total slides of all the above species were stained with picroindigocarmin (1% water solution).

Abbreviations used in the figures:

**Structural elements:** aap — arc-shaped cheliceral apodeme; ac — atrial cavity; ala — S-shaped articulation of labrum; cg — cheliceral groove; ch — chelicera; cpc — podocephalic channel; cs — capitular saddle; cv — cervix (epistome, subcheliceral plate); cxa — coxal apodeme of pedipalp; df — fixed digit of chelicera; dg — duct of infracapitular gland; dm — movable digit of chelicera; fe — femur; ge — genu; la — labrum; lap — lateral cheliceral apodeme; lf — labral fold (epipharynx); ll — lateral lip of malapophysis (hypostome); lr — lateral ridge of infracapitulum, oe — oesophagus; or — buccal orifice; pa — pedipalp; pc — preoral cavity; pch — principal article of chelicera (cheliceral body); ph — pharynx; sc — sclerite; se — dorsal septum of pharynx; sg — salivary groove; t — trachea; ta — tarsus; tb — tibia; tch — apodeme of cheliceral trochanter; tla — tendon of labral depressor; tr — trochanter of pedipalp.

**Muscular elements:** abd — abductor muscles; add — adductor muscles; con — constrictor muscles; dep — depressor muscles; dil — dilator muscles; ext — extensor muscles; lev — levator muscles; protr — protractor muscles; retr — retractor muscles; spm — salivary pump muscles.

## RESULTS AND DISCUSSION

The swallowing mechanism in mites having the suctorial gnathosoma is characterized by a specific interaction between chelicerae and infracapitulum resulting in complex relationships between salivary pump and pharynx. In spite of the differences in the trophic specialization of the studied species, there are some typical characteristics of their mouthparts.

### Adaptive changes of chelicerae

Evolutionary changes of the gnathosoma in actinotrichid mites were reflected in both: its adaptations to the feeding on mainly solid food sub-

strates (in acaridids and oribatids) and to the suction of the liquid food (prostigmatids).

The three-articulated chelicerae moving independently, like in Anactinotrichida, are supposed to be a plesiomorphic condition [Alberti, Coons, 1999]. However, they are modified in various actinotrichid groups so that cheliceral trochanter is reduced to ventral or ventrolateral apodemes [Hammen, 1982]. Moreover, the chelae were a subject to the considerable changes, as well. The numerous forms of Acaridida and Oribatida, as well as many endeostigmatic mites, have the typical powerful chelae adapted to the feeding on the solid food. Otherwise, the chelicerae of most prostigmatid mites were modified in different ways, mainly for piercing or cutting animal or plant tissues. So, the predatory bdellids possess extremely elongate chelicerae with small terminal chelae whereas the chelicerae of anystids have only sickle-shaped movable digit (Figs. 1; 2, 2; df, dm).

The adaptive changes of the chelicerae to piercing are characterized by the processes of their transformation in the stylet-like mode that cause the integration within gnathosomal structures. So, shift of the movable digit from its typical terminal position to the subterminal one, e. g. in ereynetids [Badanin, 2000] may be considered as the first step of such changes. The dynamics of the movable digit should be dependent on the processes of its retraction and protraction only (Fig. 3, 1; dm, protr. dm, retr. dm) that was found before in Penthaleidae [Di Palma, 1995]. Moreover, the chelicerae of Ereyneidae like Penthaleidae [Nuzzaci, de Lillo, 1991b] are characterized by the partial fusing of their bases. As it was stated, the chelicerae of Hydrachnidae are not simply completely fused to each other, but also with the pedipalp forming the uniform sucking organ [Mitchell, 1962].

The transformations of the chelicerae into the true stylets in prostigmatid mites are related to the more deep integrative processes of the gnathosoma. In tetranychid mites they are the result of the formation of the movable stylophore [Blauvelt, 1945; Akimov, Yastrebtsov, 1981] though in cheyletids and tarsonemids this structure is fused with the infracapitulum as stylophore capsule [Alberti, Coons, 1999]. However, these styletiform structures are not homologous resulting from their different origin. So, the cheliceral stylets of Tetranychidae, Tenuipalpidae and Cheyletidae are considered as the derivatives of the movable digits [Nuzzaci, de Lillo, 1989, 1991a; Akimov, Gorgol, 1990]. Meanwhile, the stylet-shaped chelicerae of Eryth-

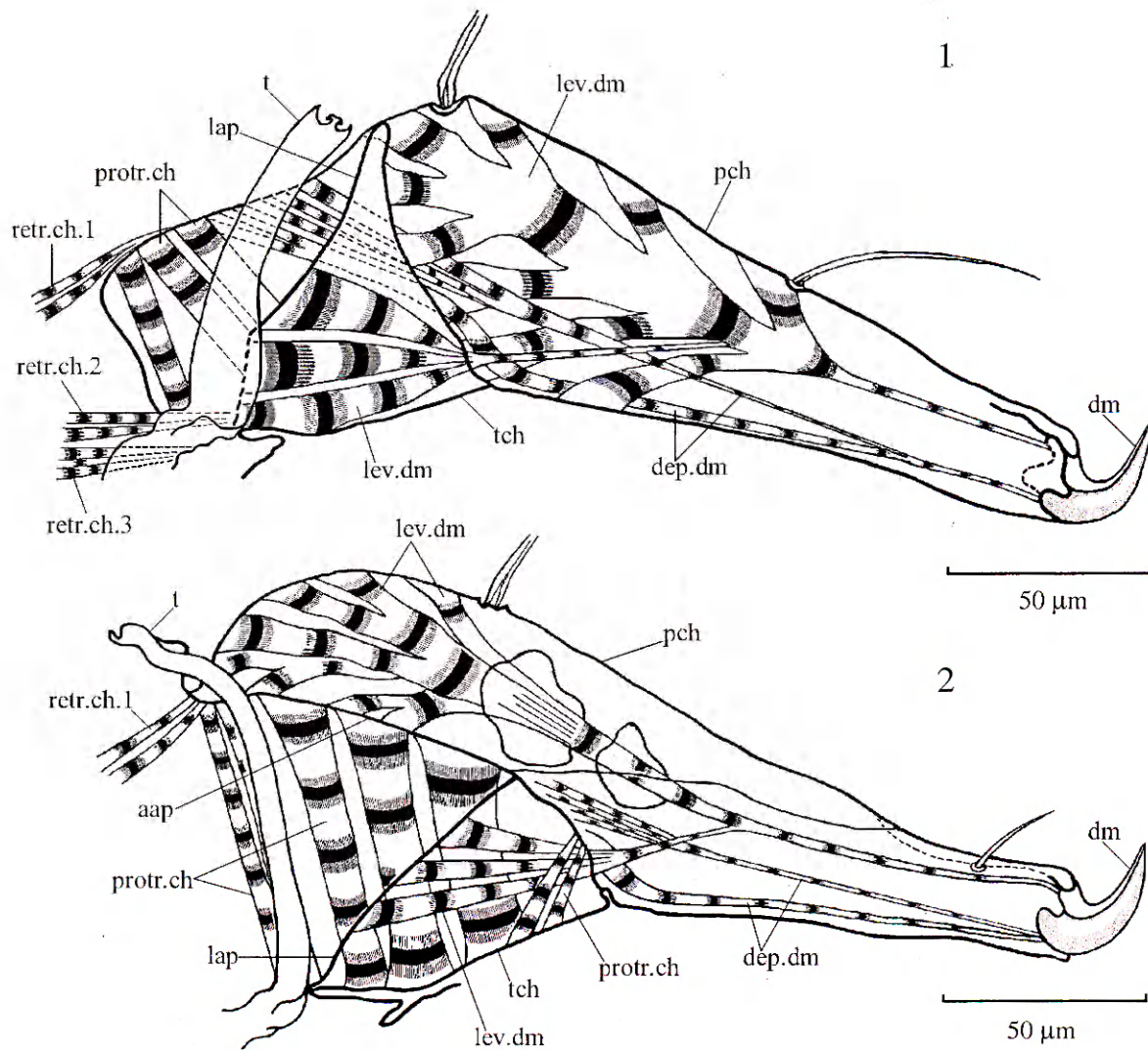


Fig. 1. Anatomical characteristics of chelicerae in anystid mites (longitudinal axial view): 1 — *Tarsotomus* sp.; 2 — *Ch. venustissima*.

Рис. 1. Анатомические особенности хелицер клещей сем. Anystidae (вид сбоку, аксиально): 1 — *Tarsotomus* sp.; 2 — *Ch. venustissima*.

raeoidea are represented by only the reduced cheliceral bodies [Witte, 1978, 1995].

#### Adaptive changes of pharynx and salivary pump

The chelicerae of the studied species are interlocked with the longitudinal grooves bordered by the lateral ridges of the infracapitulum (Figs. 3, 1; 4, 1; 1r). These cheliceral grooves are separated from each other by the median salivary groove sunk into the cervix (Figs. 2, 1, 3; 5; cg, cv, sg). The latter can also bear the capitular saddle as in bdellids (Figs. 2, 1c, d; 5, 1a; cs). Distally, the cervix is jointed with the labrum by non-condylar S-shaped articulation (Figs. 2, 1d; 3, 1; 4, 5, 2; ala, cv, la). Moreover, the paired ducts of the infracapitular glands of bdellids may be opened behind the labral

articulation [Alberti, 1973] or continued inside the lateral lips of the malapophyses (endites of the palpal coxae) to open into the preoral cavity immediately (Figs. 2, 1, 3; 5; dg, ll, pc).

Proximally, the cervix, covered by the chelicerae, forms so-called atrial cavity which volume is dependent on the pharyngeal dilators' activity. These muscles are related to the cervix in Anystidae [Akimov, Badanin, 1999], Bdellidae [Alberti, 1973] and many other prostigmatid mites. Therefore dilatation of both, the pharynx and the atrial cavity, are synchronous (Fig. 4, 1; ac, cv, dil. ph). It is important that paired podocephalic ducts are opened just into this cavity. Thus, the constriction of the latter causes an ejection of the secrets into salivary groove (Figs. 2, 1a,b, 3b; 3, 1; 4, 1; cpc, sg). Such a simple organization of the salivary pump stated before in

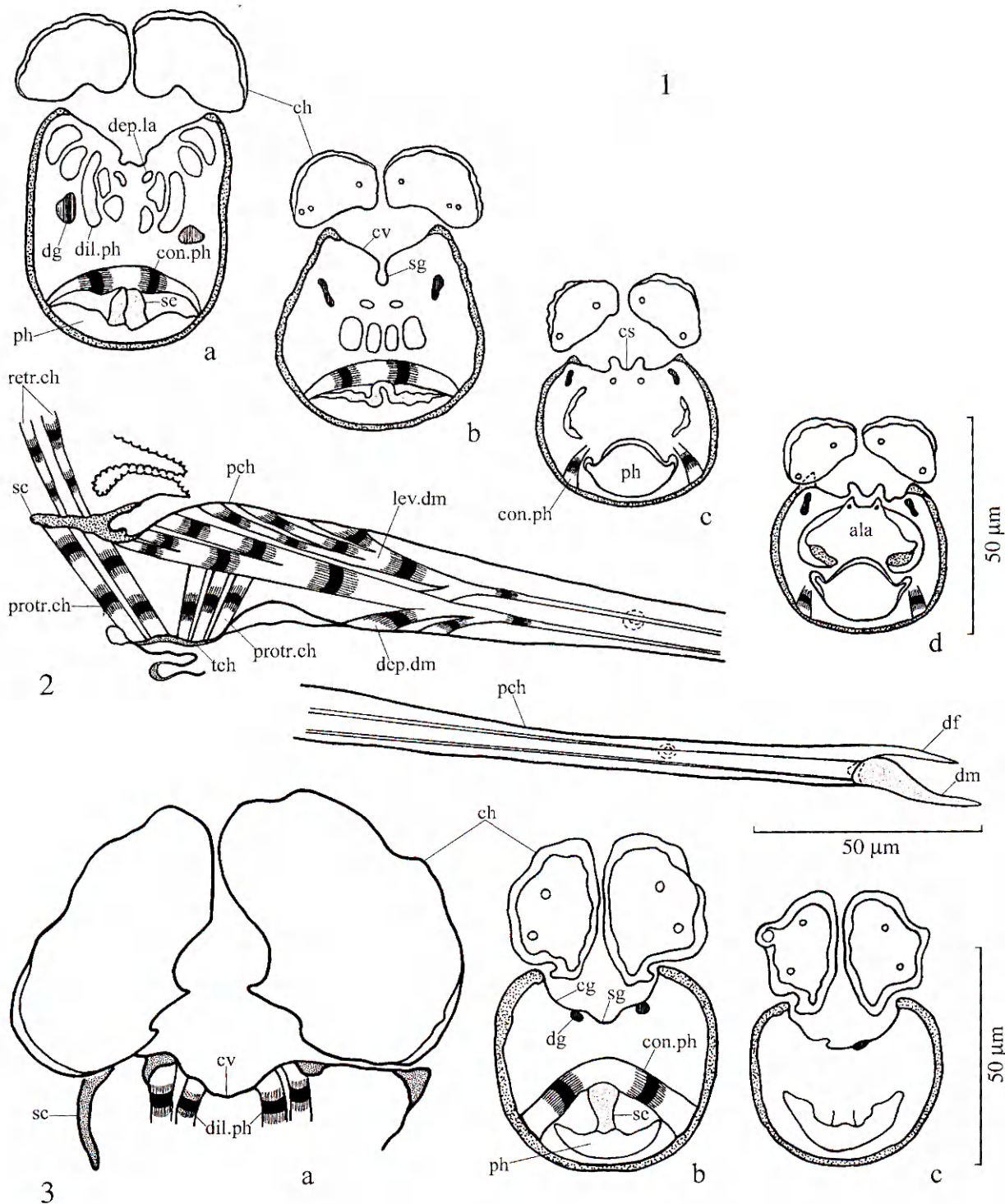


Fig. 2. Anatomical characteristics of chelicerae and infracapitulum in bdellid mites: 1 — *B. silvaticus*, cross sections through gnathosoma from its middle part (a) to the level of labral base (d); 2 — *B. silvaticus*, longitudinal axial view of chelicera; 3 — *B. iconica*, cross sections of postcoxal region of gnathosoma.

Рис. 2. Анатомические особенности хелицер и инфракапитула клещей Bdellidae: 1 — *B. silvaticus*, поперечные срезы гнатосомы от ее середины (а) до уровня основания лабрума (d); 2 — *B. silvaticus*, хелицера, вид сбоку, аксиально; 3 — *B. iconica*, поперечные срезы посткоккальной области гнатосомы.

trombiculid mites [Shatrov, 1985] is possibly typical for some groups of Prostigmata.

The further complication of the salivary pump may be associated with the formation of the close salivary groove separated from the chelicerae by

the membranous septum, like in Calyptostomatoidea and Erythraeoidea [Witte, 1991]. Proximally, the median salivary groove of ereynetids is also closed due to the fusion of the cheliceral bases. Hence, the typical atrial cavity is absent though the

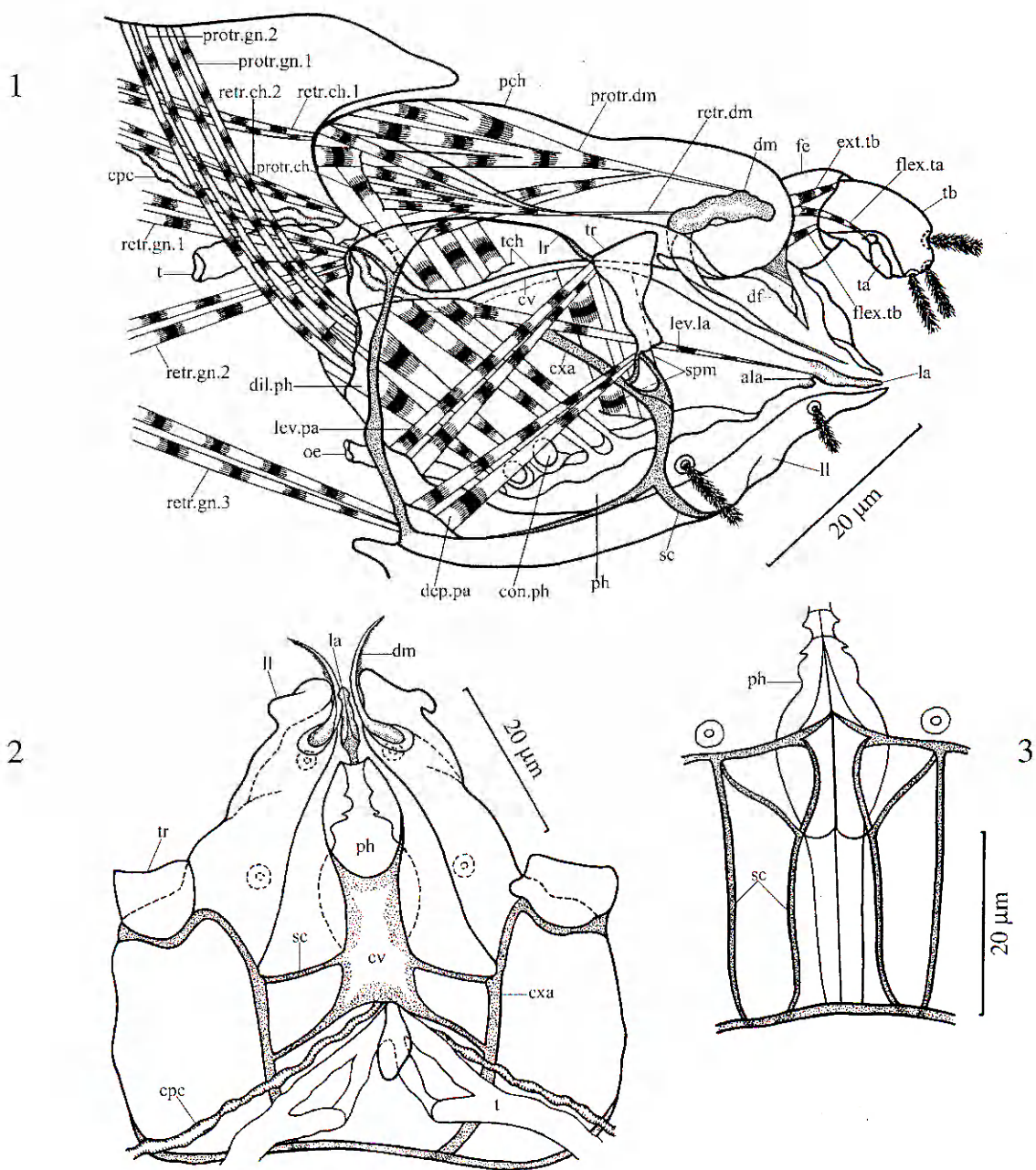


Fig. 3. Skeletal-muscular organization of gnathosoma in the mite *R.oudemansi*: 1 — topography of gnathosomal muscles, lateral view; 2 — infracapitulum, dorsal view (chelicerae removed); 3 — the characters of sclerotization of pharyngeal complex, ventral view.

Рис. 3. Скелетно-мышечная организация гнатосомы клеща *R.oudemansi*: 1 — топография мышц гнатосомы, вид сбоку; 2 — инфракапитулум, вид сверху (хелицеры удалены); 3 — особенности склеротизации глоточного комплекса, вид снизу.

cervix is still provided with specialized muscles. So, this complex is acting like some kind of the salivary pump (Fig. 3, 1; cv, spm). It is to be noted that salivary pump's muscles should be homologous to anterior pharyngeal dilators, although other dilator muscles are originated from the coxal apodemes, contrary to Anystidae and Bdellidae (cf. Figs. 3, 1, and 4, 1; cv, cxa, dil. ph, spm). Meanwhile, the attachment of the dilator muscles to the

posterior and lateral capitular apodemes was found also in various water mites [Mitchell, 1962; Zhavoronkova, 1990 a, b]. Moreover, the median salivary duct of tetranychid mites [Blauvelt, 1945] may be of interest because it is provided with anterior dilators, too. These muscles are probably homologous to the ones found in ereynetids [Badanin, 2000]. Thus, the mouthparts of Ereynetidae may be an example of the specific functional

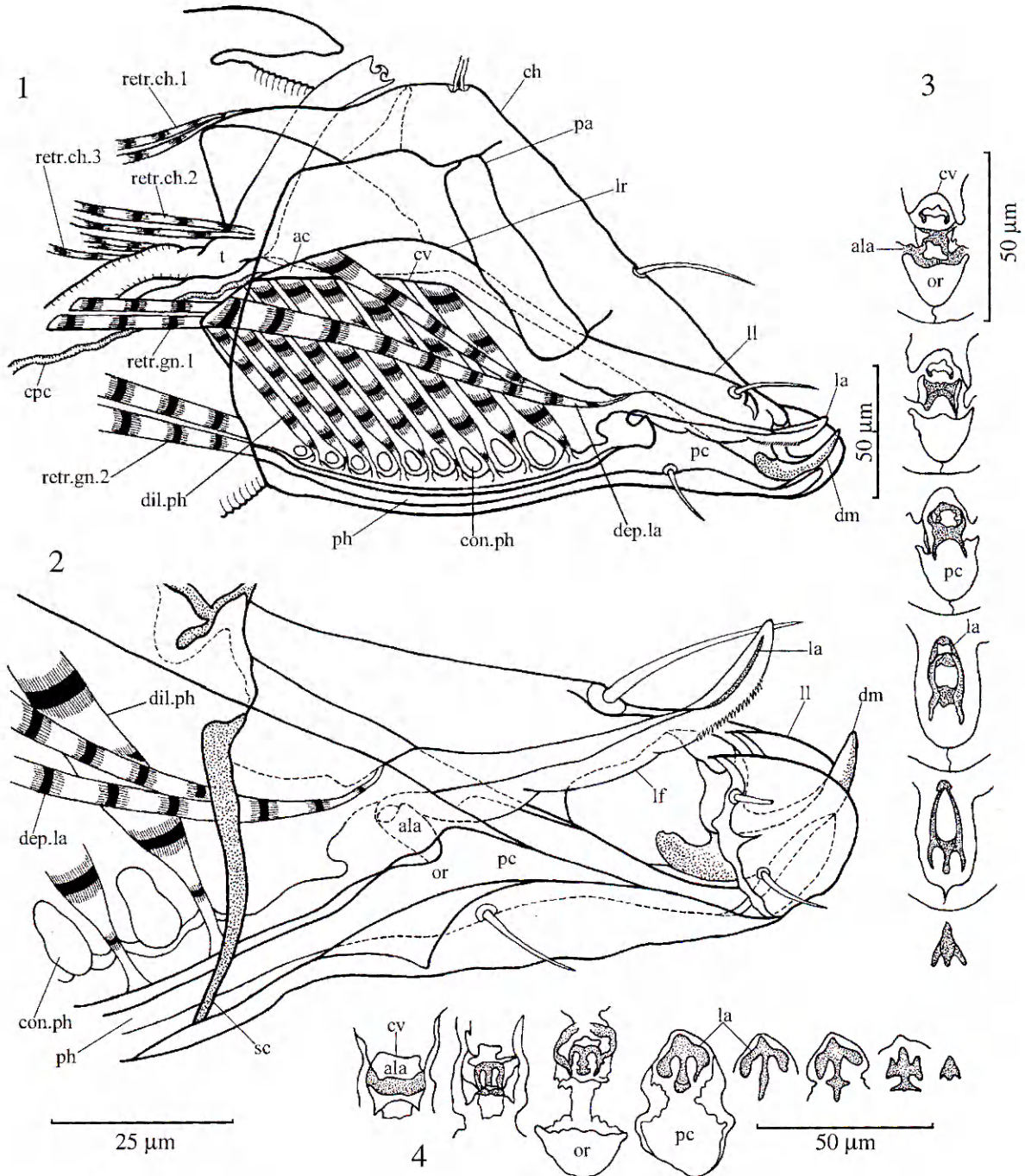


Fig. 4. Organization of pharyngeal pump and labrum in anystid mites: 1 — *Tarsotomus* sp., topography of pharyngeal and labral muscles, lateral view; 2 — *Tarsotomus* sp., structural characters of labrum, lateral view; 3 — *Tarsotomus* sp., serial cross sections of labrum (slightly oblique); 4 — *Ch. venustissima*, serial cross sections of labrum (slightly oblique).

Рис. 4. Организация глоточного насоса и лабрума клещей сем. Anystidae: 1 — *Tarsotomus* sp., топография мышц глотки и лабрума, вид сбоку; 2 — *Tarsotomus* sp., структурные особенности лабрума, вид сбоку; 3 — *Tarsotomus* sp., серия поперечных срезов лабрума (слегка наклонно); 4 — *Ch. venustissima*, серия поперечных срезов лабрума (слегка наклонно).

substitution of the gnathosomal structures. So, the cervix containing the salivary duct acts as the salivary pump, whereas the coxal apodemes are providing the background for the attachment of the pharyngeal dilators.

The pharyngeal and salivary pumps' activities are closely related to the functional organization of

the labrum provided with paired well-developed muscles. The dynamics of this structure should be determined, first of all, by the characters of its muscles' attachment (Figs. 2, 1; 3, 1; 4, 1, 2; 5, 1a, 2; dep. la, la, lev. la, tla). So, the labral muscles in anystid mites act as the depressors due to their attachment to the posterodorsal surface of the la-

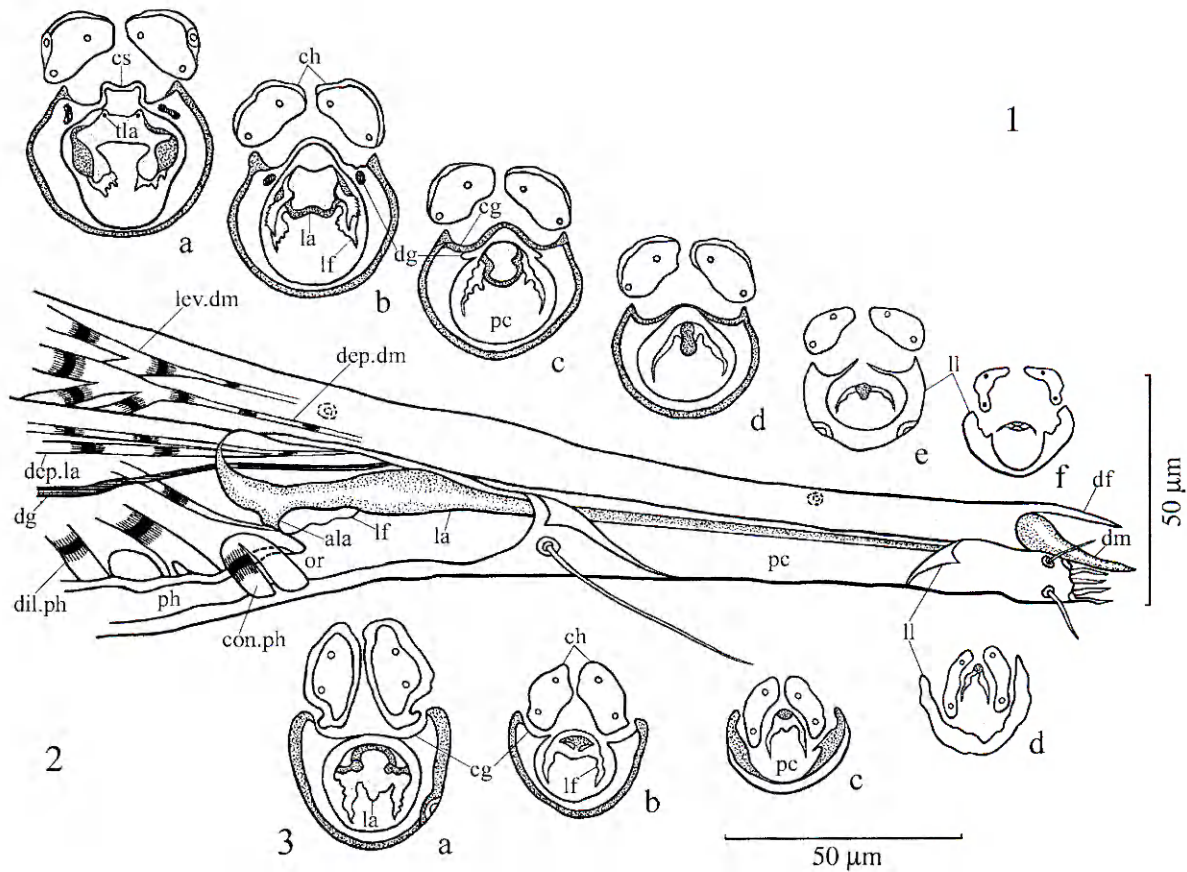


Fig. 5. Structural characteristics of labrum in bdellid mites: 1 — *B. silvaticus*, serial cross sections of labrum; 2 — *B. silvaticus*, lateral view of labrum; 3 — *B. iconica*, serial cross sections of labrum.

Рис. 5. Структурные особенности лабрума клещей сем. Bdellidae: 1 — *B. silvaticus*, серия поперечных срезов лабрума; 2 — *B. silvaticus*, лабрум, вид сбоку; 3 — *B. iconica*, серия поперечных срезов лабрума.

brum. Furthermore, *Ch. venustissima* have not only the levators of the labrum but also its depressor muscles [Akimov, Badanin, 1999; Akimov et al., 2000] The latter are typical for bdellids whereas ereynetids have the labral levators only. As a whole, the labrum is capable also to make insignificant retractable movements due to the absence of a true condylar articulation between it and the cervical apodeme.

The functional characteristics of the labrum may be of certain importance for understanding of its interaction with the pharyngeal pump. However, the suction of the liquid food should be optimal when the gnathosoma is capable to be sealed during feeding. In this respect highly adapted prostigmatid mites demonstrate the different modes of their mouthparts hermetization. Some phytophagous mites, e.g. Tetranychidae and Tenuipalpidae [Nuzzaci, de Lillo, 1989, 1991 a, b], as well as free-living and parasitic Cheyletidae [Akimov, Gorgol, 1990] possess an extremely narrow preoral cavity covered by the labrum. The latter is flanked laterad by the stylets and bordered dorsad by nearly fused

lateral lips. Furthermore, all these mite groups have the “inferior commissure channel” (decompression opening) acting as the safety valve [Nuzzaci, de Lillo, 1989] due to its possible interaction with a labrum. Another ways of the hermetization of the preoral cavity may be associated with the formation of the provisional structures like stylostome of trombiculids [Shatrov, 1983], water mites [Baker et al., 1991] or parasitic ereynetids [Baker, 1973]. The various sucker-shaped structures of the gnathosoma found in water mites [Zhavoronkova, 1990 b; Alberti, Coons, 1999] have likely certain significance for the hermetization processes, too.

In contrast to mentioned above groups the predatory anystids and bdellids have no specific adaptations for the hermetization of the preoral cavity during their feeding. However, when their highly movable powerful labrum gets down, it is formed the provisional median cavity (food channel), bordered by the inner labral walls (Figs. 4; 5; la, pc). These characteristics of the labrum may be considered as a proof of the efficiency of the hermetization processes, enabling these mites to

suck the liquid food. Moreover, the massive folds (epipharynx) of the labrum are bearing an evidence of its possible role as the remigial structure being partly capable for the filtration the food (Figs. 4, 2; 5; la, lf). The similar pectinate soft structures of the labrum were found earlier in some saprophagous acaridid mites adapted to feeding on various liquefied organic substrates [Akimov, 1985]. Meanwhile, the labrum of ereynetids is strongly reduced that may be associated with an adaptation of these mites to feeding on the mucous substrates (in particular, on the slugs' mucus) (Fig. 3, 1, 2; la).

The characters of the pharyngeal pump's organization may be dependent on the different modes of the mites feeding. So, predatory anystids are capable to suck the highly heterogeneous contents of various small arthropods, i.e. their hemolymph mixed mostly with the fragments of the digestive system. Otherwise, bdellids have an extraintestinal digestion [Alberti, 1973] that enable them to feed on the homogeneous food. The ereynetid mites are capable to eject the saliva onto the mucous substrate just before feeding [Badanin, 2000] that may be interpreted as the elements of the pre-oral digestion. As a result, the powerful pharyngeal pump of anystids provided with the polymerous antagonistic muscles may be characteristic for the least specialized type of suctorial gnathosoma (Fig. 4, 1; con. ph, dil. ph). Otherwise, the modifications of the pharynx in bdellids, having so-called dorsal septum [Alberti, 1973] and the different groups of the constrictor muscles (Fig. 2, 1, 3; con. ph, ph, se), may represent the results of their adaptation to feeding on the pre-oral digested food. Moreover, the pharynx of ereynetids is divided into strongly sclerotized anterior reservoir and sharply narrowed posterior part looking morphologically like the oesophagus (Fig. 3, 3; ph). In this case, only two constrictor muscles provide an expulsion of the mucus to the foregut (Fig. 3, 1; con. ph, oe, ph).

As a whole, the trophic specialization of prostigmatid mites may be associated with the oligomerization of the muscular complexes of the gnathosoma as well as the functional substitution of its structures due to the changes in the muscles' topography. However, the evolvement of the gnathosoma in various mite groups, being adapted to the certain nutritional patterns, is related, first of all, to its considerable morphological changes. These structural adaptations of the mouthparts usually look like more flexible if compared with their muscular system being rather more conservative.

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