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COMPARATIVE ANALYSES OF THE INTERNAL ANATOMY AND FUNCTIONAL MORPHOLOGY OF THE ELEUTHERENGONA (ACARI, TROMBIDIFORMES)

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ABSTRACT: The study summarizes data on the internal anatomy of the mites belonging to the parvorder Eleutherengona (Acariformes: Trombidiformes) mainly based on the families Tetranychidae, Cheyletidae, Syringophilidae, Myobiidae, and Demodicidae. The arrangement and functioning of the digestive tract, propodosomal glands, connective tissue, and reproductive system of both sexes are taken into account to reveal common features of the Eleutherengona as well as possible phylogenetically informative characters in particular families.

The study shows that all the examined eleutherengone families demonstrate a mixture of relatively primitive and advanced features.

The following most striking internal characters are common to all studied eleutherengone species. The postventricular midgut is represented by a simple tube-like excretory organ, which is usually in open connection with the ventriculus. The anal and genital openings of the females are close to each other and located at the terminal end of the body. The glandular component of the testicular epithelium is absent or highly reduced, as well as the male accessory glands. The number of salivary glands is reduced or these glands are lost in some parasitic forms. The coxal glands are either devoid of the proximal filter sacculus or provided by a sacculus with a considerably reduced lumen. The coxal gland epithelium does not possess a regular brush border, showing high pinocytotic activity.

KEY WORDS: mites, internal anatomy, ultrastructure, digestive tract, salivary glands, coxal glands, reproductive organs, Eleutherengona.

"The rarity of unifying characteristics within the Actinedida causes some systematics to consider this taxon as being composed of several different suborders."

J. H. Oliver Jr. (1983)

INTRODUCTION

The parvorder Eleutherengona comprises over 10 superfamilies, which represent a great diversity of lifestyles including predators, plant-feeding mites and parasites of wide range of hosts (Mironov and Bochkov 2009; Bochkov 2009) (Alternative classification, see in: Krantz and Walter 2009). The internal anatomy is known only for several taxa, in which the family Tetranychidae has been investigated most completely (Blauvelt 1945; Smith and Boudreaux 1972; Langenscheidt 1973; Crooker and Cone 1979; Weyda 1980; Pijnacker et al. 1981; Mothes and Seitz 1981a, b, c; Feiertag-Koppen and Pijnacker 1982; Mothes-Wagner 1985; Alberti and Crooker 1985; Matsubara et al. 1992). The information on the family Cheyletidae is mainly restricted to light microscopy (Akimov and Gorgol 1990) that is hardly sufficient for the anatomical reconstructions of such tiny animals. Two studies dealing with the mites from the family Demodicidae are made by means of both light and electron microscopy (Desch and Nutting 1977; Desch 1988), but these works contain few figures and are unable to illustrate all aspects of the internal organization of these highly specialized skin parasites. Two other families of parasitic mites, Myobiidae (ectoparasites of small mammals) and Syringophilidae (mites living in quills of birds' feathers), were investigated by the author (Filimonova 1999, 2001a, b, c, 2004, 2006, 2008b, 2009), but numerous unresolved questions in their anatomy have still remained. For other families of the Eleutherengona no data are still available on their internal morphology.

This study is the critical review of all data obtained by me and other researches concerning the internal anatomy of the parvorder Eleutherengona.

RESULTS AND DISCUSSION

Digestive tract

In most eleutherengone species examined up to now, the digestive tract is composed of the fore-, mid- and hindgut connecting each other (Blauvelt 1945; Alberti 1973; Mothes and Seitz 1981a; Mothes-Wagner 1985; Alberti and Crooker 1985; Akimov and Gorgol 1990; Filimonova 2001a, 2008b). Both the foregut and the hindgut possess an internal cuticle layer.

The foregut always consists of the preoral cavity, large pharynx and thin tubular esophagus, which penetrates the synganglion before joining the ventriculus (Figs. 1a, b). The mouth opening is located under the base of the labrum. In front of the mouth there is a preoral cavity surrounded by the extensions of the palpal coxae (malapophyses) (Fig. 2a). The pharynx serves as a pump for suck-

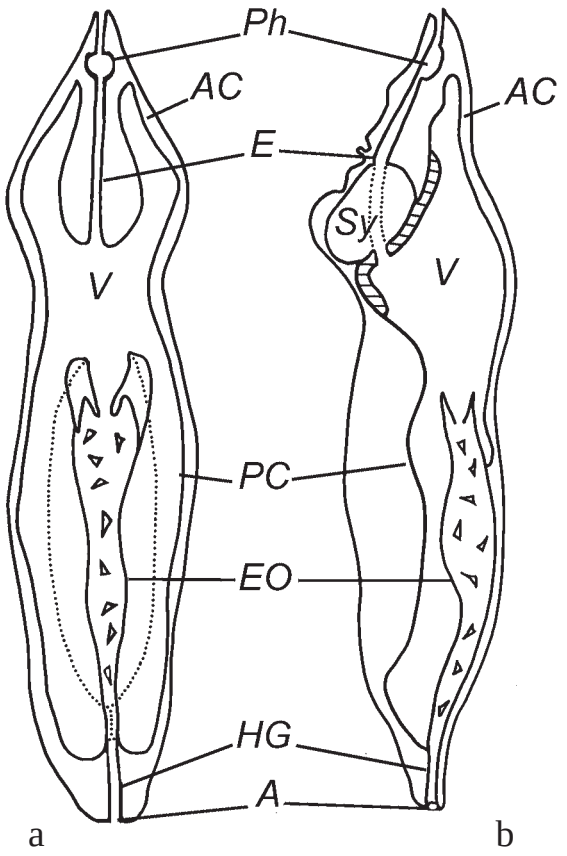

Fig. 1. Schematic drawing of the digestive tract in *Syringophilopsis fringilla*, showing the location of the modified midgut epithelium (hatched area); a — dorsal view, b — lateral view (from Filimonova 2009).
A — anus; AC — anterior caeca; E — esophagus; EO — excretory organ; HG — hindgut; PC — posterior caeca; Ph — pharynx; Sy — synganglion; V — ventriculus.

ing liquid (or semi-liquid) food. Its dorsal/ postero-dorsal wall is provided with a thick and heavily sclerotized cuticle (Figs. 2a, b). Powerful dilator muscles insert on this wall outside (Fig. 2b), whereas pharyngeal constrictors are characteristically absent (Blauvelt 1945; Anwarullah 1963; Alberti and Crooker 1985; Akimov and Gorgol 1984, 1990; Desch and Nutting 1977). Contraction of the dilators elevates the dorsal wall of the pharynx, changing its shape from the crescent to oval or round in cross section. The decrease of pressure in the pharyngeal chamber causes the intake of liquid food. When the pharyngeal muscles relax, the pharynx returns to the relaxed state due to the elasticity of its walls (Blauvelt 1945).

The esophagus is commonly described as a simply organized narrow tube serving only for the food passage (Akimov and Gorgol 1990; Alberti and Coons 1999) (Fig. 2c). In syringophilids, however, the epithelial cells of the esophagus contain numerous electron-lucent vacuoles, large residual bodies and numerous Golgi bodies, indicating their possible involvement in food processing (Filimonova 2008b) (Figs. 2d, e). This suggestion is partly confirmed by the vacuolated esophageal epithelium of demodicids (Desch and Nutting 1977). The internal cuticle layer is commonly much thinner than in the hindgut (Akimov and Gorgol 1984, 1990; Mothes and Seitz 1981a; Alberti and Crooker 1985; Filimonova 2008b). In myobiids, the cuticle of the esophagus bears irregularly-shaped teeth facing into the lumen of the organ (Filimonova, unpublished) (Figs. 2b, c). A valve, observable at the end of the esophagus in spider mites (Blauvelt 1945; Mothes and Seitz 1981a) and cheyletids (Akimov and Gorgol 1984, 1990), appears to prevent backflow of the content from the ventriculus.

In common to most Acariformes (Alberti and Coons 1999), the midgut of the Eleutherengona is divided into the anterior and posterior regions (Figs. 1a, b). The anterior midgut includes an unpaired central ventriculus and the midgut diverticuli (= caeca). Two or three anterior and two posterior midgut diverticuli are usually seen (Figs. 1a, b; 3a, b). The posterior midgut (or postventricular region) is represented by a dorsomedian excretory organ joining the hindgut posteriorly (Figs. 1a, b; 3c, d, e). The excretory organ is typically represented by a long simple tube, but in the case of *Bakericheyla chanayi* (Cheyletidae) it is bi-lobed anteriorly (Filimonova, unpublished) (Fig. 3d). This is more typical for the representatives of Parasitengona (parvorder Anystina) (Bader 1938, 1954; Mitchell 1964; Shatrov 2010). A valve occurs between the ventriculus and the excretory organ in *Tetranychus urticae* (Mothes and Seitz 1980) and in *Syringophilopsis fringilla*, in which it is accompanied by a sphincter at the entrance of the excretory organ (Filimonova 2009) (Fig. 3c). A similar valve at the entrance to the postventricular midgut seems to be typical for some other trombidiform groups (Alberti 1973; Ehrnsberger 1984). The hindgut (or rectum) ends in the anal opening, which is always dorsally to the genital opening in the Eleutherengona (Fig. 3e). The development of the gut muscle sheath varies considerably among the species. In vermiform parasitic mites, it may be partly reduced, as in syringophilids (Filimonova 2009) or entirely absent as in demodicids (Desch and Nutting 1977). In these cases the transport of the gut content is accomplished by the activity of the skeletal muscles closely attached to the digestive tract.

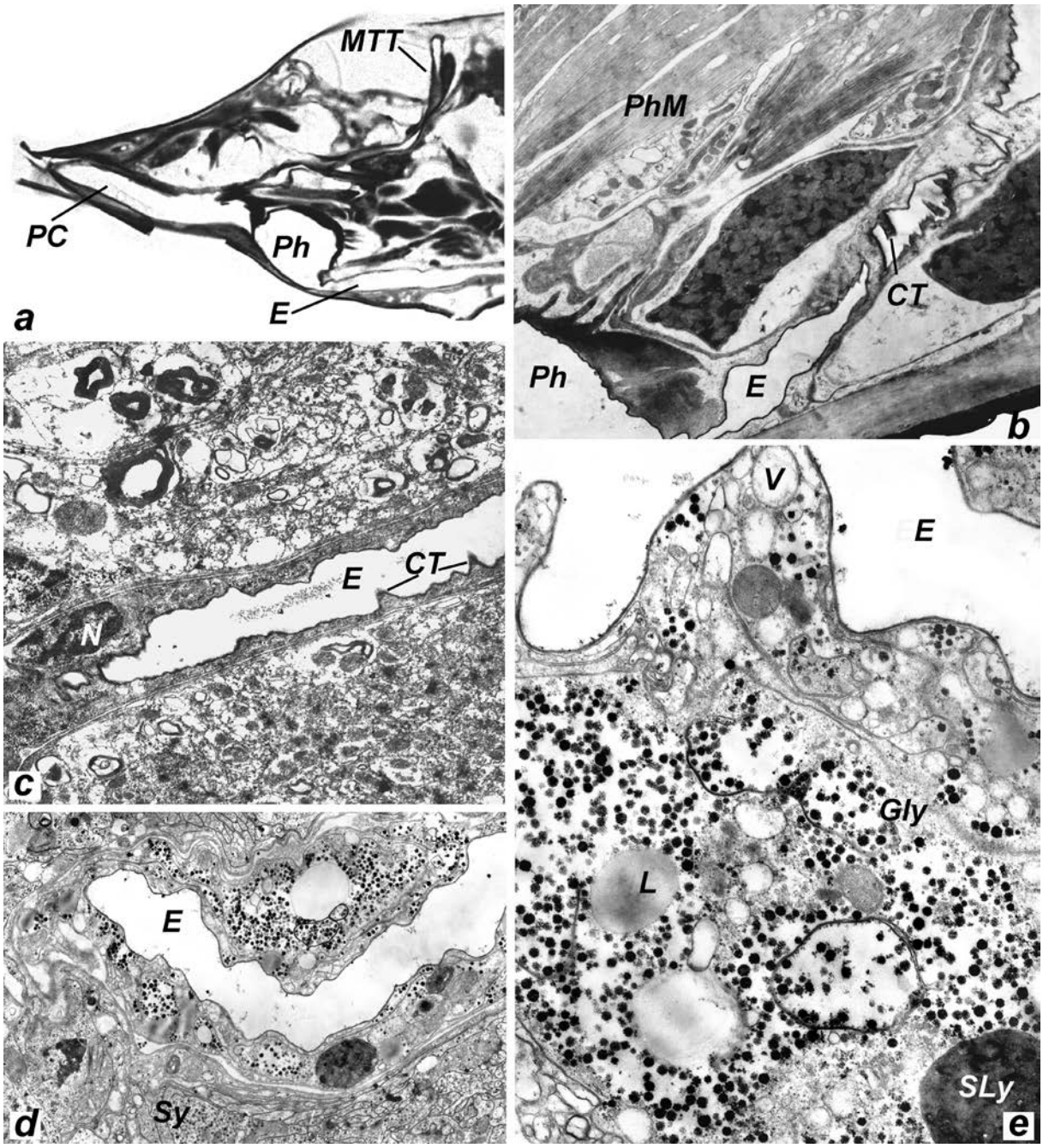

Fig. 2. The structure of the foregut, including the preoral cavity (PC), pharynx (Ph) and esophagus (E). a — longitudinal semithin section of the gnathosoma of *Syringophilopsis fringilla*; b–e — electron micrographs; b, c — longitudinal sections through the esophagus of *Myobia murismusculi* at its beginning from the pharynx (b), and inside the synganglion (c); d — esophagus of Sy*ringophilopsis fringilla* passing through the synganglion, longitudinal view; e —details of the epithelial lining of the esophagus of *Syringophilopsis fringilla.* Scale bars: a — 20 μm; b, d — 2 μm; c, e — 1 μm.
CT — cuticle teeth; E — esophagus; Gly — glycogen granules; GV — Golgi-derived vesicles; L — lipid inclusions; MTT — main tracheal trunks; N — nucleus; PC — podocephalic canals; Ph — pharynx, PhM — pharyngeal muscles; Sy — synganglion; SLy — secondary lysosomes; V — vacuole.

Digestion is mainly intracellular and takes part both in the ventriculus and caeca. To certain extent, the anterior midgut is functioning as a storage organ, which contains lipid and glycogen deposits. This is especially well expressed in demodicids (Desch and Nutting 1977) and syringophilids (Filimonova 2008 b; 2009). The excretory organ was shown to participate mainly in elimination of the nitrogenous wastes. It can enlarge considerably being filled with the excretory products. The muscle bundles following the excretory organ are always much more extensive than in the previous regions suggesting active evacuation of the wastes from the lumen of the organ (Alberti

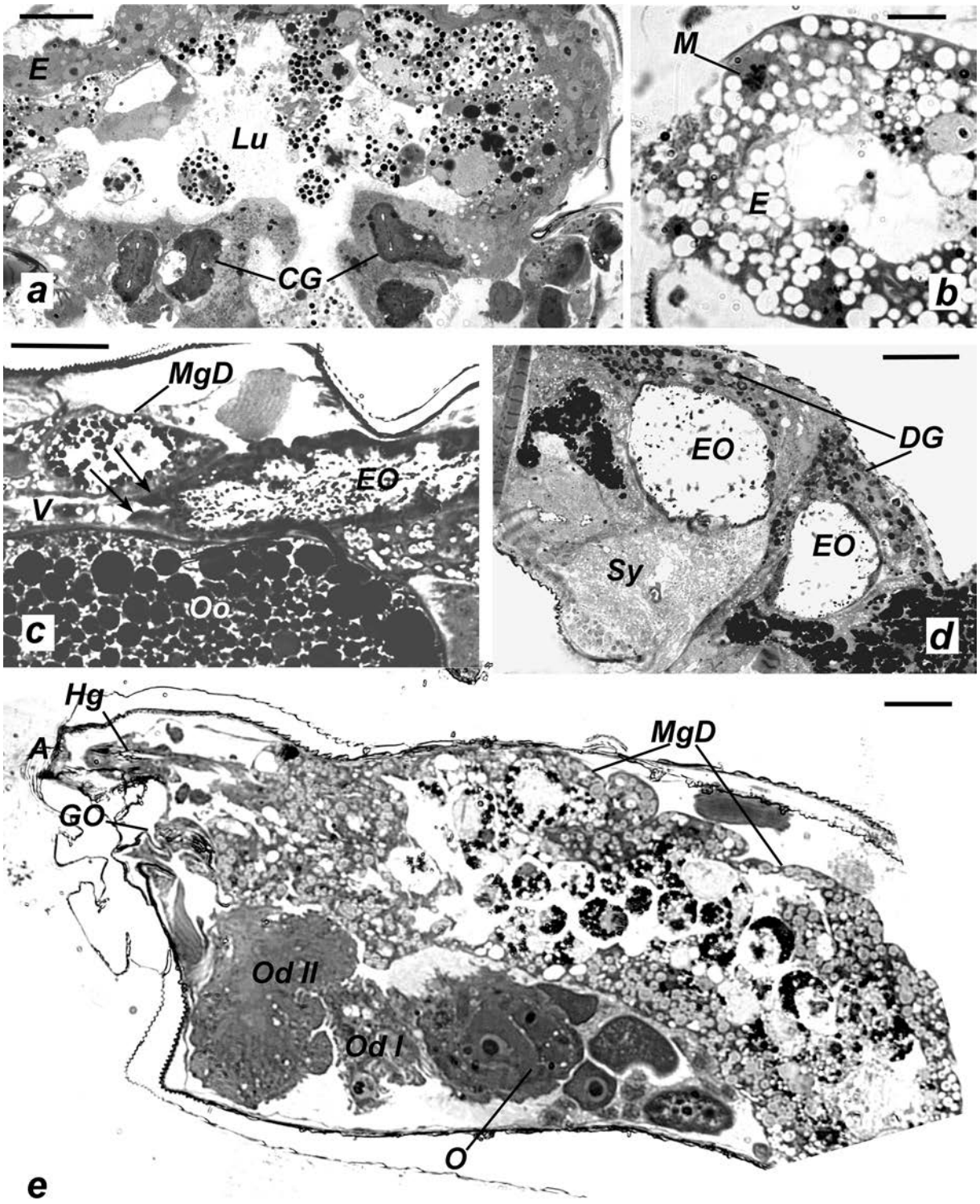

Fig. 3. General structure of the midgut of *Syringophilopsis fringilla* (a, b, c, e) and *Bakericheyla chanayi* (b) visible at the LM level; a — cross section of the ventriculus (from Filimonova 2009), b — fragment of the midgut diverticula; c — longitudinal section through the junction between the ventriculus and excretory organ (arrows indicate valves at the entrance to the excretory organ); d — cross section through the anterior portion of the excretory organ (c, d — from Filimonova 2001a); e — longitudinal view of the idiosoma. Scale bars: a, b — 10 μm; c — 20 μm; d, e — 25μm.
A — anus; CG — coxal glands; DG — dorsal glands; E —epithelium; EO — excretory organ; GO — genital opening; Hg — hindgut; Lu — lumen of the organ; M — mitosis; MgD — midgut diverticuli; O — ovary; Od I — proximal oviduct; Od II — distal oviduct; Oo — oocyte; Sy — synganglion; V — ventriculus.

and Crooker 1985; Akimov and Gorgol 1990; Filimonova 2001a, 2009).

Two exceptions from the above scheme are known within the Eleutherengona. The first one is

the digestive system of Demodicidae, in which the hindgut has been lost as well as the anal opening (Desch and Nutting 1977). Unfortunately, the description of the digestive tract of demodicids is still incomplete and nothing is known about structural differentiation of their midgut. Another exception from the general plan of the eleutherengone digestive system is the gut of *Cheyletus eruditus*. According to Akimov and Gorgol (1990), in this species the ventriculus and excretory organ were reported to be separated in contrast to other species studied from the family Cheyletidae. The blind gut is known mainly among the Parasitengona, including the families Trombiculidae (Mitchell 1964, 1970; Shatrov 1989a), Microtrombidiidae (Shatrov 2003), Calyptostomatidae (Vistorin-Theis 1977) and Hydrachnidia (Schmidt 1935; Bader 1954; Shatrov 2007). Paran (1979) described a blindly ended gut in *Myobia murismusculi* (Myobiidae), but his observation was not confirmed by the further investigation (Filimonova 2001a). On the other hand, the connection between the anterior and posterior midgut was definitely shown not only in the Eleutherengona (Blauvelt 1945; Mothes and Seitz 1981a; Alberti and Crooker 1985; Mothes-Wagner 1985; Akimov and Gorgol 1990; Filimonova 2001a, 2008 b) but in most other trombidiform taxa, including Eryophioidea (Nuzzaci and Alberti 1996), Bdellidae (Alberti 1973), Anystidae (Alberti 1973; Filimonova 2008a), Labidostommatidae (Vistorin 1980) and Rhagidiidae (Ehrnsberger 1984). Most authors described a slit opening leading to the postventricular region, which is difficult to be found as it is always closed or pressed by the muscle sphincter (Vistorin 1980; Alberti and Crooker 1985; Filimonova 2008b, 2009). Thus, the gut of *Cheyletus eruditus* requires further investigation using electron microscopy.

In all eleutherengone species examined up to now, both ventriculus and caeca are lined by the same single-layered midgut epithelium composed of polyfunctional cells**.** These cells commonly transform from the digestive into the excretory type demonstrating remarkable modifications of their shape and fine structure (Figs. 4a–c). The digestive cells are characterized by the presence of pino- and phagocytotic vesicles in their apical region (Fig. 4a) and various secondary lysosomes in the deeper layers of cytoplasm (Fig. 4b), whereas the excretory cells contain predominantly residual bodies and mineral spherites (Fig. 4c).

Special secretory cells typically observed in the midgut epithelium of some predatory trombidiform mites, such as Bdellidae and Anystidae (Alberti and Storch 1973, 1983; Vistorin 1980; Filimonova 2008a), have not been found in most eleutherengone species (Desch and Nutting 1977; Mothes and Seitz 1981a; Akimov and Gorgol 1984, 1990; Alberti and Crooker 1985; Filimonova 2001b). The only exception within the Eleutherengona is *Syringophilopsis fringilla* (Syringophilidae) in which secretory cells temporarily exist only at a certain physiological state (Filimonova 2009). These cells contain an extremely large amount of rough endoplasmic reticulum (RER) in the form of long and narrow cisternae tightly packed all over the cytoplasm, and numerous dense membrane-bounded secretory granules (Fig. 4d). The size of the granules and their appearance are very similar to those of other Trombidiformes where secretory cells are thought to produce enzymes for the extracellular digestion, which is followed by the intracellular one (Alberti and Storch 1973, 1983; Vistorin 1980; Filimonova 2008a).

A modified epithelium was shown in the Tetranychoidea in the midgut regions adjacent to the coxal glands and to the excretory organ (Mothes and Seitz 1981a; Mothes-Wagner 1985; Alberti and Crooker 1985). In both regions, the midgut cells are predominantly flat or cuboidal, provided with well-developed rough endoplasmic reticulum (RER) and lacking pinocytotic inclusions and most lysosomes. Long irregularly arranged microvilli, numerous mitochondria, and a great number of crystalline inclusions in the cytoplasm of these cells point to their involvement in the ion and water transport. The basal lamina of neighboring organs is periodically interrupted and finger-like processes of the gut cells bulge into the bases of their epithelial lining (see: Alberti and Crooker 1985). A similar modification of the ventricular epithelium was observed in the quill mites (Syringophilidae) in close contact to the coxal glands, though in this case the processes of midgut cells do not enter the coxal gland epithelium (Filimonova 2009). Alternatively, in *Myobia murismusculi* (Myobiidae) the coxal gland cells form finger-like processes penetrating the basal lamina of the adjacent midgut portions: diverticuli and excretory organ (Fig. 5a) (Filimonova 2004). This type of contacts apparently facilitates transportation of substances from the midgut to the lumen of the coxal glands or the excretory organ (Alberti and

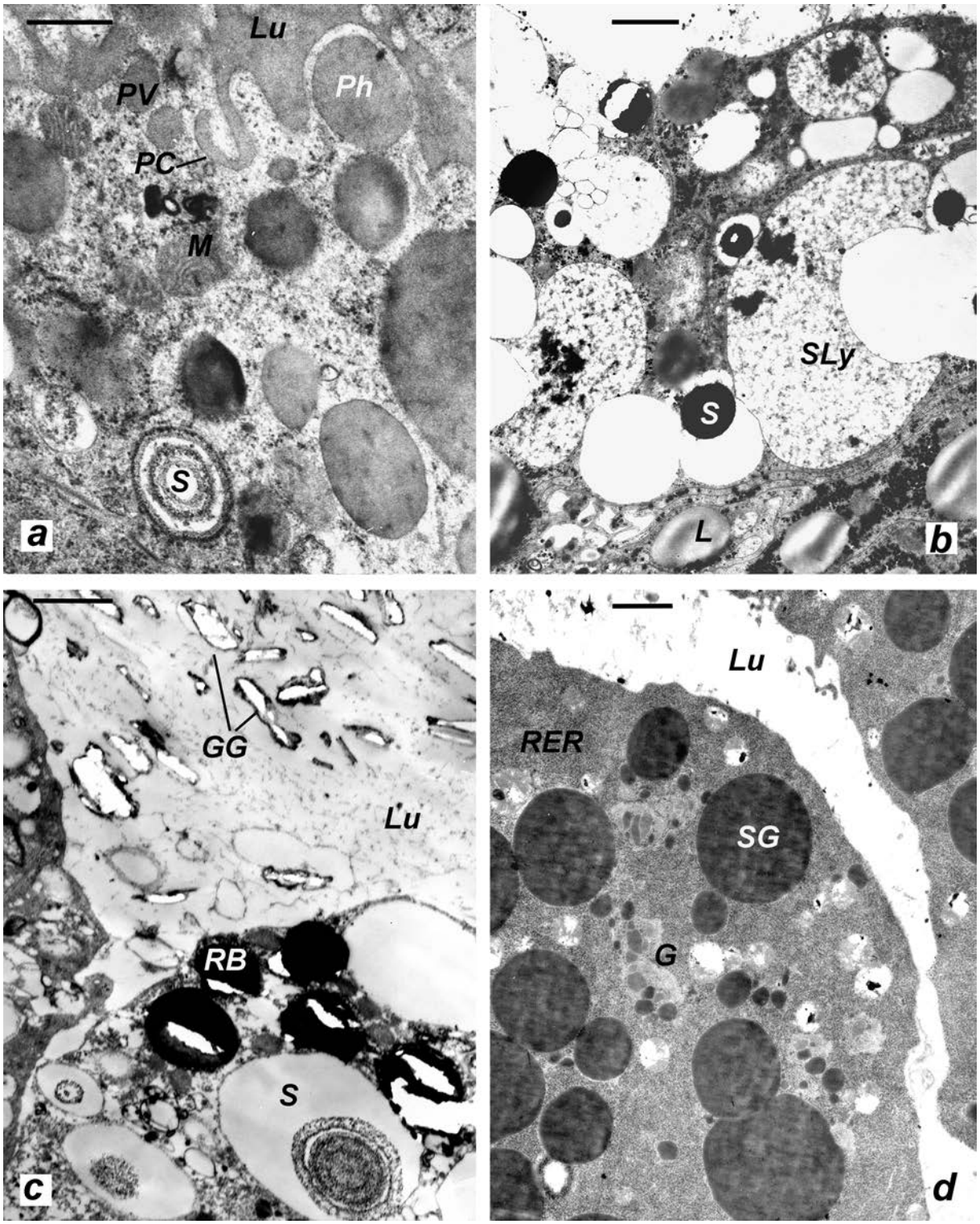

Fig. 4. Fine structure of the main cell types in the anterior midgut; a — digestive cell of *Myobia murismusculi* with high endocytotic activity (from Filimonova 2001b); digestive (b), excretory (c) and secretory (d) cells from the midgut of *Syringophilopsis fringilla* (from Filimonova 2009). Scale bars: a — 0.5 μm; b, d — 2 μm; c — 3 μm.
G — Golgi body; GG — guanine granules; Lu — lumen of the organ; M — mitochondria; Ph — phagosome; PC — pinocytotic canal; PV — pinocytotic vesicle; RB — residual bodies; RER — rough endoplasmic reticulum; S — spherites; SG — secretory granules; SLy — secondary lysosomes.

Coons 1999). In the case of *M. murismusculi*, this might be a back transport from the coxal glands to the lumen of the excretory organ.

Though many authors reported extrusions of either epithelial cells or their apical parts into the gut lumen (Blauvelt 1945; Alberti 1973; Alberti

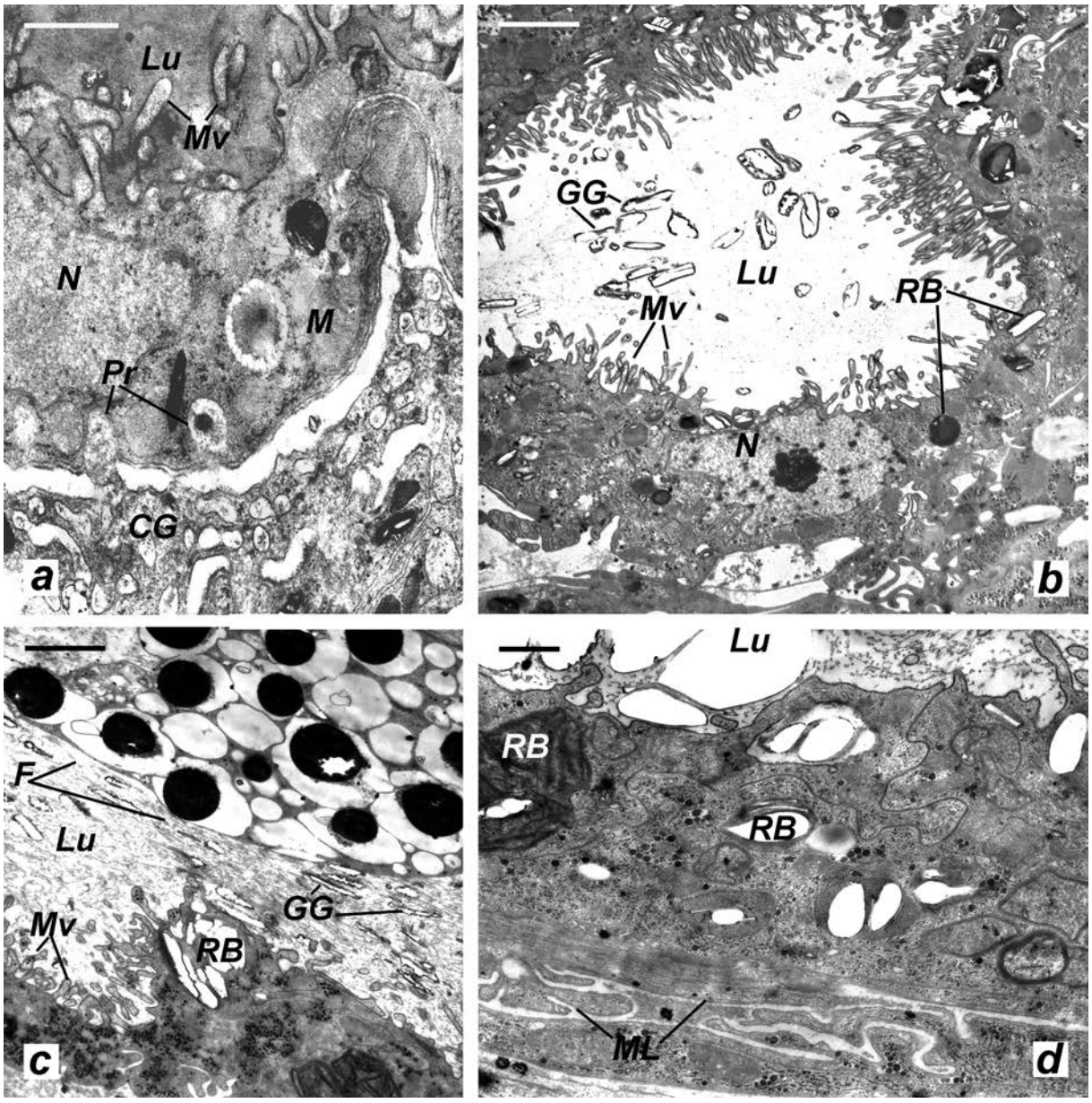

Fig. 5. Fine structure of the excretory organ of myobiids (a, b) and syringophilids (c, d); a — fragment of the epithelium in the middle portion of the organ of *Myobia murismusculi*; b — anterior portion of the organ of *Amorphacarus elongatus* (Myobiidae); anterior (c) and posterior (d) portions of the excretory organ in *Syringophilopsis fringilla.* Scale bars: a, d — 1 μm; b, c — 3 μm.

CG — proximal tube of the coxal gland; F— cell fragment floating in the gut lumen (Lu); GG — guanine granules; M — mitochondria; Mv — microvilli; ML — muscle layers; N — nucleus; Pr — processes of the coxal gland cells; RB — residual body.

and Crooker 1985; Akimov and Gorgol 1990; Filimonova 2001b), little is known about the replacement of the midgut epithelium in trombidiform mites (Alberti and Coons 1999). In contrast to *Acarus siro* (Astigmata), in which special regenerative cells have been recently found (Šobotnik et al. 2008), neither regenerative cells nor mitotic divisions have been noticed in the gut of most Trombidiformes (Alberti and Coons 1999). Akimov and Gorgol (1999) noted special reserve cells in the midgut epithelium of cheyletids, but they did not observe any mitotic figures. The latter have been recently found in the differentiated midgut cells of *Syringophilopsis fringilla* (Fig. 3b). The ultrastructural observation shows that the cells undergoing mitosis contain an usual set of organelles with a reduced number of digestive and excretory inclusions comparing to other digestive cells (Filimonova 2009).

The main histological characteristics of the excretory organ are similar in all eleutherengone taxa studied so far (Mothes and Seitz 1980,

Mothes-Wagner 1985; Alberti and Crooker 1985; Filimonova 2001a, 2009). The lumen of the organ is lined by the squamous epithelial cells that are poor in digestive inclusions and lysosomes. Numerous birefringent crystalline inclusions are always seen inside the organ (Fig. 5b). The crystal-like material was determined as guanine — the final product of nitrogenous metabolism (Mc Enroe 1961). The guanine-containing granules form so-called white pellets, which are excreted together with the black pellets, originating from the floating cells and their remnants (food boli) (Fig. 5c). The food boli also contain a number of guanine inclusions (Mothes and Seitz 1980). These two types of excrements have also been reported for other Trombidiformes (Alberti 1973; Shatrov 2000, 2007, 2010). The mechanism of the formation of guanine-containing granules is not clear enough (Mothes-Wagner 1985).

The ultrastructural investigations showed a certain difference between the epithelial lining of the excretory organ in spider mites (Mothes-Wagner 1985; Alberti and Crooker 1985) and that of syringophilids (Filimonova 2009) and myobiids (Filimonova, unpublished). In the spider mites, the dorsal and posterior lateral walls of the organ consist of the vacuolated cells possessing a large amount of RER and a few small mitochondria, while the cells of the anterior lateral walls possess deep apical invaginations and irregularly- shaped apical projections (Alberti and Crooker 1985; Mothes-Wagner 1985). The anterior lateral walls of the organ were supposed to excrete guanine, whereas the dorsal and posterior lateral walls produce the matrix in which the guanine inclusions are embedded (Alberti and Crooker 1985; Mothes-Wagner 1985). In syringophilids and myobiids, the epithelial lining of the organ is more uniform.

The excretory organ of *Syringophilopsis fringilla* is ultrastructurally divided into the anterior and posterior regions (Filimonova 2009). In the anterior region the cells bear apical microvilli-like processes (Figs. 5c, d), which are substituted in the posterior region by less numerous irregularly shaped protrusions covered by a thin surface coat of unknown nature (Filimonova 2009). In both regions crystalline inclusions were shown to be formed from the Golgi-derived vesicles, which gradually transformed into guanine-containing residual bodies (Figs. 5c, d). Interestingly, single inclusions of the same structure have been also observed in the epithelium of the anterior midgut regions: ventriculus and caeca (Filimonova 2009). In myobiids, the fine structure of the excretory organ is very similar to this description (Figs. 5a, b) (Filimonova, unpublished). The fine structure of the epithelium in the excretory organ of syringophilids, as well as myobiids, is very close to that of some other Trombidiformes: Bdellidae (Alberti 1973), Trombiculidae (Shatrov 2000) and Trombidiidae (Shatrov 2007).

Apart from the elimination of nitrogenous wastes, the excretory organ can participate in the regulation of water and ion balance and the degree of this process presumably depends on the biology of certain species. Well-developed apical brush border and deep basal infoldings, associated with great number of mitochondria, suggest the excretory organ of spider mites (Tetranychoidea) to be strongly involved in osmoregulation (Mothes and Seitz 1980; Mothes-Wagner 1985; Alberti and Crooker 1985). In the corresponding organ of *Syringophilopsis fringilla* (Filimonova 2009), as well as in all investigated parasitengones belonging to the Trombiculidae, Microtrombidiidae, Teutonidae, and Pionidae, only apical concentration of mitochondria was observed without typical basal labyrinth (Shatrov 2000, 2007, 2010; Alberti and Coons 1999). This evidently indicates considerably less level of ion transport directed to the body cavity in the mentioned species. In syringophilids, the absence of modified midgut epithelium in the region adjacent to the excretory organ might also be caused by the relatively low ion and water transport activity of the organ comparing to that of the spider mites.

The homology of the excretory organ to a certain postventricular region of other Trombidiformes is not presently obvious**.** Hafiz (1935) demonstrated the ectodermal origin of the excretory organ in *Cheyletus eruditus*. For a long time it has been considered as a part of hindgut in spider mites (Mothes and Seitz 1980; Alberti and Crooker 1985). Another embryological study on the parasitic eleutherengone mite *Acarapis woodi* (Tarsonemina) revealed the presence of internal group of entodermal cells apparently giving rise to the excretory organ or a part of it (Klumpp 1954). Akimov and Gorgol (1990) reported histological difference between the anterior and posterior portions of the excretory organ in cheyletids. In syringophilids, the posterior portion of the organ is characterized by much less microvilli covered with a special surface layer (Filimonova 2009), but there is no reason to suggest its ectodermal origin since the cuticle layer was not observed on

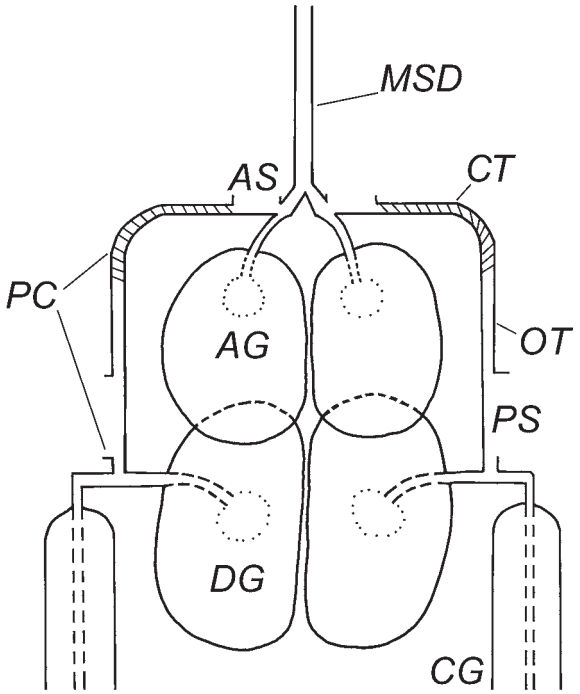

Fig. 6. Schematic drawing of the podocephalic system of *Tetranychus urticae* (after Mills 1973, with minor modification).
AG — anterior gland; AS — anterior slit of podocephalic canal; CG — coxal gland; CT — closed tube of the podocephalic canal; DG — dorsal gland; MSD — median salivary duct; PC — podocephalic canal; PS — posterior slit; OT — open trough of the podocephalic canal.

the surface of the epithelial cells. Nowadays, most authors believe the excretory organ to be a homologue of the postcolon (Ehrnsberger 1984; Alberti and Coons 1999). If it is so, the trend of colon reduction is highly realized in Eleutherengona. Another version is that the two portions of the excretory organ might correspond respectively to the colon and postcolon of other trombidiform mites such as Bdellidae or Labidostommatidae. Unfortunately, little is known about fine structure and functional meanings of these two postventricular regions in other trombidiform taxa (Alberti and Coons 1999).

Propodosomal glands

In the Trombidiformes propodosomal glands are typically united in a podocephalic system that is composed of several pairs of glands consequently sending their ducts into the common podocephalic canal (Grandjean 1938; Bader 1938; Brown 1952; Moss 1962; Mitchell 1964; Mills 1973; Alberti and Storch 1973, 1974) (Fig. 6). Each podocephalic canal receives the exit ducts of 3–5 salivary alveolar (or acinous) glands producing enzymes for preoral digestion as well as the tubular coxal gland functioning as an osmoregulatory organ (Figs. 7a–e). The presence of paired podocephalic canals is considered to be one of the most striking synapomorphic features of the Acariformes **(**Lindquist 1984; Alberti and Coons 1999; Alberti 2005). Plesiomorphically, podocephalic canals are represented by the open grooves on the lateral sides of propodosoma in some lower Trombidiformes, whereas in many trombidiform taxa common salivary ducts run inside the mite body (Grandjean 1938).

Within the Eleutherengona, open podocephalic canals have been definitely observed in the representatives of the Tetranychoidea (Grandjean 1938; Summers and Witt 1971; Mills 1973) and Syringophilidae (Filimonova and Mironov 2010) (Figs. 6, 7e). The latter family is commonly assumed to be close to the Cheyletidae (Bochkov 2002), though in *Cheyletus eruditus* podocephalic canals were described as the closed tubes passing beneath the integument (Grandjean 1938). According to our preliminary data, the other cheyletid mite, *Bakericheyla chanayi*, also demonstrates closed podocephalic canals (Fig. 7b) (Filimonova, unpublished).

In addition to the podocephalic system, an unpaired tracheal gland was found in a number of trombidiform mites as well as certain paired glands provided with independent exit ducts (Bader 1938; Brown 1952; Mitchell 1955, 1964; Moss 1962; Mills 1973; Alberti and Storch 1974; Shatrov 1989b, 2000, 2003).

In the species of spider mites capable of silk secretion, a large unicellular silk gland has been found terminating at the tip of each pedipalp (Alberti and Storch 1974; Mothes and Seitz 1981b; Alberti and Crooker 1985). A huge cell of the silk gland contains proteinaceous secretory granules accumulated in the reservoir-like apical region of the cell. The absence of the similar unicellular glands in the genera *Bryobia* and *Tetranychina*, which do not produce silk, confirms them to be the main silk glands in spider mites (Alberti and Storch 1974), though other propodosomal glands might be also involved in the silk production (Mills 1973).

Alveolar propodosomal glands

Within the Eleutherengona, the number of alveolar propodosomal glands is reduced comparing to those of other trombidiform taxa (see Alberti and Coons 1999; Shatrov 2005). The podocephalic system is most completely represented in the Tetranychidae, in which two alveolar salivary

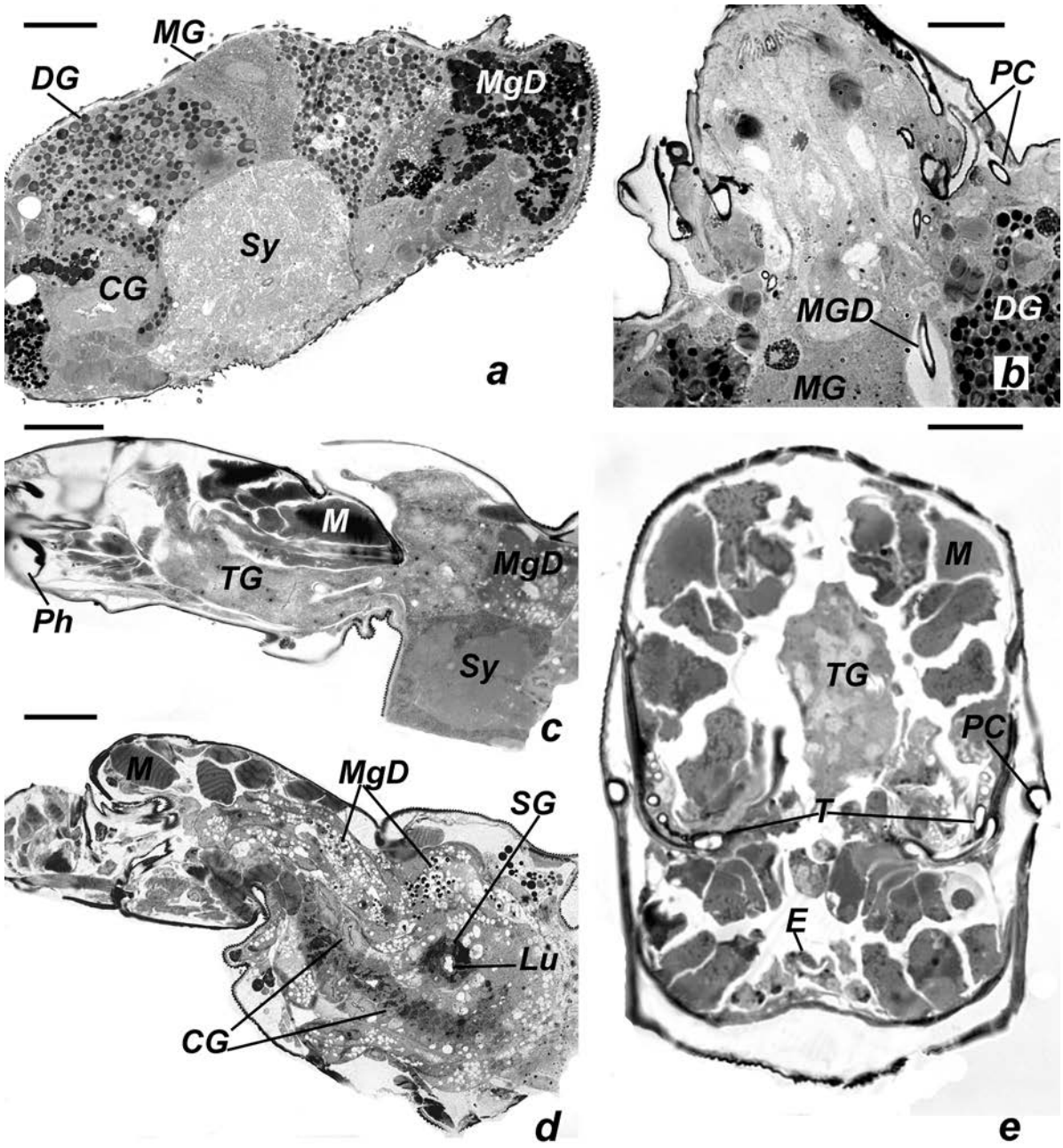

Fig. 7. General morphology of the podocephalic system visible in semithin sections; a — cross section of *Bakericheyla chanayi* at the level of synganglion (Sy); b — frontal section of the same species anterior to the previous region; sagittal (c) and parasagittal (d) sections of propodosoma of *Syringophilopsis fringilla*; e — cross section of *S. fringilla*, showing the open part of the podocephalic canals (on the right). Scale bars: a — 25 μm; b, e — 20 μm; c — 40 μm; d — 70 μm.
E — esophagus; CG — coxal glands; DG — dorsolateral glands; Lu — lumen of the coxal gland; M — muscles; MgD — midgut diverticuli; MG — medial glands; MGD — medial gland duct; Ph — pharynx; PC — podocephalic canal; Sy — synganglion; SG — secretory granules; T — tracheae; TG — tracheal gland;

glands and a tubular coxal gland are united by the common podocephalic canal on each side of the body (Mills 1973; Alberti and Storch 1974; Mothes and Seitz 1981b) (Fig. 6). Mills (1973), who thoroughly examined the anatomy of the podocephalic system in *Tetranychus urticae*, reported the junction of the coxal and dorsal glands just at the origin of the podocephalic canal (= common silk duct by this author) (Fig. 6). At the base of the coxa I the podocephalic canal enters outside the mite body through the slit-like opening (posterior slit by Mills 1973), and runs forward as an open trough provided from outside by interdigitating cuticular lips partly covering its lumen. Running a certain distance forward, the trough-like portion of the podocephalic canal makes a turn toward the median direction and at this point becomes a closed tube which passes through the integument and

gives rise to the anterior slit just before the corresponding cheliceral body. The duct of the anterior gland enters the anterior end of this slit after which the paired podocephalic canals continue into the common median salivary duct (or rostral silk duct, by Mills 1973) (Fig. 6). Running forward this duct conducts complex secretory product to the labral base (Alberti and Storch 1974; Mothes and Seitz 1981 b; Alberti and Crooker 1985). Both alveolar salivary glands of tetranychids are equipped with organelles characteristic for protein synthesis and produce a great number of proteinaceous secretory granules (Alberti and Storch 1974; Mothes and Seitz 1981b; Alberti and Crooker 1985).

The family Cheyletidae demonstrates much more diversity in food specialization, which is reflected in the variable content of their propodosomal glands. In their comparative light-optical study, Akimov and Gorgol (1990) reported a pair of medial salivary glands for *Cheyletus eruditus*, paired dorsal glands for *Ornithocheyletia* sp. and two pairs of alveolar propodosomal glands (dorsal and medial) for *Bakericheyla chanayi* (Fig. 7a). In all species studied, the alveolar glands occupy a large area from the anterior end of the ovary to the mouthparts. They are typically composed of large cells encircling a central cuticle-lined duct. The authors described each gland to have its own salivary duct leading independently to the tip of the gnathosoma, but the ducts' terminations were not traced exactly in their study (Akimov and Gorgol 1990) (Fig. 7b). The cells of the dorsal glands of *Ornithocheyletia* sp. and dorso-lateral glands of *Bakericheyla chanayi* are both filled with uniform protein-like secretory granules. The number of granules does not change during the digestion being associated with the stage of oogenesis. Considerably more granules have been shown in the females containing oocytes at the late stage of vitellogenesis, whereas the agranular state corresponds to the period following oviposition. The dorso-lateral glands of *Bakericheyla chanayi*, each composed of two giant cells, were thought to be silk producing (Akimov and Gorgol 1984). Medial glands of the predatory mite *Cheyletus eruditus* were shown to decrease in size and release their secretion in the course of food uptake. A high proteolytic activity, which was demonstrated in the homogenates of these glands, implies the secretory product to be enzymes involved in the preoral digestion (Gorgol and Barabanova 1979).

In the Demodicidae, the paired teardrop-shaped salivary glands lie within the latero-dorsal region of propodosoma extending backwards above the synganglion. Each gland is composed of one large cell surrounded by 6 to 8 smaller, flattened cells all containing vacuoles and dark-staining granules (Desch and Nutting 1977). Each gland opens into a salivary duct at the level of the legs II. The salivary ducts pass into the gnathosoma and open laterally in the posteroventral region of the preoral cavity (Desch and Nutting 1977; Desch 1988).

Paran (1982) briefly referred to a single salivary gland in *Myobia murismusculi* (Myobiidae) but did not give any description of its structure. Our study has revealed no propodosomal glands in this species apart from the paired coxal glands (see below) (Filimonova 2001a).

Tracheal gland

An unpaired tracheal gland of tetranychids lies independently in the antero-dorsal part of the propodosoma. The duct of this gland extends medioventrad along the median cheliceral septum discharging secretion onto the upper surface of the stylets (Blauvelt 1945; Mills 1973; Alberti and Storch 1974; Mothes and Seitz 1981b; Alberti and Crooker 1985). The cells of the tracheal gland contain a great volume of smooth endoplasmic reticulum associated with numerous electron-lucent droplets, which have been considered to be lipids. Mothes and Seitz (1981b) assume that this secretion facilitates the movements of the stylets inside the infracapitular gutters. However, this suggestion contradicts the fact that in Bdellidae a tracheal gland was found not to be an obligate structure even for the closely related species with similar biology (Alberti and Coons 1999).

Though Akimov and Gorgol (1990) have not noticed a tracheal gland in the examined cheyletids, Di Palma and coauthors (2009) have recently reported a typical tracheal gland in *Cheletogenes* sp. with its duct joining the proximal end of the median salivary duct (the unpaired continuation of the podocephalic canals).

Recently tracheal gland has been observed in *Syringophilopsis fringilla* from the family Syringophilidae also belonging to the superfamily Cheyletoidea (Filimonova 2008b) (Figs. 7c, e). It is a long tubular gland extending from the synganglion to the point in which the main tracheal trunks are running down from the roof of the gnathosoma (Fig. 7c). The epithelial lining of the gland contains a great number of electron-lucent granules presumably of lipid nature. Contrary to *Cheleto-*

genes sp., the duct of the tracheal gland in *S. fringilla* does not join median salivary duct but communicates directly to the prelabral cavity via an independent highly sclerotized duct, passing in the median septum. In this case the median salivary duct running forward above the labrum contains only the secretion of the coxal glands (Filimonova and Mironov 2010).

Tubular propodosomal glands

Tubular glands (or coxal glands) are paired excretory organs characteristic of the Arachnida. It is assumed that they play a main role in osmoregulation (Berridge 1970). Each coxal gland of arachnids is generally composed of the proximal sacculus and distal tubulus. The sacculus is distinctly involved in formation of an ultrafiltrate (primary urine) from the hemolymph passing through the basal lamina of the organ. The mechanism of filtration is counted to be similar to that of mammal's nephron.

A long convoluted tubulus modifies this ultrafiltrate by means of reabsorption (Berridge 1970). The cuticular exit duct of the gland connects to the corresponding podocephalic canal at the base of the coxa I (see above). The most detailed study on the coxal gland structure in the Acari was performed by Alberti and Storch (1977). They investigated 17 species from 11 cohorts of trombidiform mites, three of which, *Cheyletus eruditus* (Cheyletidae), *Bryobia praetiosa* and *Tetranychus urticae* (Tetranychidae), are presently referred to the Eleutherengona (see Krantz and Walter 2009). According to the data obtained by these authors, only *Cheyletus eruditus* demonstrates typical coxal gland arrangement. The sacculus in this species is of tubular shape, with a narrow central lumen connecting to several lateral pouches. It is lined by the typical podocytes with their basal processes (pedicels) resting on a thin basal lamina. The podocytes demonstrate certain pinocytotic activity, which is expressed in the presence of pinocytotic vesicles in their apical region and lysosome-like dense bodies in the central cytoplasm (Alberti and Storch 1977).

In the Tetranychidae, the sacculus was shown to be lost (Alberti and Storch 1977); subsequent studies confirm the coxal gland of tetranychids consist only of the tubulus, which terminates with the cuticle-lined excretory duct (Mothes and Seitz 1980, 1981b; Alberti and Crooker 1985). Apart from the Tetranychidae and Cheyletidae, the loss of the sacculus was also reported for most Parasitengona (the cohort Anystina) (Bader 1938; Moss 1962; Mitchell 1964; Alberti and Storch 1977; Shatrov 1995, 2000, 2006). This is conventionally interpreted as a feature caused by living in dry conditions (Alberti and Storch 1977). In this case, the proximal tubule is suggested to be the place of primary urine formation (Alberti and Coons 1999). Details of this process are still unclear taking into account the absence of remarkable muscle sheath in this portion of the gland.

The tubulus typically runs along the longitudinal axis of the body and makes several bends. The number and arrangement of the bends varies greatly among different taxa (see Alberti and Coons 1999). According to Alberti and Storch (1977), in cheyletids and tetranychids the tubulus is very similar and includes the proximal tube, middle region and distal tube, — all of the same diameter. The fine structure of the corresponding tubular portions of both taxa has also much in common (Alberti and Storch 1977; Mothes and Seitz 1980; Alberti and Crooker 1985). The proximal tube is characterized by a system of apical invaginations or canals which give rise to a number of pinocytotic vesicles. Alberti and Storch (1977) reported the same arrangement of the apical region for the coxal glands of the Eupodidae and *Cunaxa* (Cunaxidae), both presently belonging to the parvorder Eupodina (according to Kethley 1982, Mironov and Bochkov 2009). Contrary to these groups of mites, the proximal tube epithelium of Bdellidae, Labidostommatidae, Anystidae and Parasitengona is devoid of apical canals but bears a highly developed apical brush border (Alberti and Storch 1977; Shatrov 1995, 2000, 2006).

The middle region of the tubulus does not exhibit any special features representing an intermediate state between the proximal and distal tubes (Alberti and Storch 1977), whereas the distal tubule of both tetranychids and cheyletids does not demonstrate endocytotic activity lacking apical system of invaginations and is characterized by deep infoldings of basal plasmalemma associated with numerous long mitochondria (basal labyrinth) (Alberti and Storch 1977; Mothes and Seitz 1980; Alberti and Crooker 1985). Basal labyrinth has also been described in the distal tube epithelium of most other trombidiform mites (Alberti and Storch 1977) pointing to high ion and water transport activity.

A special kind of coxal glands devoid of a sacculus has been described in a parasitic mite *Myobia murismusculi* (Myobiidae) (Filimonova

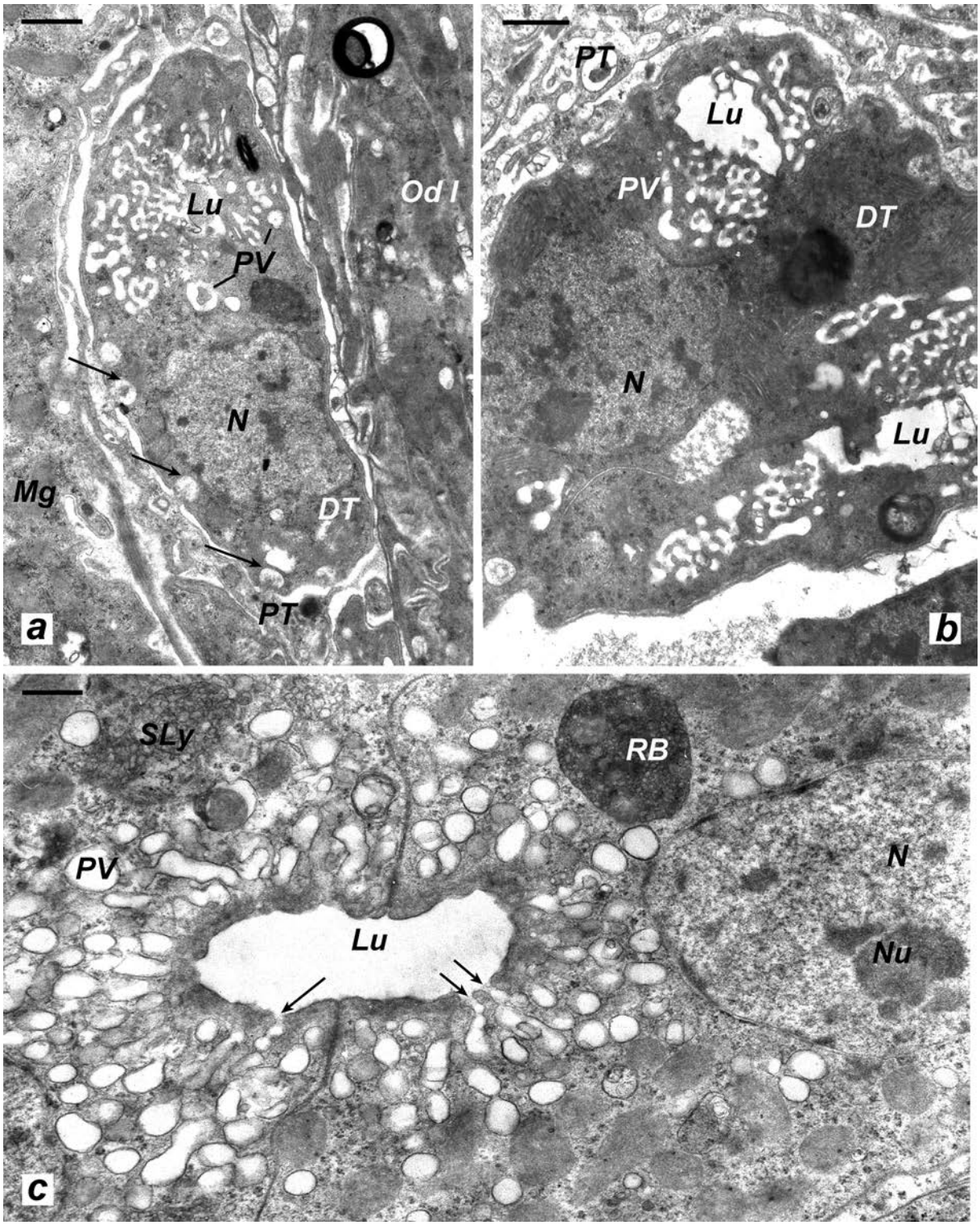

Fig. 8. Ultrastructure of the tubular portion of the coxal gland of *Myobia murismusculi* (from Filimonova 2004); a — cross-section through the most posterior end of the distal tube, to which a thin proximal tube is closely attached (arrows indicate proximal tube projections entering the distal tube cell); b — a cross section through the posterior region of the distal tube, composed of the two larger cells than in a; c — cross-section through the anterior region of the distal tubule. Note numerous pinocytotic canals connecting to the gland lumen (arrows). Scale bars: a, b — 1 μm; c — 0.5 μm.
DT — distal tube; Lu — gland lumen; M — mitochondria; Mg — midgut; N — nucleus; Nu — nucleolus; Od I — proximal oviduct; PC — pinocytotic canals; PT — proximal tube; PV—pinocytotic vesicle; RB — residual body; SLy — secondary lysosomes.

2004). Apart from the long tubular portion, the myobiid coxal gland contains a distal glandular enlargement (sac), which is directly connected to the terminal excretory duct. The tubulus compris-

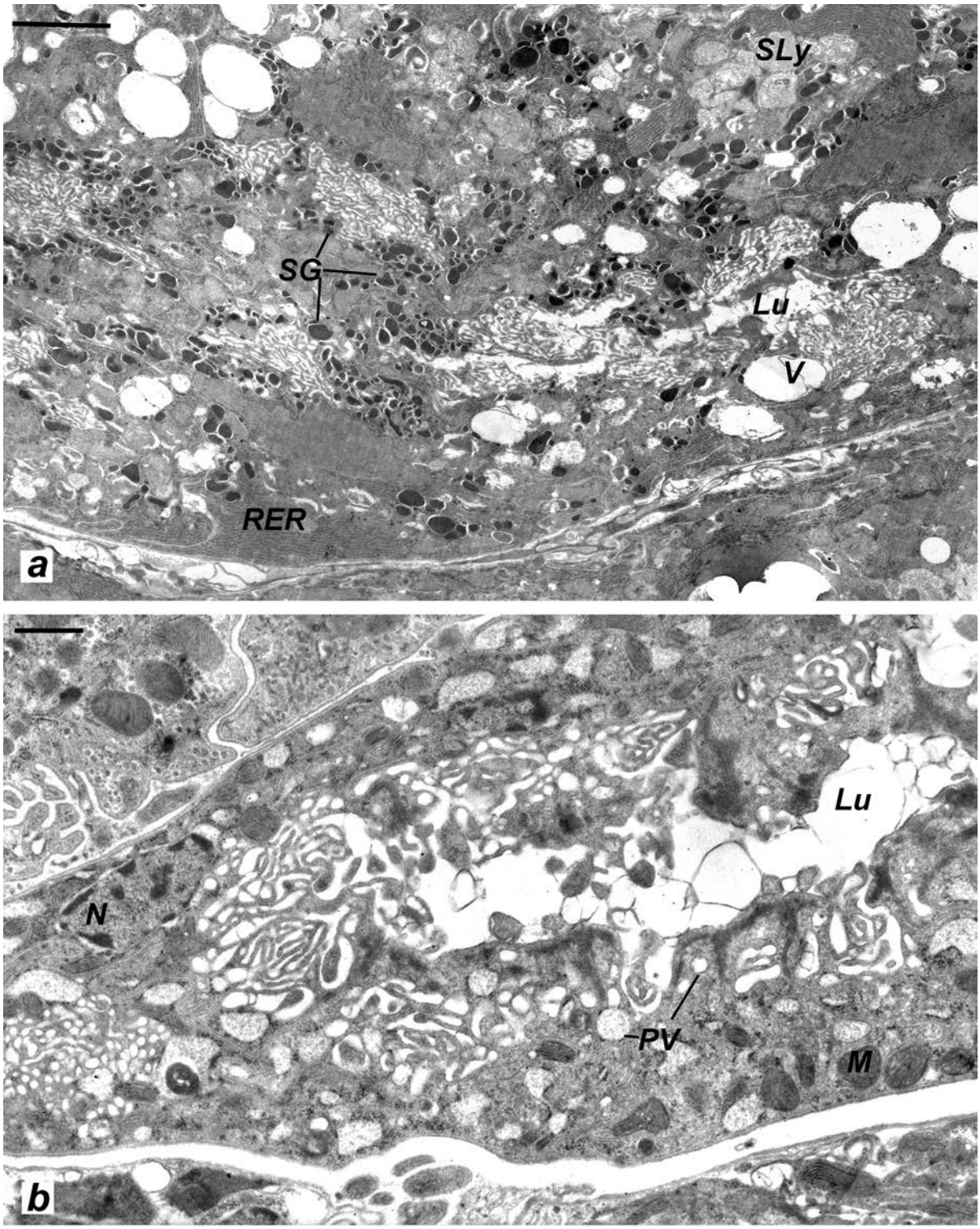

Fig. 9. Ultrastructure of the sac portion of the coxal gland of *Myobia murismusculi* (from Filimonova 2004). Longitudinal sections of the female (a) and male (b) sacs. Scale bars: a, b — 1 μm.
Lu — lumen of the organ; M — mitochondria; N — nucleus; PV — pinocytotic vesicle; RER — rough endoplasmic reticulum; Sly —secondary lysosomes; SG — secretory granules; V — vacuole.

es looped proximal and distal tubes running in close association with each other with their diameter constantly increasing from the proximal to the distal end (Figs. 8a–c). The proximal tube does not have a discernable lumen being represented by a row of flat cells with numerous processes directed to the body cavity (Figs. 8a, b). Some of these processes project into the neighboring organs (distal tube, midgut caeca or excretory organ) through the pores in their basal lamina (Fig. 5a). Both

proximal and distal tubes show high pinocytotic activity, which is most extensive in the sac (Figs. 8a–c, 9a, b). Being a distal part of the gland and being devoid of podocytes, this organ cannot be considered as a homologue of the proximal filter sacculus of other arthropods. It is formed by the high columnar epithelial cells with especially high pinocytotic activity and numerous mitochondria in the basal region of the epithelium. They are involved in the intracellular digestion of the organic substances taken from the coxal fluid. In addition to this, the sac cells produce dense protein like secretory granules. The secretion was only observed in the female coxal glands, so it was supposed to be of pheromone nature (Filimonova 2004) (Figs. 9a, b).

During our preliminary investigation, similar secretion has been recently found in the coxal glands of *Syringophilopsis fringilla* (Syringophilidae), in which the protein-like secretion is also restricted to the most distal part of the coxal gland (Filimonova 2008b) (Fig. 7d).

Male genital system and sperm structure

A considerable lack of knowledge is evident concerning the arrangement of the male genital system of the Eleutherengona. Since natural populations of many parasitic species contain much less number of males, most studies are restricted with the description of the females only. Arrhenotokous males are typical to the Eleutherengona. Such superfamilies as Tetranychoidea, Cheyletoidea, Tarsonemoidea, Pygmephoroidea**,** demonstrate no sign of meiosis during spermatogenesis (see Norton et al 1993). Neither mitotic, nor meiotic figures have been observed in the testes of *Demodex folliculorum* (Desch and Nutting 1977) and *Myobia murismusculi* (Myobiidae) (Filimonova 2006).

True copulation is characteristic for Eleutherengona and no exceptions are known up to now. This implies the presence of aedeagus and a simply organized male genital tract without special accessory glands (Fig. 10). As it was shown for spider mites (Tetranychidae), each of the paired sac-like testes is lined by a thin epithelium lacking outer muscle sheath. Alberti and Storch (1976) and later Mothes and Seitz (1981d) described proximal germ and distal glandular regions in the testis of *Tetranychus urticae.* Pijnacker (1985) named the glandular region vesicula seminalis and considered it to be a part of the short vas deferens. A thin epithelium of the glandular region of the testis is composed of the cells rich in RER and

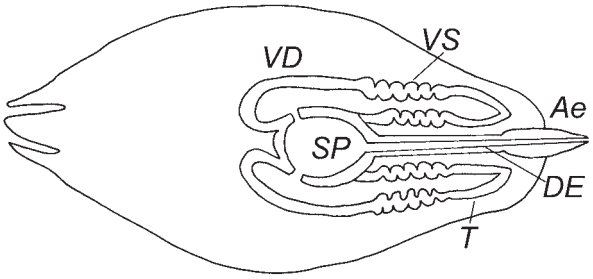

Fig. 10. Scheme of the male genital system in *Tetranychina harti* (after Matsubara et al. 1992, with minor modification). Ae — aedeagus; DE — ductus ejaculatorius; SP — sperm pump; T — testis; VD — vas deference; VS — vesicula seminalis.

Golgi complexes and produce protein-like secretion. This secretion fills the lumen of the organ and a few spermia embedded in it (Alberti and Storch 1976; Mothes and Seitz 1981d; Matsubara et al. 1992). The vasa deferentia join to form a single pear-shaped sperm pump (Alberti and Crooker 1985; Pijnacker 1985) (or seminal vesicle by some authors: Blauvelt 1945; Matsubara et al. 1992) which is equipped with a remarkable muscular sheath surrounding the internal epithelial layer. The contraction of the muscles presses the sperm cells into the narrow ejaculatory duct, which runs inside the aedeagus (or penis) (Alberti and Storch 1976; Alberti and Crooker 1985; Pijnacker 1985; Matsubara et al. 1992) (Fig. 10). There are two types of gate cells in the epithelial lining of the sperm pump located near the beginning of the ejaculatory duct. These cells, provided with processes, possibly control discharging of spermia into the ejaculatory duct, which diameter is less than the size of a single sperm cell (Matsubara et al. 1992).

The male genital system of *Brevipalpus obovatus* from the family Tenuipalpidae (former Phytoptipalpidae, superfamily Tetranychoidea) is very similar to the above (Pijnacker et al. 1981). Paired testes, which are very typical for trombidiform mites in whole (Alberti and Coons 1999), are shown in all eleutherengone families (Pijnacker and Drenth-Diephus 1973; Alberti and Storch 1976; Pijnacker 1985; Filimonova 2006) except for the Demodicidae, in which Desch and Nutting (1977) reported an unpaired testis.

Position of the male genital opening is an important characteristic used in the taxonomy of trombidiform mites. In a plesiomorphic state, the male genital opening is situated on the ventral side of the body (for example, in Parasitengona) (Alberti and Coons 1999) but in the Eleutherengona it

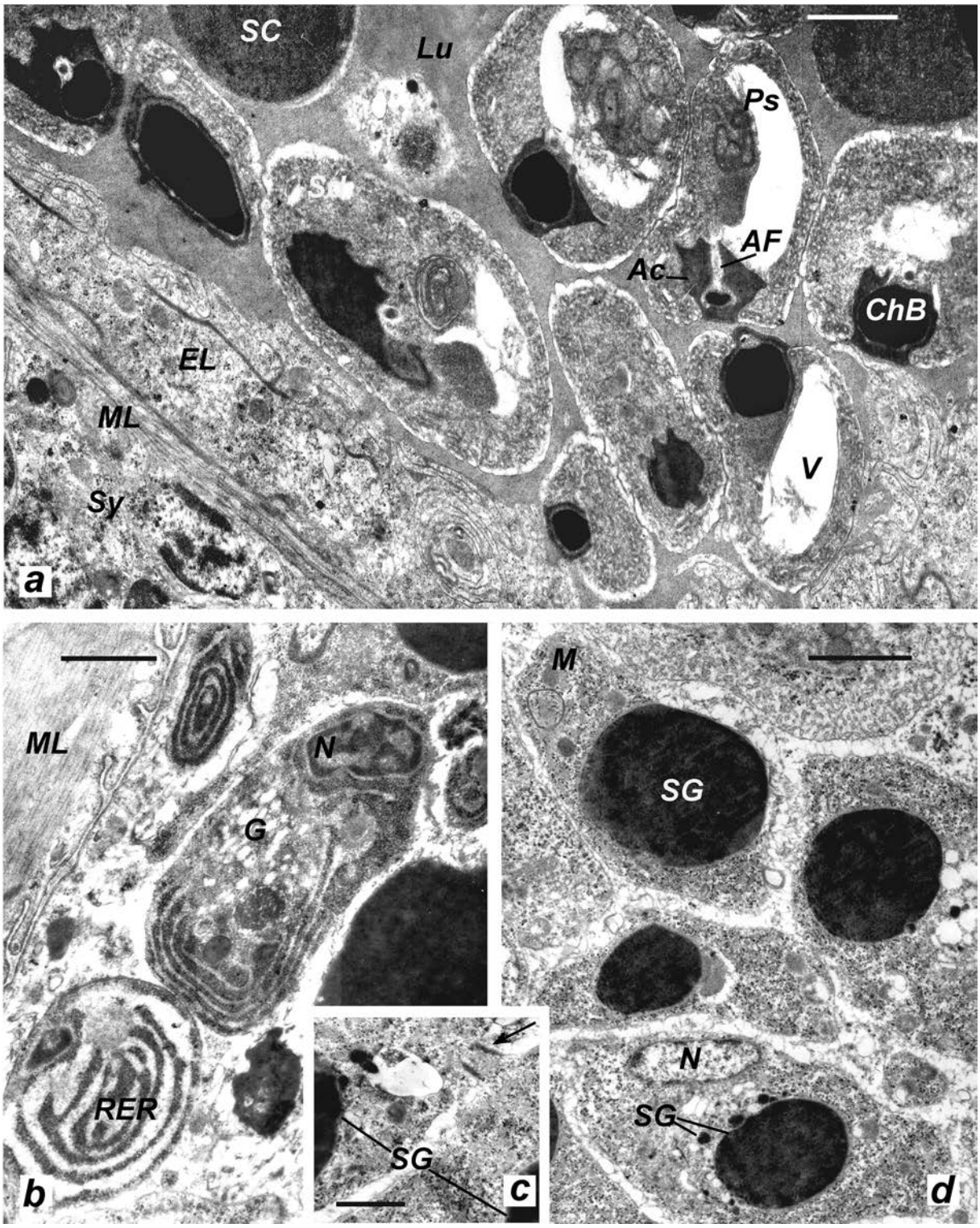

Fig. 11. Ultrastructure of the testes in *Myobia murismusculi* (from Filimonova 2006); a — fragment of the testis close to the synganglion; b — developing secretory cells; c — an intercellular bridge (arrow) between sister secretory cells; d — formation of a single secretory granule in the cytoplasm of secretory cells. Scale bars: a–c — 1 μm; d — 2 μm.
Ac — acrosomal vesicle; AF — acrosomal filament; ChB — chromatin body; EL — epithelial lining; G — Golgi body; Lu — lumen of the testis; M — mitochondria; ML — muscle layers; N — nucleus; Ps — prospermium (term needs to be explained); RER — rough endoplasmic reticulum; Sy —synganglion; SC — secretory cells; SG — secretory granules; V — vacuole.

is located either on the terminal end of the body (in Tetranychoidea) (Alberti and Storch 1976) or even dorsally, as in Demodicidae, Psorergatidae (Cheyletoidea), Podapolipidae (Tarsonemoidea), and Myobiidae (Myobioidea) (Alberti and Coons 1999).

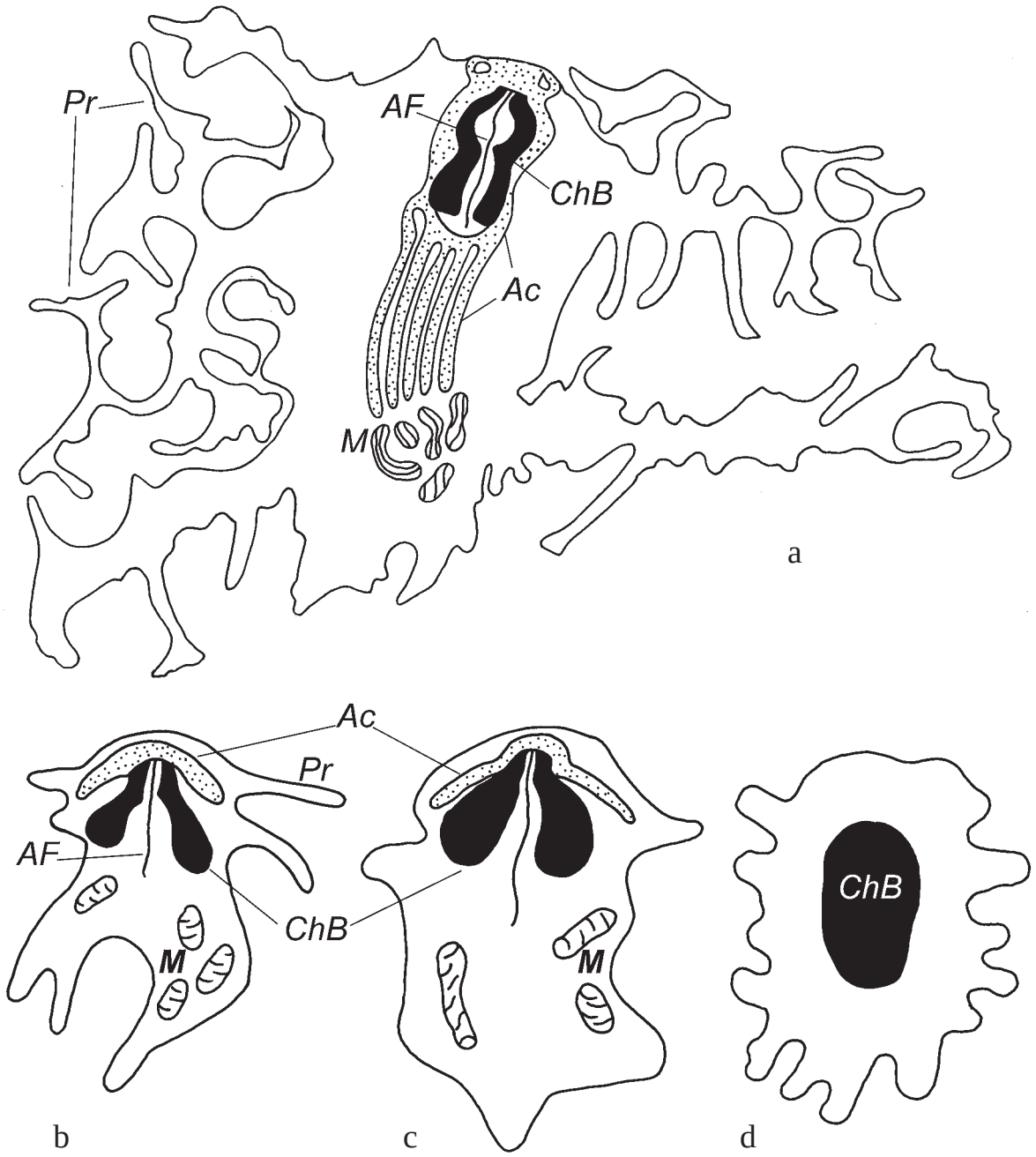

Fig. 12. Schematic drawings of the mature sperm cells from the receptaculum seminis of *Myobia murismusculi* (a) (after Filimonova 2006); *Eustigmaeus* sp. (b) (after Alberti 1980, with minor modification); *Demodex folliculorum* (c) (after Desch and Nutting 1977, with minor modification), and *Tetranychus urticae* (d) (after Alberti and Crooker 1985, with minor modification).
Ac — acrosomal vesicle; AF — acrosomal filament; ChB — chromatin body; M — mitochondria; Pr — processes.

Internal insemination does not acquire much mucous substance to preserve spermia alive like in the case of the spermatophores. Thus, special accessory glands are typically absent in the Eleutherengona (Alberti and Coons 1999). There is also a tendency to reduce the glandular portion of the testicular epithelium comparing to most other trombidiform taxa, where large glandular cells present in the epithelial lining of the testes (Alberti and Coons 1999). The testes of the eleutherengone species examined so far, demonstrate thin epithelium in which secretory region has been reported only for tetranychids (Alberti and Storch 1976; Desch and Nutting 1977; Pijnacker et al. 1981; Filimonova 2006) (Fig. 11a). In *Demodex folliculorum,* the bulbous seminal vesicle is not of glandular nature actually representing the vas deferens filled with the mature

spermia (Desch and Nutting 1977). In *Myobia murismusculi*, the glandular component of the testicular wall appears to be substituted by the single secretory cells floating in the lumen of the organ among the germ cells (Filimonova 2006) (Fig. 11a). Similar to the spermatids, secretory cells undergo their development in cell clusters formed after incomplete cytokinesis (Figs. 11b, c). Each secretory cell contains prominent RER and Golgi complex and develops a single dense granule in the cytoplasm. Growing gradually, the granule fills the whole volume of the cell (Fig. 11d). Mature secretory cells disintegrate and the secretory product discharges into the testicular lumen (Filimonova 2006). Thus, the high glandular epithelium of the testes, which is plesiomorphic for trombidiform mites (Alberti 1980b), at least in some eleutherengone taxa, changes to a thin epithelial layer which does not enclose the developing spermatocytes as it commonly occurs in most other Acari (Alberti and Coons 1999).

A comparative investigation of 24 species from different families of Trombidiformes indicates that all of them have aflagellate spermia, which lose their nuclear envelope in the course of differentiation (Alberti 1980b). Unfortunately, spermiogenesis has not been studied in details for most eleutherengone families, and the species examined up to date, demonstrate a remarkable diversity of sperm ultrastructure (Alberti 1980b; Alberti and Coons 1999). According to Alberti (1980b), plesiomorphic spermia of the Trombidiformes are characterized by a full complex of internal components, including acrosomal vacuole, and filament, as well as typical mitochondria. Within the Eleutherengona this kind of sperm cells have been found in the families Demodicidae (Desch and Nutting 1977), Rhaphignathidae, Stigmaeidae (Alberti 1980b), and Myobiidae (Filimonova 2006), all demonstrating very similar mode of chromatin elimination during spermiogenesis, and provided by pseudopodia-like processes in a mature state (Figs. 12a–c).

Alternatively, spermia of the spider mites are small simply organized cells devoid of acrosomal complex and mitochondria (Albert and Storch 1976; Alberti 1980b; Pijnacker 1985) (Fig. 12d). This reflects the main evolutionary trend of trombidiform sperm cells to be tiny and simply organized contrary to the spermia of Parasitiformes (Alberti 1980a; Alberti and Coons 1999).

Capacitation, the term used for sperm transformation inside the female body, is widely spread in various animal taxa, including both orders of the Acari (see Alberti and Coons 1999). Mature spermia of most eleutherengone species form short slender arms after entering female genital tract. This is true for *Raphignathus* sp. (Raphignathidae), *Eustigmaeus* sp. (Stigmaeidae) (Alberti 1980b), *Demodex folliculorum* (Demodicidae) (Desch 1984), and *Tetranychus urticae* (Tetranychidae) (Alberti and Storch 1976; Alberti 1980b, Mothes and Seitz 1981c, d) (Figs. 12b, c, d). In all mentioned species it is associated with the loss of peripheral channels of sperm cells. In the case of *Myobia murismusculi*, the arms are extremely long and abundant. As in other species they are accompanied by subplasmalemmal filaments, appearing to provide their motility (Fig. 12a).

One of the most striking features of *M. murismusculi* is the presence of the large electron-lucent vacuole at the late stages of sperm development (Fig. 11a). Up to now, no vacuoles have been observed during spermiogenesis in the order Acariformes (Alberti and Coons 1999). Vacuolated spermia are considered to be synapomorphic for the Parasitiformes (Alberti 1980a, 2005). In all Parasitiformes, the vacuole is a very complex structure with regular invaginations inside (see Alberti and Coons 1999), which is not comparable to the vacuole found in the *Myobia* late spermiogenesis. Inside the female body, the *Myobia* spermia lose their large vacuole but retain large acrosomal vesicle of unusual shape. The apical part of the acrosomal vesicle encircles the nuclear body, while its basal region exhibits long extensions (Figs. 13a, b).

Female genital system and oogenesis

The anatomy of the female reproductive system considerably varies among different trombidiform taxa, including paired or unpaired state of the ovaries, their shape, as well as the presence of sperm access system and accessory glands (Alberti and Coons 1999). At the same time, the data obtained on the representatives of Tetranychidae (Blauvelt 1945; Langenscheidt 1973; Weyda 1980; Mothes-Wagner and Seitz 1984; Alberti and Crooker 1985; Matsubara et al. 1992), Tenuipalpidae (Pijnacker et al. 1981), Demodicidae (Desch and Nutting 1977), Cheyletidae (Akimov and Gorgol 1990), Myobiidae (Filimonova 1999) and Syringophilidae (Filimonova 2008b) showed remarkable similarity of the female genital system within the Eleutherengona. Its main components are as follows: an unpaired ovary, a glandular ovi-

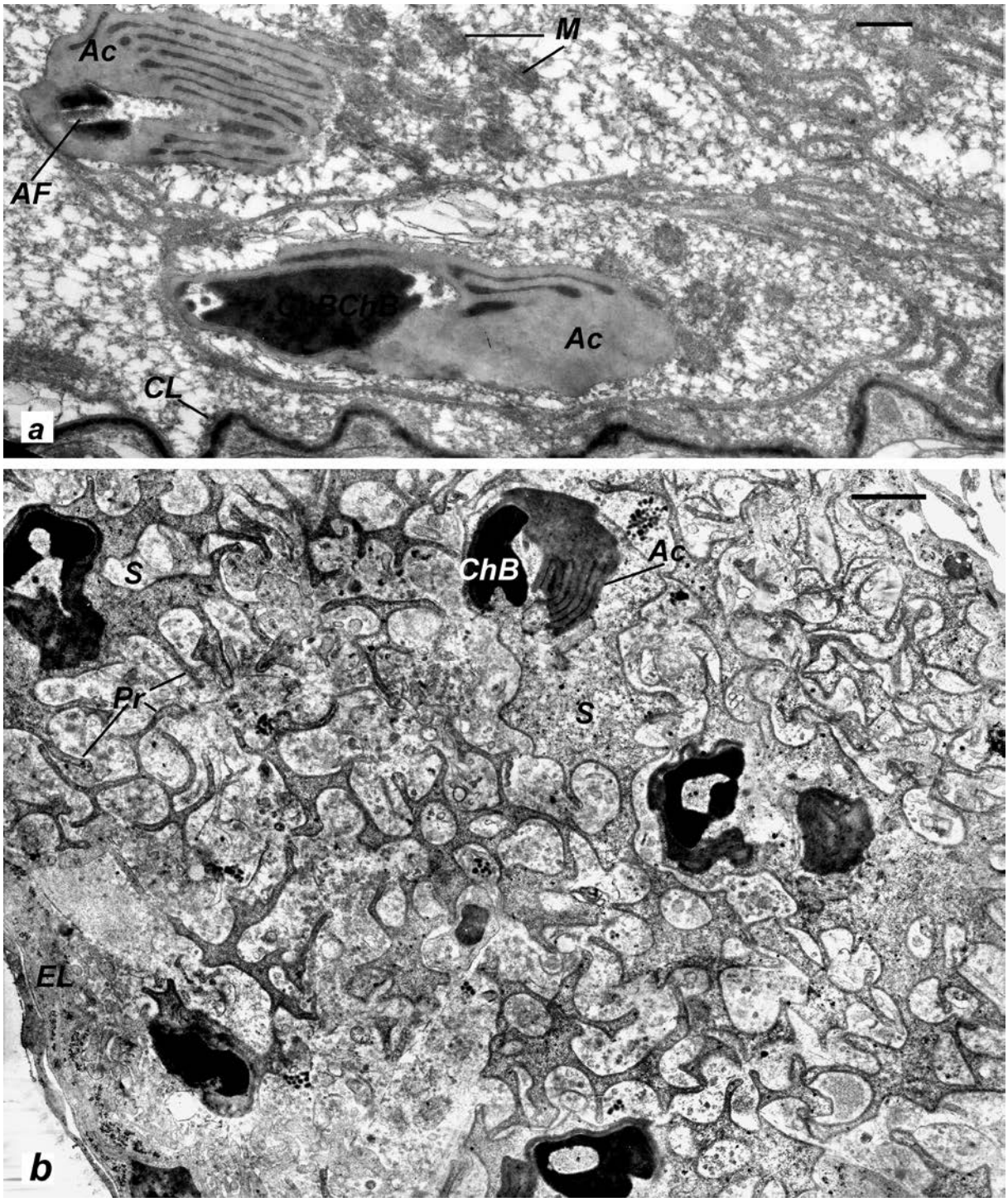

Fig. 13. Fine structure of the mature spermia of *Myobia murismusculi* (from Filimonova 2006);
a — two modified prospermia in the lumen of the receptaculum seminis; b — a group of mature spermia in the lumen of the duct, connecting the receptaculum seminis and the oviduct. Note long amoeboid processes of the sperm cells. Scale bars: a — 0.5 μm, b — 1 μm.
Ac — acrosomal vesicle; AF — acrosomal filament; CL — cuticle lining of the receptaculum seminis; ChB — chromatin body; EL — epithelial lining of the duct; M — mitochondria; Pr — processes of the sperm cells; S — mature spermia.

duct commonly divided into two portions, and a cuticle-lined vaginal cavity leading to a (primary) genital opening that serves for egg laying (Figs. 14 a–c, 15a). Receptaculum seminis was also found in most species (Blauvelt 1945; Alberti and Storch 1976; Weyda 1980; Mothes-Wagner and Seitz 1984; Alberti and Crooker 1985; Matsubara 1992; Filimonova 1999, 2001a, 2008b), including parthenogenetic *Brevipalpus obovatus* (Tenuipalpidae) (Pijnacker et al. 1981).

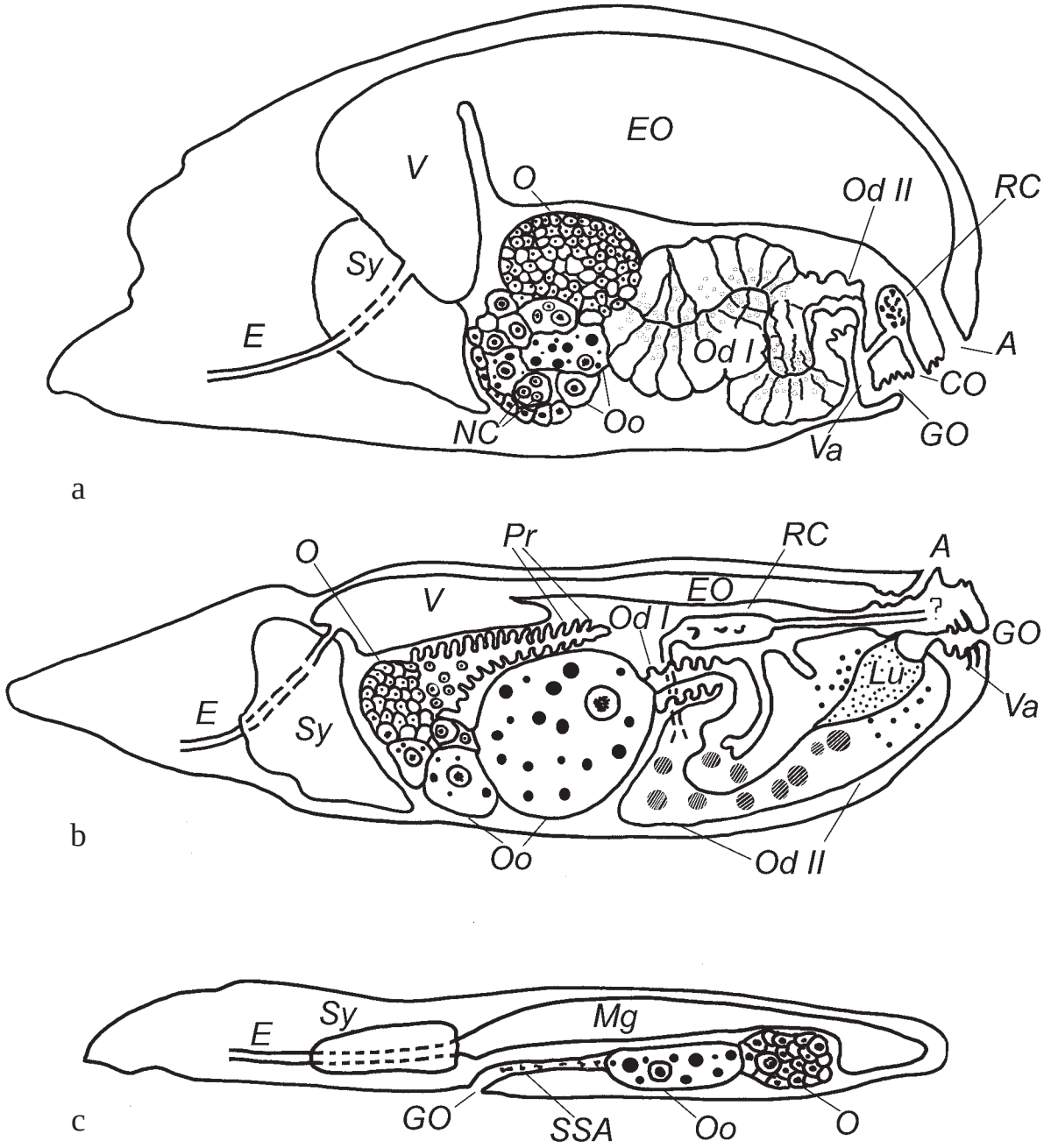

Fig. 14. Schematic drawing of the female genital system of *Tetranychus urticae* (after Matsubara et al. 1992, with minor modification) (a), *Myobia murismusculi* (b) (after Filimonova 2001a, with minor modification), and *Demodex folliculorum* (c) (after Desch and Nutting 1977, with minor modification).
A — anus; CO — copulatory opening; E — esophagus; EO — excretory organ; GO — genital opening; Lu — enlarged oviduct lumen; Mg — midgut; NC — nurse cells; O — ovary; Oo — oocytes; Od I — proximal oviduct, Od II — distal oviduct; Pr — zone of processes; RC — receptaculum seminis; SSA — sperm storage area; Sy — synganglion; V — ventriculus; Va — vagina.

An unpaired ovary commonly occupies the central part of the body immediately behind the synganglion (Alberti and Coons 1999). Blauvelt (1945) suggested the ovary of tetranychids to be originally paired. This was later proved by Langenscheidt (1973), whose embryological study demonstrated that a single ovary of *Tetranychus urticae* originally develops from the paired imaginal buds. Another embryological study dealing with *Cheyletus eruditus* (Hafiz 1935) reported the same data.

The ovary in eleutherengone mites is conventionally divided into the germarium, previtellogenic and vitellogenic regions, without clearly

discernable border between these regions (Mothes and Seitz 1981c; Mothes-Wagner and Seitz 1984; Alberti and Crooker 1985). Typically for most Acari, growing oocytes lack true follicular cells (Alberti and Coons 1999). The somatic cells constituting the ovarian sheath are sometimes called "follicular epithelium" (Mothes and Seitz 1981d; Mothes-Wagner and Seitz 1984), though they do not really form a continuous epithelial lining along the ovary. The nuclei of the somatic cells have been noted either at the top of the ovary as in *Myobia murismusculi* (Myobiidae) (Filimonova 1999) and some spider mites (Mothes-Wagner and Seitz 1984; Alberti and Crooker 1985), or also in the region connected to the oviduct in *Tetranychina harti* (Matsubara et al. 1992). In the spider mites, some somatic cells are present in the germarium in a form of supporting tissue located among the germ cells (Weyda 1980; Mothes-Wagner and Seitz 1984; Alberti and Crooker 1985; Matsubara et al. 1992).

Commonly to most other Acari (see Alberti and Coons 1999), the growing oocytes of eleutherengones stretch the sheath of the ovary to form special pouches in which their development occurs (Weyda 1980; Alberti and Crooker 1985; Akimov and Gorgol 1999; Filimonova 1999). The basal lamina of the ovarian sheath is the only component of the reduced somatic tissue encircling oocytes and separating them from the surrounding midgut until the egg-shell layers are formed (Fig. 15b). Specialized contacts between the ovary and the midgut have been observed in *Tetranychina harti,* in which the vitellogenic oocytes contact to the midgut basal lamina by means of minute microvilli-like processes (Matsubara et al. 1992). Single muscle bundles follow the ovary, but form a continuous muscle layer only around the oviducts (Weyda 1980; Alberti and Crooker 1985; Filimonova 1999).

In *Myobia murismusculi,* the ovary is hook-shaped with its top curled posterodorsally along the main part of the ovary (Filimonova 1999). Somatic cells constituting the top region form a great number of thin long processes arranged in regular rows and deeply extending into the body cavity (Filimonova 1999) (Fig. 14b). These processes occupy a large area between the ovary and the midgut which can be visible even at LM level, and evidently provide exchanging of certain substances between these organs. A similar complex of long processes has been recently found in the ovary of *Syringophilopsis fringilla* (Syringophilidae) (Filimonova 2008 b) (Figs. 15a, c).

In addition to somatic cells and oocytes, special nurse (or nutritive) cells have also been described in the ovary of the spider mites (Tetranychidae) (Blauvelt 1945; Langenscheidt 1973; Weyda 1980; Mothes-Wagner and Seitz 1984; Alberti and Crooker 1985; Matsubara et al. 1992), *Brevipalpus obovatus* (Tenuipalpidae) (Pijnacker et al. 1981) and some cheyletids (Akimov and Gorgol 1990) (Fig. 14a). The nurse cells of the cheyletids have not been investigated with regard to the ultrastructure, and no special characteristics have been given by the authors to distinguish these cells from the supporting tissue (Akimov and Gorgol 1990). In the spider mites, the nurse cells were shown to derivate from the precursors common to the germ cells, which do not differentiate into oocytes. Each of the nurse cells possesses three large nuclei provided with active nucleoli and a considerable amount of RER in the cytoplasm (Mothes-Wagner and Seitz 1984; Alberti and Crooker 1985; Matsubara et al. 1992; Weyda 1980). The intercellular bridges (or stalks) connecting the nurse cells with the oocyte are surrounded by the somatic cells named "follicular cells" (Mothes and Seitz 1981d; Mothes-Wagner and Seitz 1984; Alberti and Crooker 1985). Through these stalks some cytoplasmic components pass from the nurse cells into the oocyte. Similar intercellular bridges have been described between the oocyte and the nurse cells in *Brevipalpus obovatus* from the same superfamily Tetranychoidea (Pijnacker at al. 1981). In both groups of mites the stalks remain during most vitellogenesis and then degenerate (Pijnacker et al. 1981; Feiertag-Koppen and Pijnacker 1982; Mothes-Wagner and Seitz 1984; Alberti and Crooker 1985).

In demodicids and myobiids, no nurse cells have been found (Desch and Nutting 1977; Filimonova 1999). The solitary oogenesis (when developing oocytes form all necessary substances all by themselves), is regarded to be plesiomorphic for Trombidiformes (Alberti and Coons 1999). Interestingly, the representatives of the parvorder Anystina also demonstrate both types of oogenesis (solitary and nutrimentary): such mites as *Diplodontus despiciens* (Hydrachnidia, Hydryphantidae), *Allotrombium lerouxi* (Trombidiidae), *Hirsutiella zachvatkini* (Trombiculidae), *Platytrombidium fasciatum* (Microtrombidiidae) lack the ovarian nurse cells (Schmidt 1935; Mathur and Le Roux 1970; Shatrov 1997, 2002), while in *Abrolophus rubipes* (Erythraeidae**)** and *Calyptostoma velutinus* (Calyptostomatidae) these cells have been definitely shown (Witte 1975; Vistorin-Theis 1977).

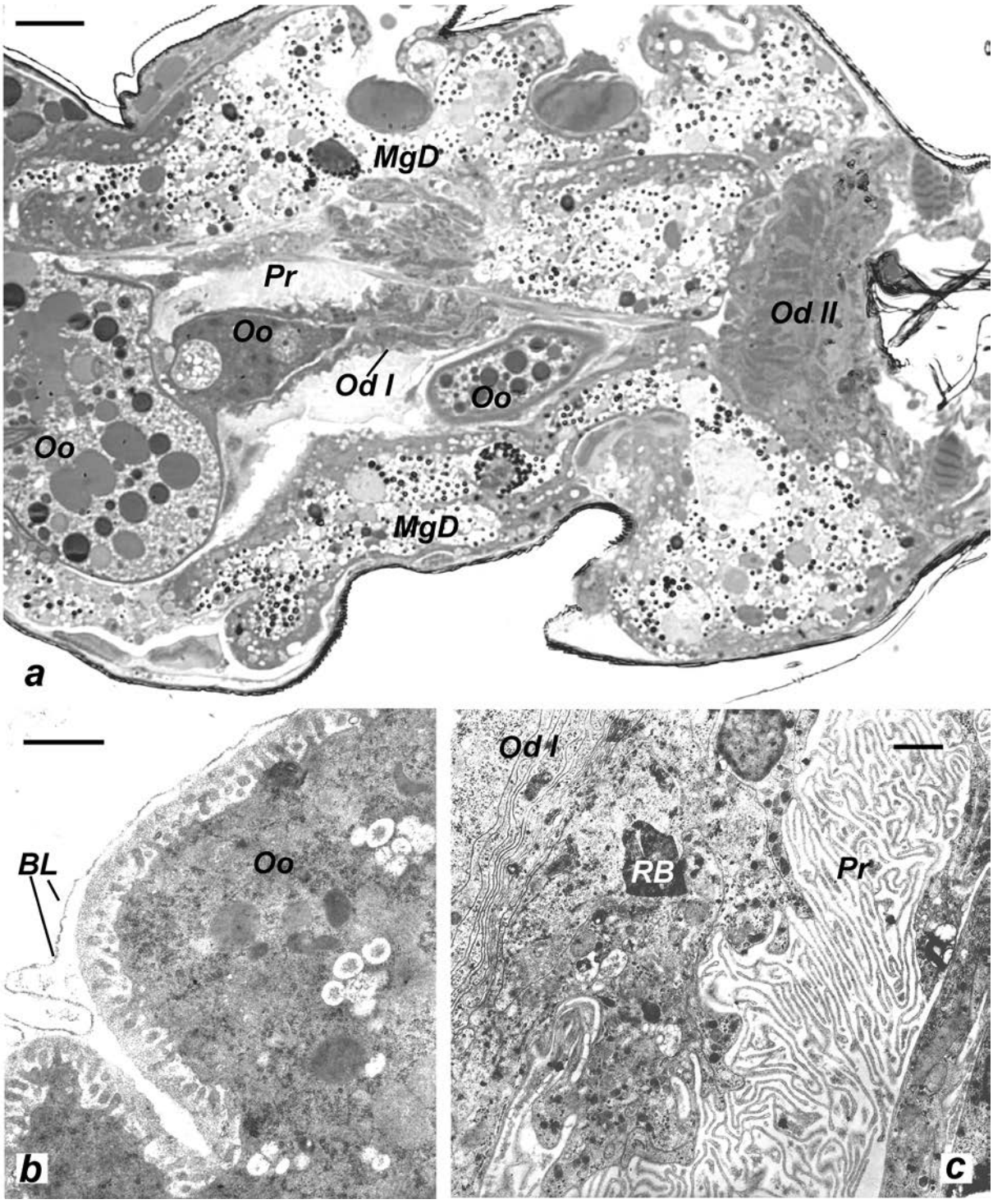

Fig. 15. The peculiarities of the female genital system in myobiid and syringophilid mites; a — frontal semithin section of the opisthosoma of *Syringophilopsis fringilla*, showing large zones of projections between the proximal oviduct and adjacent midgut diverticuli; b — ultrathin section of the young vitellogenic oocyte of *Myobia murismusculi*; c — fine structure of the zone of projections in *S. fringilla.* Scale bars: a — 25 μm; b, c — 1 μm.
BL — basal lamina; MgD — midgut diverticuli; Od I, II — regions of the oviduct; Oo — oocyte; Pr — zone of projections; RB — residual body.

In most Eleutherengona, the oviduct is a large glandular organ composed of two histologically distinct portions: the proximal and distal oviducts, each producing two or more different secretory products. In all species examined, the vitellogenesis undergoes inside the proximal oviduct (= uterus) either in part, as in Tetranychidae (Crooker and Cone 1979; Weyda 1980; Matsubara et al. 1992), Tenuipalpidae (Pijnacker et al. 1981), Cheyletidae (Akimov and Gorgol 1990) and Myo-

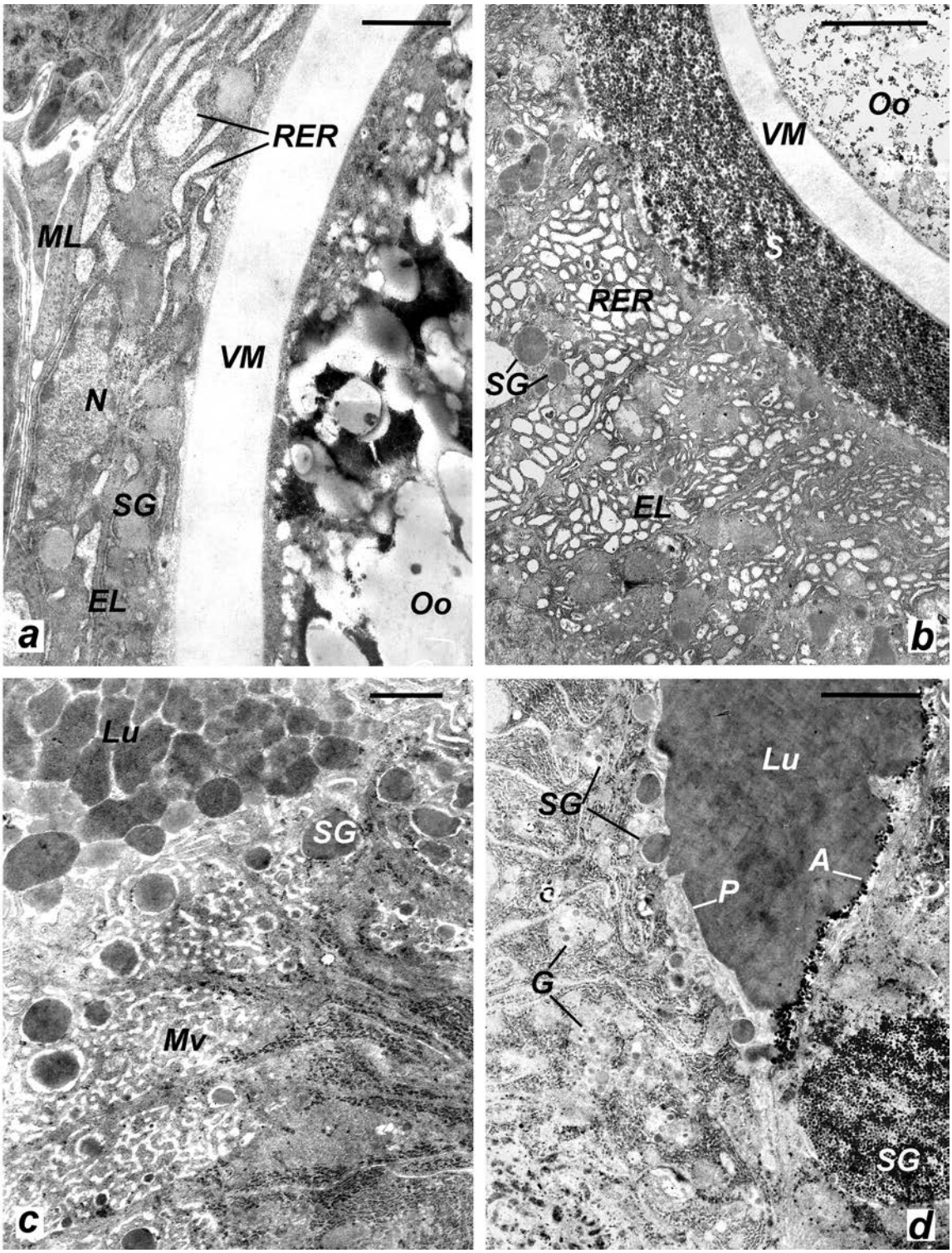

Fig. 16. Different types of secretion in the oviduct of *Myobia murismusculi* (from Filimonova 1999); a — proximal oviduct with the growing oocyte in its lumen; b — the oocyte in the most anterior portion of the distal oviduct; c — posterior portion of the distal oviduct with its lumen filled with secretion; d — the border between anterior and posterior portions of the distal oviduct. Scale bars: a, c — 1 μm; b, d — 2 μm.
A — anterior portion of the distal oviduct; EL — epithelial lining; G — Golgi bodies; Lu — lumen of the distal oviduct; Mv — microvilli; ML — muscle layer; N — nucleus; Oo — oocyte; P — posterior portion of the distal oviduct; RER — rough endoplasmic reticulum; S — secretion; SG — secretory granules; VM — vitelline membrane.

biidae (Filimonova 1999), or entirely, as it was shown in the Demodicidae (Desch and Nutting 1977). In the spider mites, the proximal oviduct is much bigger than the distal one (Blauvelt 1945; Smith and Boudreaux 1972). It is a voluminous convoluted tube lined by the high columnar epi-

thelial cells, demonstrating remarkable secretory activity (Crooker and Cone 1979; Weyda 1980; Matsubara et al. 1992). The distal oviduct consists of the lower cells, each of them containing a single large vacuole (Fig. 14a). Mature oocytes have never been noticed in this region. Both oviduct regions take part in the formation of the external egg-shell layers (chorion) (Smith and Boudreaux 1972; Weyda 1980; Mothes-Seitz and Wagner 1984; Matsubara et al. 1992).

In cheyletids, the proximal oviduct (uterus) is not as large as the distal one. The secretion of the distal oviduct serves to fasten the eggs together and to protect them from drying (Akimov and Gorgol 1990).

In demodicids, the proximal uterus is the place of vitellogenic growth of a single oocyte. It is composed of a thin epithelium, producing material for the chorion formation. The distal oviduct (which is named "sperm storage area") is a glandular organ with a narrow lumen filled by the spermia (Desch and Nutting 1977) (Fig. 14c).

In *Myobia murismusculi* (Myobiidae), the proximal oviduct is lined by a relatively low columnar epithelium which is highly folded in the empty state being stretched to a thin layer after oocyte entering the organ (Fig. 14b). In this region the most advanced oocyte completes its vitellogenic growth and the formation of the vitelline membrane occurs (Filimonova 1999) (Fig. 16a). The distal oviduct is much more voluminous though mature eggs have not been noted in its lumen. Histologically the distal oviduct of *Myobia murismusculi* is divided into the anterior and posterior portions with different types of secretion (Figs. 16b–d). The epithelial lining of the anterior portion is characterized by the presence of the huge secretory granules, containing chorion precursors (Filimonova 1999) (Figs. 16b, d). The distal portion of the organ consists of especially high columnar cells encircling a wide lumen. They produce a great amount of the basophilic secretory product, which completely fills the lumen of the organ (Figs. 16c, d).

According to our preliminary data (Filimonova 2008 b), the distal oviduct of *Syringophilopsis fringilla* (Syringophilidae) has much in common with that of myobiids. The lumen of the organ is also enlarged and filled with the secretion, which is released outside during oviposition. In both species, the oviduct secretion evidently serves like a glue to stick eggs to the host's hair or quill wall respectively (Filimonova 1999, 2008b).

In tetranychids and myobiids, oviposition is accompanied by the eversion of an ovipositor from the progenital chamber (Alberti and Crooker 1985; Alberti and Coons 1999; Filimonova, unpublished).

Receptaculum seminis was found in most of the studied eleutherengone taxa. In all cases it is represented by a flexible sac-like organ displaced from the midline in the ventral part of idiosoma (Alberti and Storch 1976; Filimonova 1999, 2001a, 2008b). In tetranychids, a thin cuticle-lined duct leads from the receptaculum seminis to a small orifice visible on a slight prominence between the anal and genital openings (Dosse and Langenscheidt 1964; Pijnacker and Drenth-Diephuis 1973, Crooker and Cone 1979; Mothes and Seitz 1981c; Alberti and Crooker 1985). Autoradiographic study confirms this orifice to be a copulatory opening (or insemination pore) (Smith and Boudreaux 1972) (Fig. 14a). Similar opening leading to the insemination duct was also described in the related family Tenuipalpidae (Castagnoli 1974). Another duct connects the receptaculum seminis with the distal oviduct not far from the point when the oviduct joins the vaginal cavity (Fig. 14a). This part of sperm accessory system was traced both in *Tetranychus urticae* (Crooker and Cone 1979; Weyda 1980) and *Tetranychina. harti* (Matsubara et al. 1992). In both species it was considered to be a tract delivering spermia to the mature ova. This seems much more evident than direct sperm transferring first through the wall of the receptaculum seminis into the body cavity and then through the wall of the oviduct inside its lumen, which was supposed by some authors (Smith and Boudreaux 1972; Mothes and Seitz 1981c, d; Alberti and Crooker 1985; Alberti and Coons 1999). The duct connecting the receptaculum seminis with the distal oviduct was also observed in *Myobia murismusculi* (Myobiidae) (Filimonova, unpublished).

Nothing is known about sperm access system in cheyletids, as receptaculum seminis has not been observed in the species examined up to now (Akimov and Gorgol 1990). In demodicids, the receptaculum seminis has not been found either, but according to Desch and Nutting (1977) the distal oviduct is functioning as the "sperm storage area" in *Demodex folliculorum*.

Tissues of the body cavity

Connective tissue is reduced to some extent in all the Trombidiformes. This is particularly true

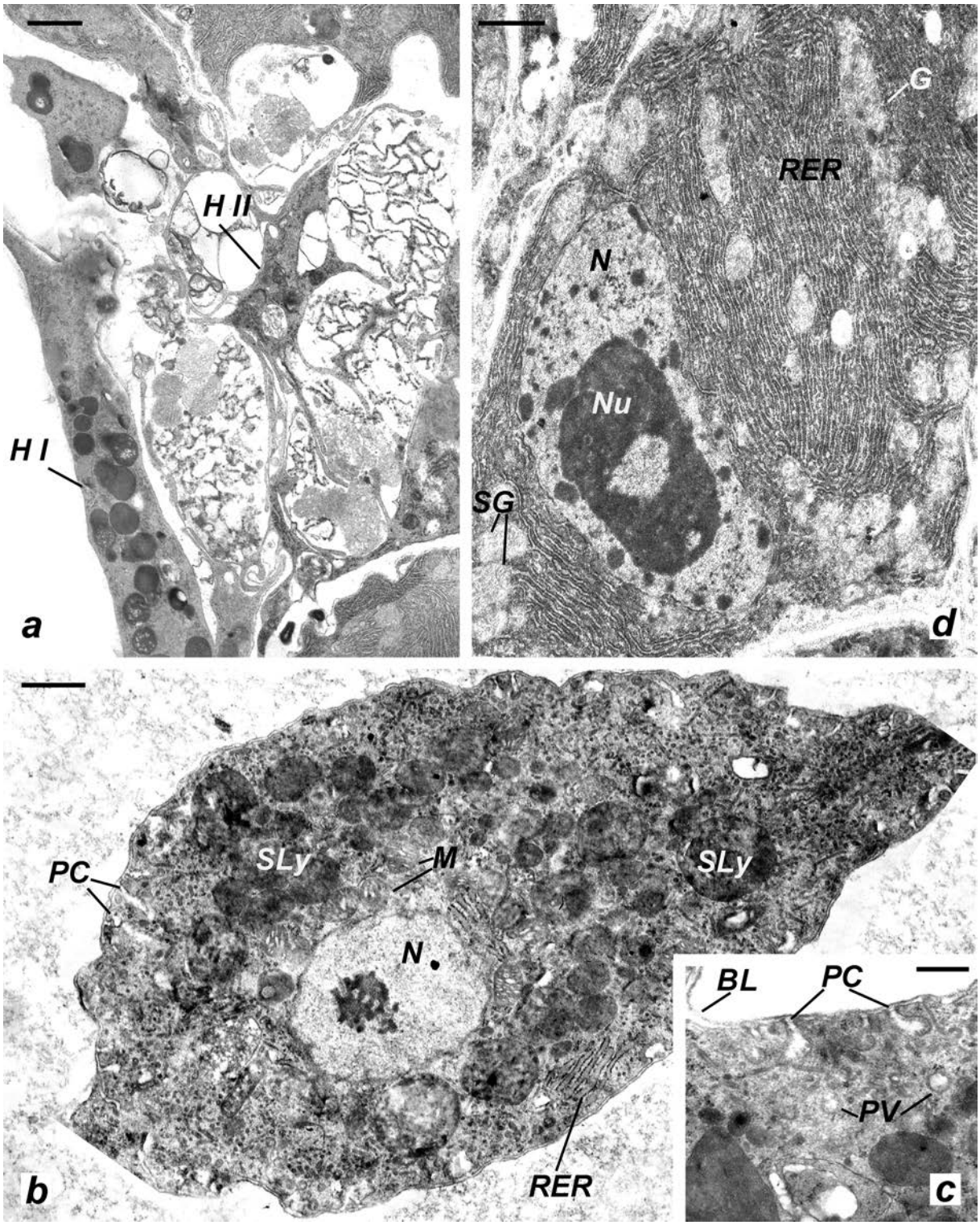

Fig. 17. TEM. Main types of the free cells visible in the body cavity of *Myobia murismusculi* (from Filimonova 2001a, with minor alterations); a — the two types of hemocytes; b — nephrocyte c — the surface of the nephrocyte at higher magnification; d — common view of the fat body cell. Scale bars: a, b, d — 1 μm; c — 0.5 μm.
BL — basal lamina; G — Golgi body; H I — granulocyte and H II — amoeboid-like hemocytes; M — mitochondria; N — nucleus; Nu — nucleolus; PC — pinocytotic canals; PV — pinocytotic vesicles; RER — rough endoplasmic reticulum; SLy — secondary lysosomes; SG — secretory granules.

with respect to small parasitic Eleutherengona in which midgut serves not only for digestion but is also involved in the exchange of substances between internal organs. So, in Demodicidae, Myobiidae and Syringophilidae connective tissue was not observed in a conventional form of interstitial membranes or a sheath covering internal organs, as it was described in some other mites (Alberti

and Coons 1999). In these mites, connective tissue is evidently represented mainly by free hemocytes, which have been poorly studied up to now. Two types of hemocytes have been described in *Myobia murismusculi* (Filimonova 2001a) (Fig. 17a). One of them contains membrane-bounded granules of medium electron density and resembles the type of hemocytes observed in *Syringophilopsis fringilla* (Syringophilidae) (Filimonova 2008 b) as well as in many other Acari (Alberti and Coons 1999). The other type of myobiid hemocytes is represented by the star-like cells which are presumably capable to burst releasing their internal content into the body cavity (Fig. 17a).

Nephrocytes typical for most of the Acari (Amosova 1983; El Shoura 1986, 1989; Coons et al. 1990; Shatrov 1998) were also observed in *Myobia murismusculi* (Filimonova 2001a). They are large cells containing peripheral network of pinocytotic canals from which numerous coated vesicles originate (Figs. 17b, c). Large membrane-bound granules of moderate electron density were also seen in their cytoplasm (Filimonova 2001a) (Fig. 17b).

The hemolymph of *Syringophilopsis fringilla* was shown to contain large granulated hemocytes but no nephrocytes have been observed in this species (Filimonova 2008a). The absence of typical nephrocytes has been also reported for cheyletids (Akimov and Gorgol 1990).

Though exact function of acarine nephrocytes is not detected, their structural identity to those of insects suggests similar function: in the Acari these cells may also maintain internal homeostasis selectively eliminating certain substances from the hemolymph.

While a distinct fat body has been found in all suborders of Acariformes (see Alberti and Coons 1999; Alberti et al. 2003), regarding the Trombidiformes it has received only a brief attention in a limited number of papers (Whitmoyer et al. 1972; Jonczy and Kropczinska 1974; Alberti 1974; Witte 1975; Nuzzaci and Alberti 1996; Filimonova 2001a, c). Among the eleutherengone mites studied up to date, the only example is *Myobia murismusculi* (Myobiidae), in which fat body is represented by a layer of very large cells attached to the midgut and by another group of cells concentrated at the terminal end of the body (Filimonova 2001a, c). The large size of the cells and their huge nuclei suppose probable polyploidy (Fig. 17d). A prominent nucleolus, extensive rough endoplasmic reticulum (RER), and numerous Golgi bodies producing secretory granules, all point to the active protein synthesis (Filimonova 2001c) (Fig. 17d). As the fat body cells occur only in the mature females of *Myobia*, it was suggested that the secretory product might be one of vitellogenin precursors, releasing into the hemolymph of the mite like it was demonstrated for ixodids (Coons et al. 1982). Appearance of the fat body cells in *Myobia* is very similar to that described in ixodids (Coons et al. 1982, 1990), and some other Trombidiformes, including representatives of Eriophyidae (Whitmoyer et al. 1972), Bdellidae (Alberti 1974) (both belonging to the parvorder Eupodina), and Anystidae (parvorder Anystina) (Filimonova, unpublished). In contrast to the observations obtained on some other mites (Alberti et al. 2003; Alberti 2005), the processes of *Myobia* fat body cells do not penetrate the basal lamina of the midgut epithelium (Filimonova 2001c).

Blauvelt (1945) and Langenscheidt (1973) reported the presence of fat body cells in *Tetranychus telarius* and *T. urticae* respectively (Tetranychidae), but these data have not been confirmed later (Alberti and Crooker 1985). Very thin layer of connective tissue was mentioned in *Tetranychina harti* close to the ovary (Matsubara et al. 1992), but no special investigation has been carried out.

CONCLUSIONS

As it was shown in the present paper, the representatives of the parvorder Eleutherengona studied up to present remarkably differ from the mites belonging to the other two parvorders of Trombidiformes (Eupodina and Anystina) by some important internal characters. 1. Their postventricular midgut is not divided into the colon and postcolon being represented by a simple tube-like excretory organ. The latter has an open communication with the ventriculus contrary to the corresponding organ of Parasitengona. 2. The female genital opening is situated on the posterior end of the body, while in most other trombidiform taxa it is ventrally located. Thus, the anal and genital openings are close to each other in the females. 3. The glandular component in the epithelial lining of the testis is much reduced (if present). 4. The salivary glands are not so large and numerous as those in most other Trombidiformes being reduced to two pairs in Tetranychoidea and to a single pair in Cheyletidae and Demodicidae. In Myobiidae and Syringophilidae, these glands have not been found (the tracheal gland of syringophilids is not evidently involved in digestion). 5. The coxal

glands are long tubes extending up to the level of legs IV). They are either devoid of the proximal filter sacculus (in tetranychids, and myobiids) or provided by a sacculus with a considerably reduced lumen (in cheyletids). The epithelial lining of the tubules do not demonstrate regular brush border (as it is in the Parasitengona), showing high pinocytotic activity.

All the eleutherengone species examined so far, belong to the section Rhaphignatha, among which the families Myobiidae (superfamily Myobioidea) and Tetranychidae (Tetranychoidea) have been recently considered as the inferior Rhaphignatha**,** while the superfamily Cheyletoidea (including Cheyletidae, Demodicidae and Syringophilidae) have been referred to as the higher Rhaphignatha (= subsection Stylostomatina) (Bochkov et al. 2008, 2009; Mironov and Bochkov 2009). The present study demonstrates that the phenomenon of heterobatmy is characteristic for all the examined eleutherengone families and all of them demonstrate the mixture of relatively primitive and advanced characters.

As it was mentioned above, the Tetranychoidea have genital opening in both sexes in a relatively primitive position. The female genital opening of spider mites is ventrally located (similar to most trombidiforms), though in other eleutherengone taxa it occupies terminal position. Aedeagus of tetranychids ends posteriorly, whereas in all other eleutherengone families it is displaced to the middle of the dorsal side and is directed anteriorly.

At the same time, the Tetranychoidea is characterized by two strong apomorphic features: the absence of a sacculus in the coxal glands and the simply organized sperm cells devoid of mitochondria and acrosomal complex. Interestingly, the spermia of tetranychids inside the female genital tract develop the processes like the sperm cells of Myobiidae, Rhaphignathidae, and Stigmaeidae.

The sperm structure of *M. murismusculi* with its large acrosoma, associated with full acrosome complex and unmodified mitochondria is very similar to that of *Rhaphignathus* (Rhaphignathidae) and *Eustigmaeus* (Stigmaeidae), confirming Myobiidae as the early derivative Rhaphignatha (Bochkov et al. 2008). On the other hand, *Myobia murismusculi*, the only species examined presently from this family, shows a unique arrangement of the testis in which the glandular cells develop in the lumen of the organ and discharge the secretory product after their disintegration. This is also the only example with vacuolated prospermia which have been observed among Trombidiformes.

A further striking feature of myobiids is the occurrence of fat body cells (Filimonova 2001c) which have not been found in other eleutherengones. This may be a special physiological feature of myobiids which are characterized by a relatively small volume of midgut (another potential source of vitellogenins) comparing to the corresponding organs of cheyletids, syringophilids and demodicids (Filimonova 2001a; 2008b). On the other hand, within the parvorder Anystina, the fat body cells have been found in the females of Anystidae (Filimonova, unpublished) but not in the more derived Parasitengona (Shatrov 2000; Alberti and Coons 1999).

The Syringophilidae share several striking internal characters with Myobiidae and Tetranychidae (both the low Rhaphignatha, according to Bochkov 2009). Like myobiids, they are lacking typical salivary glands and show a remarkable glandular region in the distal portion of the coxal gland. Another similarity of these taxa concerns the highly modified somatic part of the ovary provided with a great number of long processes which occupy the area between the ovary and the gut. Besides this, syringophilids demonstrate open podocephalic canals, a plesiomorphic character, which they share with the Tetranychoidea.

Undoubtedly, at least a part of the internal characters observable in different families have been convergently developed as the adaptation to parasitic life. So, all obligate parasites, as the Myobiidae, Syringophilidae, and Demodicidae, show remarkable reduction of the internal visceral musculature. In myobiids and syringophilids, the esophagus and anterior midgut do not have a continuous muscle layer, and it is completely lost in the gut of demodicids. The feeding on the lymph of vertebrate hosts, which is rich in simple organic substances, might cause the reduced number or even the absence of salivary glands. A glandular region in the coxal glands of myobiids and syringophilids appears to substitute the loss of voluminous salivary glands in these tiny animals.

Small size of the mites is accompanied by the reduction of the body cavity and hemolymph volume in the parasitic Eleutherengona comparing to much bigger predators like Parasitengona or Bdellidae. The reduction of hemolymph volume seems to be the main functional reason to lose a typical filter sacculus in the coxal glands of most eleutherengone species. Remarkable reduction of

the connective tissue leads to the development of special contacts between the internal organs, such as specialized finger-like processes connecting the coxal glands and midgut in tetranychids, myobiids and syringophilids, a set of long processes originating from the somatic cells of the ovary both in myobiids and syringophilids, as well as various small extensions, with which most internal organs (including fat body, muscle cells or epidermis) communicate. Finally, highly specialized parasitic Demodicidae lost even respiratory and circulatory systems with the other systems of organs strikingly reorganized (Desch and Nutting 1977).

The findings of the present study demonstrate numerous parallel-developed features, which have evidently appeared in the course of the divergent evolution of the taxa. Our knowledge in this area is still fragmentary. Practically, no data are available concerning the internal anatomy of the superfamilies Pterygosomatoidae and Rhaphignathoidea. Much more species are necessary to be examined to define steady differences among the various eleutherengone families. The data on the internal organization of Heterostigmata, which is assumed to be the sister group of the Rhaphignatha (Lindquist 1984; Kethley in: Norton et al. 1993; Bochkov et al. 2008), would be of special interest. Besides this, information concerning internal anatomy of other parvorders of Trombidiformes is also quite necessary to clarify the questions arisen in literature and to define new internal characters useful for phylogenetic reconstructions.

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