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The ground pattern of midgut structure in Julidae (Julida: Juloidea): a study on selected species

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Abstract

The middle endodermal region of the digestive system (midgut) of arthropods is responsible for processes related to digestion but is also considered an organ participating in homeostasis maintenance. Therefore, many experimental studies, for example, related to the effect of various stressors on the organism, are conducted on the epithelium of this intestine. However, it is important to know the basic structure and ultrastructure of the midgut tissues. In myriapods (e.g., millipedes), the midgut has the form of a simple tube lined with a single layer of epithelium, surrounded by hepatic cells and visceral muscles. Considering the fact that millipedes can inhabit various terrestrial environments, feed on a variety of foods, and are important links in food chains, they can be considered good models for ecotoxicological studies. Thus, we selected eight species belonging to the family Julidae (order Julida) to investigate whether any distinct ground pattern for this organ appears within one millipede systematic group and whether it is possible to translate it into the general pattern of the midgut epithelium in millipedes: *Leptoiulus sarajevensis* (Verhoeff, 1898), *Leptoiulus trilineatus* (C. L. Koch, 1847), *Cylindroiulus boleti* (C. L. Koch, 1847), *Megaphyllum bosniense* (Verhoeff, 1897), *Pachyiulus cattarensis* (Latzel, 1884) and *Pachyiulus hungaricus* (Karsch, 1881) as representatives of the epigean fauna as well as *Leucogeorgia longipes* Verhoeff, 1930 and *Leucogeorgia gioi* Antić and Reip, 2020 as true cave-dwelling species. The study was performed using light and transmission electron microscopy. The results revealed a general pattern of all cells forming the midgut epithelium in Julidae, as well as the hepatic cells surrounding the midgut. Some small differences were observed, which are probably related to the type of food consumed.

Keywords

digestive system, midgut epithelium, millipedes, regenerative cells, storage material

1. Introduction

The digestive system of arthropods, including myriapods, consists of three regions that differ in their embryonic origin: ectodermal fore- and hindgut, and endodermal midgut. The middle region is lined with a single layer of epithelium on the non-cellular basal lamina and is surrounded by visceral muscles. It may take the form of a simple tube differentiated (or not) into regions; it may be a large gland or a combination of a tube and a gland. It is considered an organ not only responsible for processes related to digestion or being a niche for microbiota, but also constituting an important barrier in the body against the penetration of pathogenic microorganisms or toxic substances. Through its continuous degeneration and regeneration processes, homeostasis is maintained in the body (Malagoli et al. 2010; Wilczek et al. 2014; Bonelli et al. 2019). Studies on the model species *Drosophila melanogaster* Meigen, 1830, indicate that this organ is highly complex and dynamic (Chen and St Johnston 2022). Therefore, many experimental studies (e.g., toxicological, cytotoxicological) are conducted, which use knowledge of the structure of this organ not only in *D. melanogaster* (Affleck and Walker 2019; Dreszer et al. 2023) but also in other arthropods (Wilczek et al. 2014; Bonelli et al. 2019; Rost-Roszkowska et al. 2022; Ostróżka et al. 2022). As it turns out, depending on the structure of the arthropod midgut, there can be many different cells in the epithelium, but the most important are digestive, regenerative, and secretory cells. The ultrastructure of all cells forming the midgut epithelium is related to their functions, but it can often be changed by e.g., various stressors from the natural environment (Zhang et al. 2024).

In myriapods, data on the structure or ultrastructure of the midgut epithelium are mainly known from Diplopoda and Chilopoda. The midgut in these animals is a simple tube lined by an epithelium composed of certain types of cells (Koch et al. 2011; Fontanetti et al. 2015). The type of epithelium, which is related to its functions, influences the distribution of cellular organelles (Cioffi 1984). Apparent differences have been described in different species, such as centipedes (Chajec et al. 2012, 2014) or millipedes (Sosinka et al. 2014). Considering also the fact that they can inhabit various terrestrial environments, feed on a variety of foods, and are important links in food chains, they can be considered good models for ecotoxicological studies (Buch et al. 2018; Ion and Murariu 2023). However, for such studies to be conducted, it is important to know the structure and ultrastructure of the tissues forming the midgut in these animals. Abundant data can be found on the midgut of species belonging to millipedes (Fontanetti et al. 2015). However, we attempted to investigate whether any distinct ground pattern for this organ appears within one millipede systematic group and whether it is possible to translate it into the general pattern of the midgut epithelium in millipedes. Thus, we selected specimens from the order Julida due to the distribution of these animals worldwide that would be available for eco- or cytotoxicological studies. With approximately 700 described species, the monophyletic millipede family Julidae is the most speciose of the 16 families of the Julida (class Diplopoda). This group is predominantly found in the Palaearctic, with extensions into the Indomalayan region in Southeast Asia (Enghoff 2015). The greatest diversity is found in Europe, with around 530 species described (Kime and Enghoff 2017). Like most other millipedes, the representatives of this family are important elements of temperate forest ecosystems, where they play a crucial role as detritivores (Golovatch and Kime 2009). In addition, this family also includes a considerable number of cave-dwelling taxa, some of which have transitioned from an exclusively terrestrial way of life and detritivorous diet to a semi-aquatic and hygropetricolous lifestyle and filtering diet or a diet based on collecting small organic particles from the cave water, wet walls and cave hygropetric by scratching with modified mouthparts (Enghoff 1985; Antić et al. 2017, 2023; Antić and Reip 2020; Antić and Akkari 2023).

In addition to describing the general pattern of the epithelium forming the midgut in selected species of Julidae, the further aims of this study were to determine whether, within one systematic group (family), the ultrastructure of the midgut epithelium has a distinct pattern, and, if any differences occur, whether the living environment or the type of food consumed influence them. The general knowledge of cell structure at the ultrastructural level will be able to be used in the future in numerous experimental studies conducted on millipedes.

2. Material and methods

2.1. Material examined and photography

We selected several species of European julids (Fig. 1A–H) from six different tribes with a preference for different habitats for this study. From the tribe Leptoiulini, we analyzed the Balkan endemic species *Leptoiulus sarajevensis* (Verhoeff, 1898) as a mountain forest dweller and *Leptoiulus trilineatus* (C. L. Koch, 1847), a trans-Adriatic species occurring predominantly in the Balkans with extension to Anatolia, with a wide range of habitats from forests to open habitats and caves (Kime and Enghoff 2017). From the tribes Cylindroiulini and Brachyiulini, we used a single species each, viz., *Cylindroiulus boleti* (C. L. Koch, 1847) and *Megaphyllum bosniense* (Verhoeff, 1897). *Cylindroiulus boleti* is a lowland species widely distributed in south-eastern and central Europe, often occurring in dead wood, while *M. bosniense* is a Balkan subendemic species, occurring mainly in woodlands, but sometimes also in pastures and suburban areas (Kime and Enghoff 2017). Two common Balkan species from the tribe Pachyiulini were also included in this study. *Pachyiulus cattarensis* (Latzel, 1884) is a subendemic Balkan species that occurs in various habitats but favors warm, open habitats, while the Carpathian-Balkan *Pachyiulus hungaricus* (Karsch, 1881), one of the largest European millipedes, is very common, especially in deciduous forests. Finally, in addition to the six epigean species, two troglobiotic Caucasian endemics from the tribe Leucogeorgiini were also studied, viz., *Leucogeorgia gioi* Antić and Reip, 2020 and *Leucogeorgia longipes* Verhoeff, 1930. *Leucogeorgia gioi* is a typical terrestrial, cave-dwelling species known from a few caves in the Chiatura district of Georgia (Antić and Reip 2020). *Leucogeorgia longipes*, on the other hand, is a millipede species with modified mouthparts and semi-aquatic and hygropetricolous lifestyle. This species is found in cave streams, on very humid cave walls, and in the cave hygro-

Figure 1. Julidae species examined. Photos: D. Antić.

Table 1. Collecting data of specimens.

Millipede species	Location
Leptoiulus sarajevensis	SERBIA, Vrdnik, Fruška Gora Mountain, mixed forest with *Fagus* dominant, 19.04.2023, D. Antić, D. Stojanović, Ł. Chajec and M. Rost-Roszkowska leg.
Leptoiulus trilineatus	SERBIA, Belgrade, Avala Mountain, Čarapićev Brest, *Fagus* forest, 28.10.2023, D. Antić, D. Stojanović, Ł. Chajec and M. Rost-Roszkowska leg.
Cylindroiulus boleti	SERBIA, Belgrade, Ada Ciganlija, Sava River embankment, *Populus* and *Salix*, 20.10.2023, D. Antić leg.
Megaphyllum bosniense	SERBIA, Belgrade, Ada Ciganlija, Sava River embankment, *Populus* and *Salix*, 20.10.2023, D. Antić leg.
Leucogeorgia longipes	GEORGIA, Ambrolauri, Racha karst massif, Tskhrajvari cave, 22.06.2023, D. Antić leg.
Leucogeorgia gioi	GEORGIA, Imereti, Chiatura, Zemo Imereti plateau, Kotia Cave, 24.06.2023, D. Antić & A. Faille leg.
Pachyiulus cattarensis	SERBIA, Pčinja, Starac Mountain, litter, 16.05.2023, D. Stojanović leg.
Pachyiulus hungaricus	SERBIA, Belgrade, Avala Mountain, Čarapićev Brest, *Fagus* forest, 28.10.2023, D. Antić, D. Stojanović, Ł. Chajec and M. Rost-Roszkowska leg.

petric, where it apparently feeds by filtering or collecting fine organic particles by scratching with modified mandibles (Antić and Reip 2020, Antić et al. 2023). This species is endemic to caves in the Kutaisi, Ambrolauri, and Chiatura districts of Georgia (Antić and Reip, 2020). The material was collected in a natural, unpolluted environment (Table 1). The specimens were in good condition, actively moving and feeding.

The animals were photographed directly in the field or a few hours later at the University of Belgrade – Faculty of Biology using Olympus Stylus Tough TG-6 and Canon PowerShot SX120IS digital cameras. Adult specimens used for this study were collected. After some hours, they were anesthetized with chloroform (5 specimens of each species examined) and decapitated in 2.5% glutaraldehyde in a 0.1 M sodium phosphate buffer. The midgut was isolated and fixed in 2.5% glutaraldehyde in a 0.1 M sodium phosphate buffer (University of Belgrade). Then the material was prepared for analysis using the methods described below (University of Silesia in Katowice). The exception was cave species, which, after collection, were immediately decapitated, fixed in 2.5% glutaraldehyde in a 0.1 M sodium phosphate buffer, and sent to the laboratory at the University of Silesia in Katowice.

2.2. Methods

2.2.1. Light and transmission electron microscopy

The isolated middle region of the digestive system (midgut) was fixed with 2.5% glutaraldehyde for at least 24 h (pH 7.4, 4°C), postfixed in 1% osmium tetroxide in a 0.1 M phosphate buffer (4°C, 2 h), dehydrated (50%, 70%, 90%, 96%, 100% x 4, acetone, each for 15 min, RT) and embedded in epoxy resin (Epoxy Embedding Medium Kit; Sigma). After a few days of polymerization, Epon blocks were trimmed and prepared for cutting using a Leica EM UC7 ultramicrotome (University of Silesia in Katowice). Semithin sections (0.8 μm thick), after staining with 1% methylene blue in 0.5% borax, were examined using an Olympus BX60 light microscope (University of Silesia in Katowice). Ultrathin sections (70 nm) were stained with 13% uranyl acetate (15 min) and 1% lead citrate (15 min) and analyzed using a Hitachi H500 transmission electron microscope at 75 kV (University of Silesia in Katowice).

2.2.2. Histochemical methods

Semithin sections that were not stained with 1% methylene blue were used for the histochemical methods: the periodic acid–Schiff (PAS) method (detection of glycogen and polysaccharides), bromophenol blue (BPB; detection of proteins), and Sudan Black B (detection of lipids). The protocols were precisely described by Sosinka et al. (2014) and Rost-Roszkowska et al. (2018a). The material was examined using an Olympus BX60 light microscope (University of Silesia in Katowice).

3. Results

The midgut of the julid species studied is a simple tube, separated from the fore- and hindgut by valves. The single-layer epithelium lining the midgut is formed by digestive, regenerative, and secretory cells. It rests on a non-cellular basal lamina surrounded by two layers of the visceral muscles (inner circular layer and outer longitudinal layer) and hepatic cells (Fig. 2A–H).

3.1. Ultrastructure of digestive cells in the midgut epithelium

Distinct regionalization in the distribution of cell organelles was observed in all studied species' cytoplasm of digestive cells. Thus, we could distinguish an apical region with a distinct cortical layer, a perinuclear region and a basal region. The cortical layer lying just beneath the apical cell membrane contains numerous filaments extending into it from microvilli (Fig. 3A–H). It is slightly less pronounced in *M. bosniense*, *L. longipes* and *L. trilineatus* (Fig. 3C–E). In general, the cortical layer is poor in cell organelles: it contains only single mito-

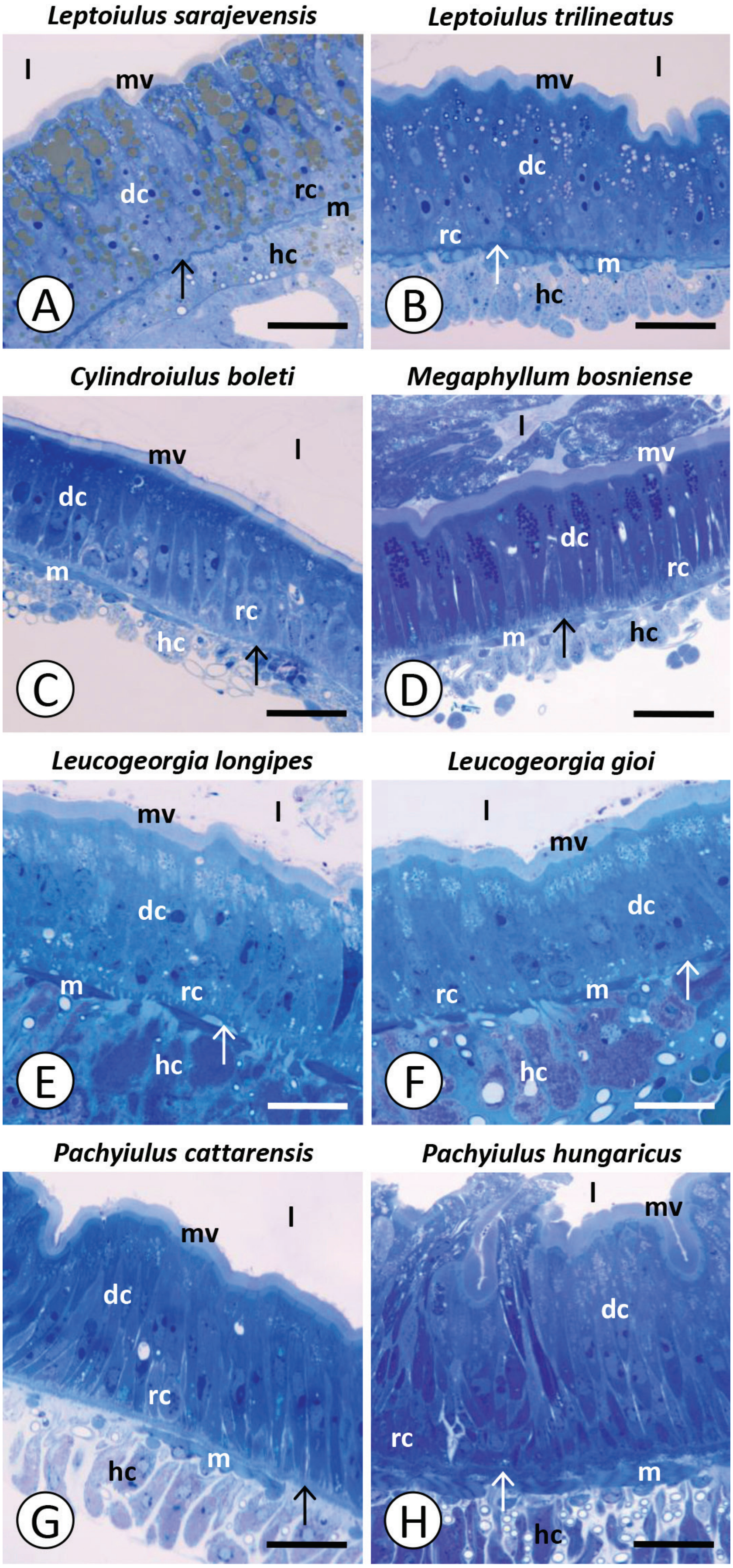


Figure 2. Fragments of the midgut epithelia of selected Julidae species. Longitudinal sections, methylene blue staining, light microscope. — Abbreviations and symbols: dc – digestive cells, hc – hepatic cells, l – lumen, m – visceral muscles, mv – microvilli, rc – regenerative cells, arrow – basal lamina.— Scale bars: **A** 15 μm, **B** 17 μm, **C** 18 μm, **D** 16 μm, **E** 13 μm, **F** 17 μm, **G** 15 μm, **H** 14 μm.

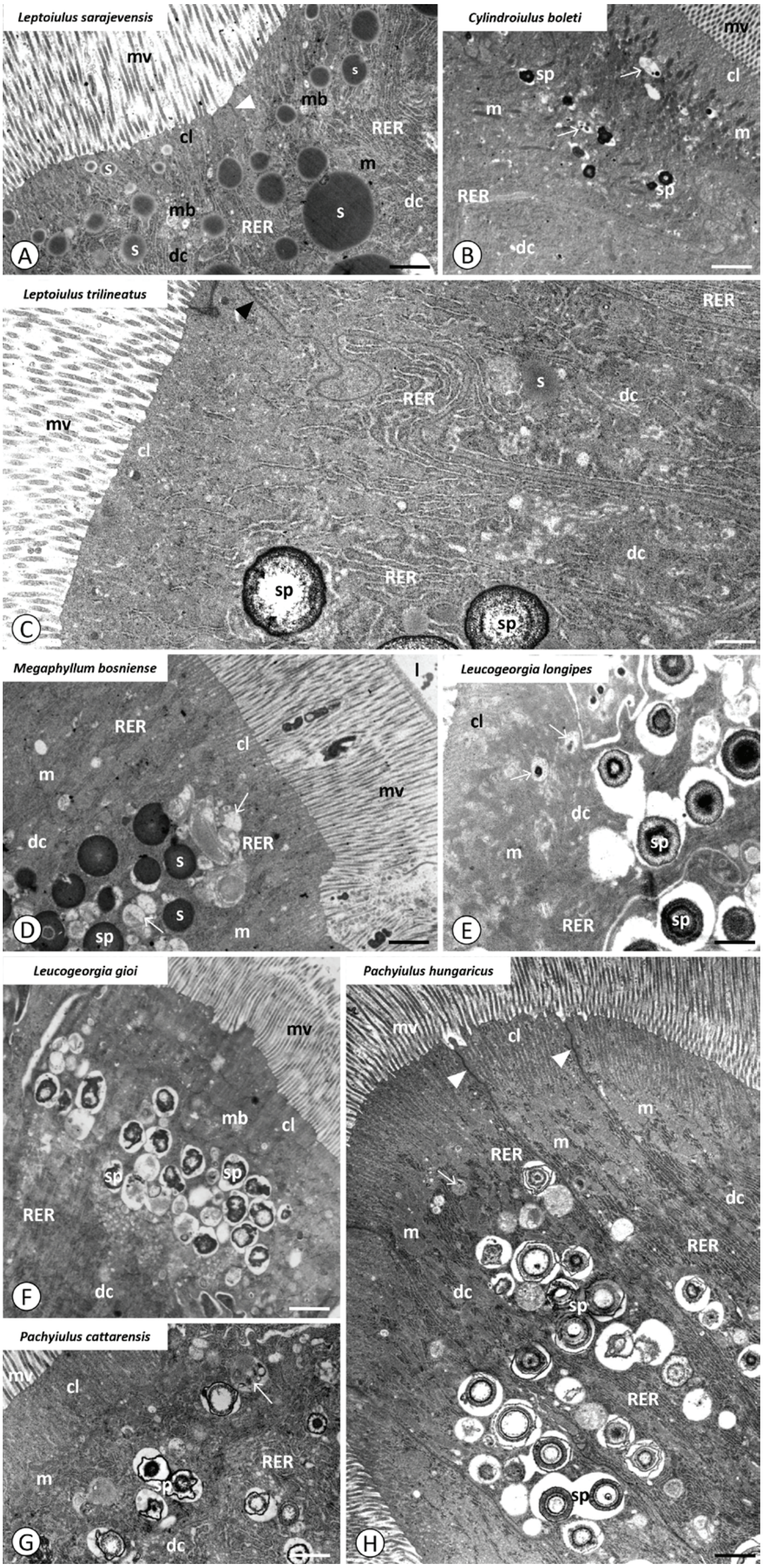


Figure 3. The midgut epithelium of selected Julidae species. Apical cytoplasm of the digestive cells (dc) in *L. sarajevensis* (**A**), *C. boleti* (**B**), *L. trilineatus* (**C**), *M. bosniense* (**D**), *L. longipes* (**E**), *L. gioi* (**F**), *P. cattarensis* (**G**), *P. hungaricus* (**H**). Longitudinal sections, TEM. — Abbreviations and symbols: cl – cortical layer, l – lumen, m – mitochondria, mb – multivesicular bodies, mv – microvilli, RER – cisternae of the rough endoplasmic reticulum, s – storage material, sp – spherites, arrows – autophagic structures, arrowhead – smooth septate junctions. — Scale bars: **A** 0.8 µm, **B** 1.1 µm, **C** 0.5 µm, **D** 0.6 µm, **E** 0.9 µm, **F** 1.2 µm, **G** 1.1 µm, **H** 1.1 µm.

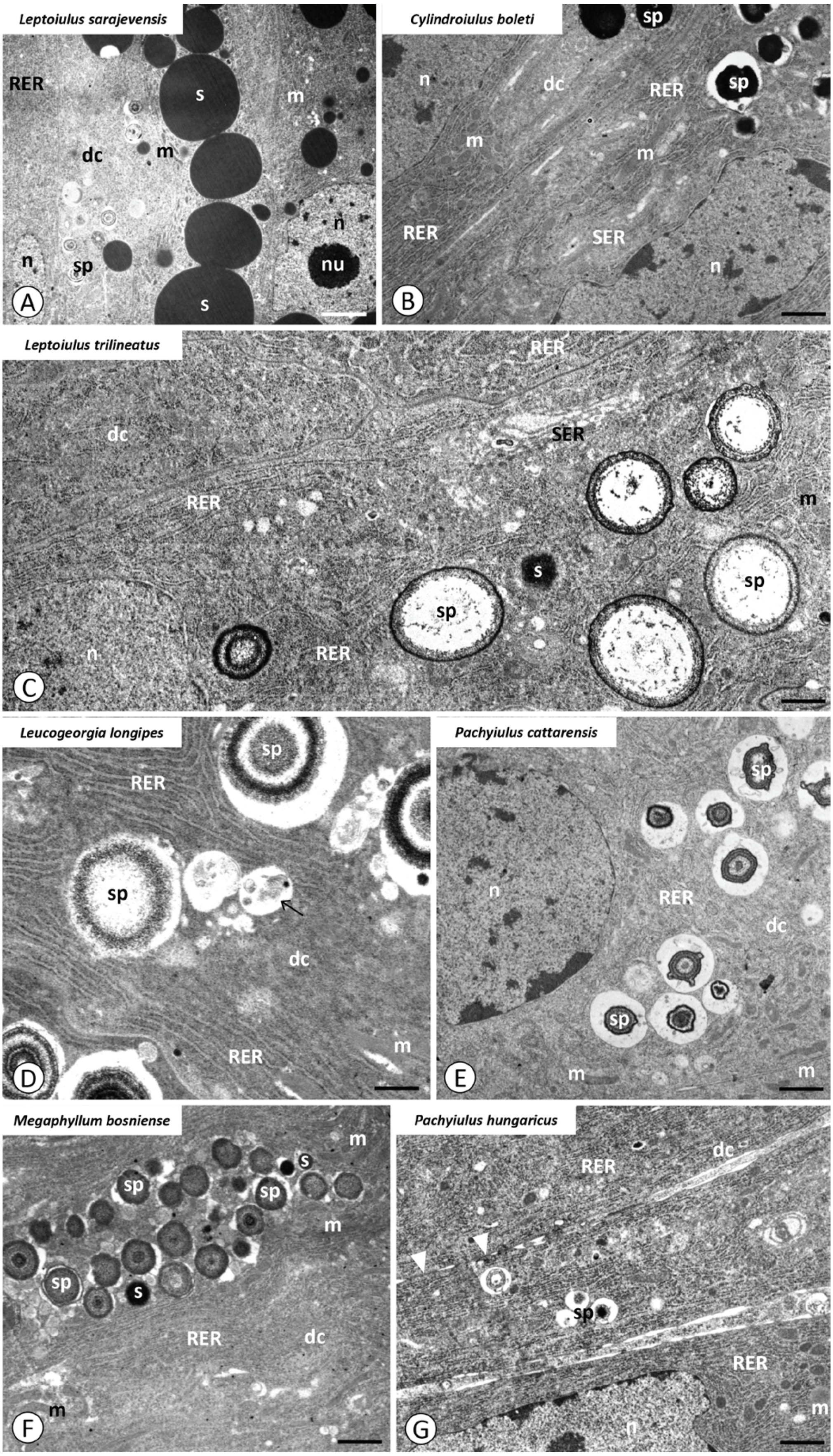


Figure 4. The midgut epithelium of selected Julidae species. Perinuclear cytoplasm of the digestive cells (dc) in *L. sarajevensis* (**A**), *C. boleti* (**B**), *L. trilineatus* (**C**), *L. longipes* (**D**), *P. cattarensis* (**E**), *M. bosniense* (**F**), *P. hungaricus* (**G**). Longitudinal sections, TEM. — Abbreviations and symbols: m – mitochondria, n – nucleus, nu – nucleolus, RER – cisternae of the rough endoplasmic reticulum, s – storage material, SER – cisternae of the smooth endoplasmic reticulum, sp – spherites, arrow – autophagic structures. — Scale bars: **A** 0.8 µm, **B** 0.6 µm, **C** 0.5 µm, **D** 0.4 µm, **E** 1 µm, **F** 0.7 µm, **G** 1 µm.

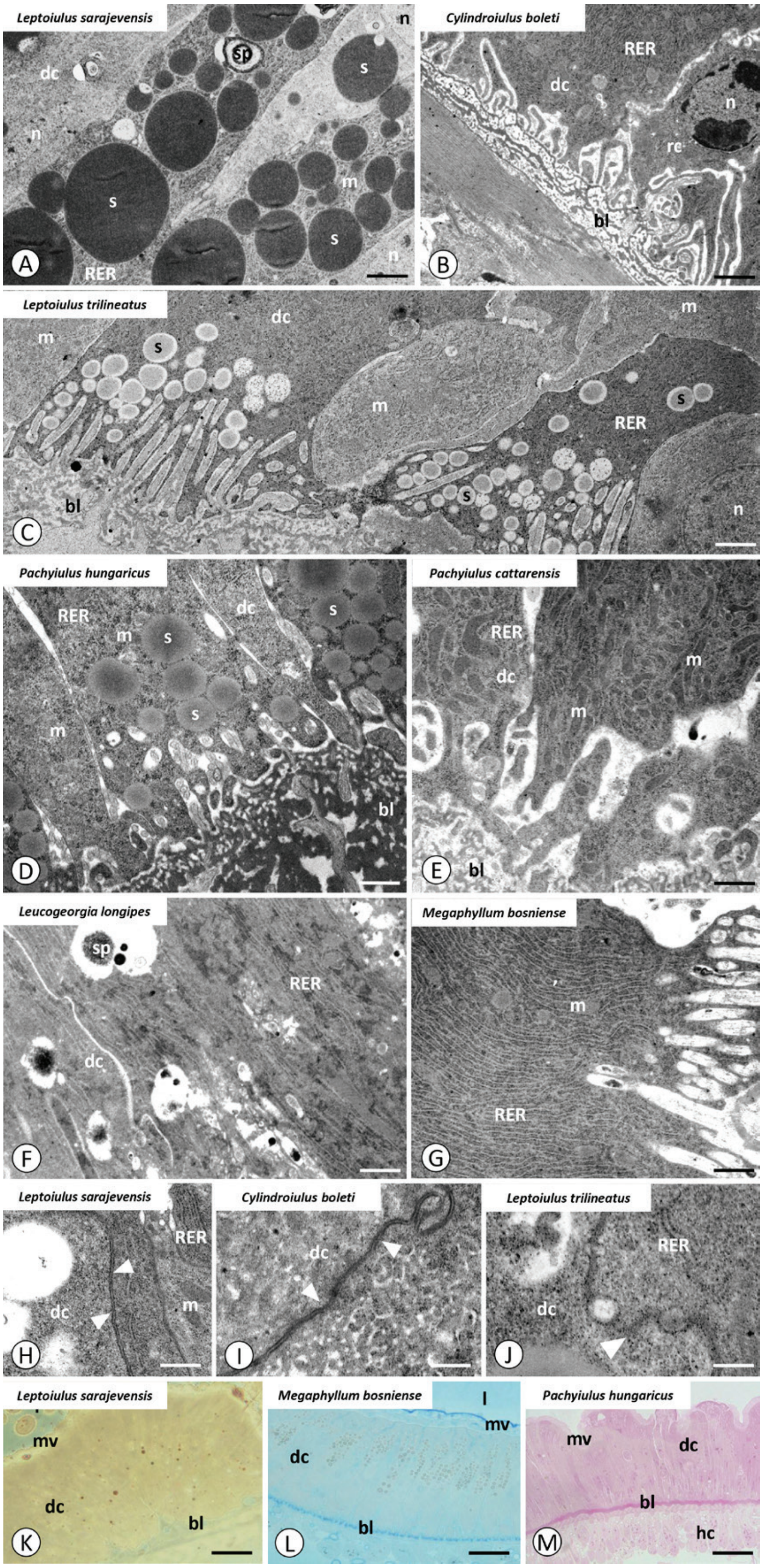
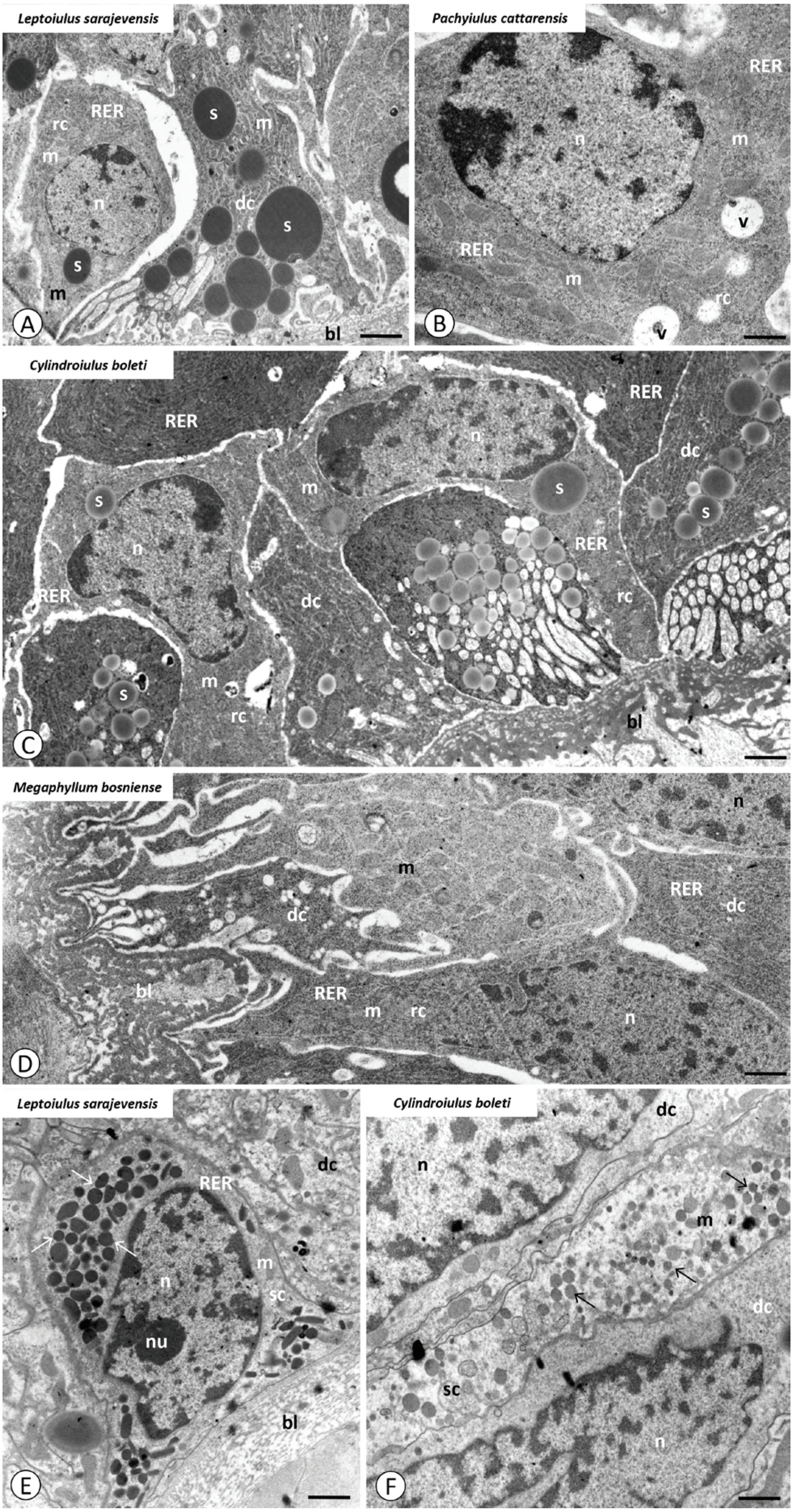


Figure 5. The midgut epithelium of selected Julidae species. Basal cytoplasm of the digestive cells (dc) in *L. sarajevensis* (**A**, **H**, **K**), *C. boleti* (**B**, **I**), *L. trilineatus* (**C**), *P. hungaricus* (**D**, **M**), *P. cattarensis* (**E**), *L. longipes* (**F**), *M. bosniense* (**G**, **L**). Longitudinal sections, TEM. (A–J), histochemical methods (K – Sudan Black B, L – BPB, M – PAS)— Abbreviations and symbols: bl – basal lamina, hc – hepatic cells, l – lumen, m – mitochondria, mv – microvilli, n – nucleus, rc – regenerative cells, RER – cisternae of the rough endoplasmic reticulum, s – storage material, sp – spherites, arrow – autophagic structures, arrowheads – gap junctions (in I and J) or septate junctions (in H). — Scale bars: **A** 0.7 µm, **B** 0.7 µm, **C** 0.5 µm, **D** 1.3 µm, **E** 1.1 µm, **F** 1 µm, **G** 0.3 µm, **H** 0.2 µm, **I** 0.1 µm, **J** 0.1 µm, **K** 15 µm, **L** 13 µm, (M) 15 µm.



Leptoiulus sarajevensis

Pachyiulus cattarensis

Cylindroiulus boleti

Megaphyllum bosniense

Leptoiulus sarajevensis

Cylindroiulus boleti

Figure 6. The midgut epithelium of selected Julidae species. Regenerative cells (rc) (**A**–**D**) and secretory cells (sc) (**E**, **F**) distributed among basal regions of the digestive cells (dc). Longitudinal sections, TEM. — Abbreviations and symbols: bl – basal lamina, m – mitochondria, n – nucleus, nu – nucleolus, RER – cisternae of the rough endoplasmic reticulum, s – storage material, arrows – electron-dense granules. — Scale bars: **A** 0.7 µm, **B** 0.8 µm, **C** 0.7 µm, **D** 0.7 µm, **E** 0.6 µm, **F** 0.5 µm.

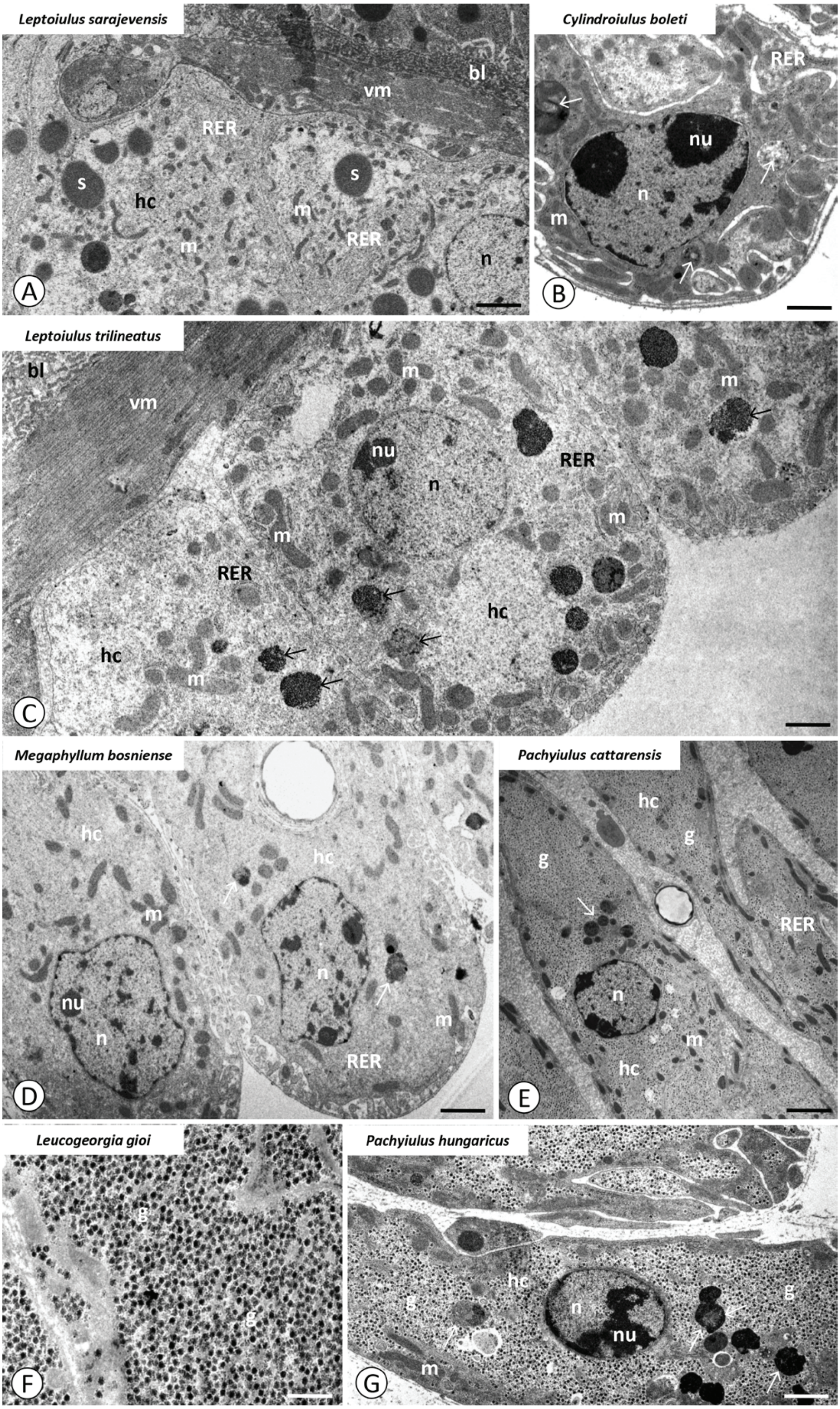


Figure 7. Hepatic cells surrounding the midgut epithelium in selected Julidae species. *L. sarajevensis* (**A**), *C. boleti* (**B**), *L. trilineatus* (**C**), *M. bosniense* (**D**), *P. cattarensis* (**E**), *L. gioi* (**F**), *P. hungaricus* (**G**). Longitudinal sections, TEM. — Abbreviations and symbols: bl – basal lamina, hc – hepatic cells, m – mitochondria, n – nucleus, nu – nucleolus, RER – cisternae of the rough endoplasmic reticulum, s – storage material, vm – visceral muscles, arrows – autophagic structures. — Scale bars: **A** 1.1 µm, **B** 0.5 µm, **C** 0.6 µm, **D** 1.1 µm, **E** 0.5 µm, **F** 0.7 µm, **G** 1.4 µm.

chondria and cisternae of the rough endoplasmic reticulum located between filaments (Fig. 3A–H). However, spheres of storage material with medium electron density were observed in *L. sarajevensis* (Fig. 3A). The apical cytoplasm under the cortical layer in all species studied contains numerous mitochondria, rough endoplasmic reticulum cisternae, and autophagic structures (autophagosomes, autolysosomes, residual bodies) (Fig. 3A–H). The latter are more abundant in *M. bosniense*, *C. boleti* and *P. cattarensis* (Fig. 3B, D, G). In *L. sarajevensis* and *L. gioi*, multivesicular bodies accumulate (Figs 2A, B, 3C). *C. boleti*, *M. bosniense*, *L. longipes*, *L. gioi*, *P. cattarensis*, and *P. hungaricus* have numerous spherites (Figs 2D–G, 3A–E). Additionally, reserve materials were observed in *L. sarajevensis*, *L. trilineatus*, and *M. bosniense* (Fig. 3A, F). Smooth septate junctions constitute the intercellular junctions that connect digestive cells in their apical regions in all millipedes examined (Fig. 3A, C, H).

The perinuclear cytoplasm of the digestive cells in all examined millipedes is rich in rough and smooth endoplasmic reticulum cisternae, Golgi apparatus, and numerous spherites (Fig. 4A–G). The nuclei have small patches of electron-dense heterochromatin located near the nuclear envelope (Fig. 4A, B, E, G). Additionally, in *L. sarajevensis*, *C. boleti*, and *M. bosniense*, there are numerous electron-dense spheres of storage material (Fig. 4A, B, F). The basal membrane of digestive cells in all analyzed species shows characteristic invaginations forming the so-called labyrinth (Fig. 5A–G). Between the invaginations, there are numerous mitochondria and rough endoplasmic reticulum cisternae (Fig. 5B–D, G). Additionally, in *L. sarajevensis*, *P. hungaricus*, and *C. boleti*, storage materials of the high electron densities were observed in the basal cytoplasm; however, it has a medium electron density in the remaining species (Figs 5A, B, D, 6A, C). The reserve material accumulated in the cytoplasm of digestive cells is presented in Table 2 (Fig. 5K–M).

Merocrine secretion has been observed in the digestive cells of the midgut epithelium in all the millipedes examined. However, in *M. bosniense*, *L. gioi*, and *L. trilineatus*, a microapocrine secretion was detected (not shown). Between neighboring digestive cells, specialized intercellular junctions appeared: smooth septate junctions (apical regions), gap junctions, and septate junctions (perinuclear and basal regions) (Fig. 5H–J).

3.2. Ultrastructure of regenerative cells in the midgut epithelium

Regenerative cells (midgut stem cells) (Fig. 6A–D) of all species studied rest on the basal lamina and are individually distributed between the basal regions of digestive cells. Thus, they do not form regenerative nests. They do not reach the midgut lumen. Regenerative cells' cytoplasm is poor in organelles and contains mainly mitochondria and cisternae of the rough endoplasmic reticulum. However, small spheres of storage material with different electron densities were observed in *L. sarajevensis* (Fig. 6A) and *C. boleti* (Fig. 6C). The reserve material accumulated in the cytoplasm of regenerative cells is the same as in the digestive cells: lipids and polysaccharides. Vacuoles with electron-lucent content appeared in *L. gioi*, *P. cattarensis* (Fig. 6B), and *P. hungaricus*. Intercellular junctions between regenerative and digestive cells were not detected.

Table 2. Reserve material accumulated in the cytoplasm of digestive cells in all the Julidae examined. Lp – lipids, Ps – polysaccharides, Pr – proteins.

Species / reserve material	Lp	Ps	Pr
Leptoiulus sarajevensis	+	+	—
Leptoiulus trilineatus	+	+	—
Cylindroiulus boleti	+	+	—
Megaphyllum bosniense	+	+	—
Leucogeorgia longipes	+	-	—
Leucogeorgia gioi	+	—	—
Pachyiulus cattarensis	+	+	—
Pachyiulus hungaricus	+	+	—

3.3. Ultrastructure of secretory cells in the midgut epithelium

The secretory cells in all analyzed millipedes are scarcely distributed among the basal regions of digestive cells in the midgut epithelium. They do not reach the midgut lumen. The entire cytoplasm is rich in granules of different electron density distributed evenly throughout the cytoplasm. Among the organelles, only single mitochondria and cisternae of the rough endoplasmic reticulum occurred (Fig. 6E, F). Intercellular junctions between secretory and digestive cells were not detected.

3.4. Ultrastructure of hepatic cells

The hepatic cells (Fig. 7A–G) surrounding the midgut epithelium have a lobular shape, but in two species (*P. cattarensis* and *P. hungaricus*) they are elongated (Fig. 7E, G). Their long cytoplasmic processes enter the midgut epithelium through the basal lamina of the epithelium between the basal regions of digestive cells. They are characterized by a cytoplasm rich in glycogen granules (Fig. 7F). They also contain single mitochondria and rough endoplasmic reticulum cisternae near the nucleus, which contains a distinct nucleolus and small amounts of heterochromatin near the nuclear envelope. In all species, the hepatic cells possess numerous autophagic structures (Fig. 7B–E, G).

4. Discussion

As a section of the digestive system of endodermal origin, the midgut of invertebrates is responsible for many functions related to the digestion of ingested food. Because it has direct contact with the food, it is also exposed to numerous xenobiotics. Therefore, numerous mechanisms have been developed in the cells forming the epithelium that lines them, which will counteract any changes that disturb homeostasis. Therefore, it is considered an organ that, together with the epidermis, will constitute a barrier for the entire organism against the effects of harmful substances (Wilczek et al. 2014; Bonelli et al. 2019; Rost-Roszkowska et al. 2018a, 2019, 2022, 2024; Ostróżka et al. 2022). Some studies have been conducted on changes that can occur in the epithelium lining the midgut of myriapods under the influence of different stressors (Rost-Roszkowska et al. 2020, 2021a, 2022; de Souza et al. 2020; Błaszczyk et al. 2023). Thus, changes in the cytoplasm of cells forming the midgut epithelium have been demonstrated. The processes of autophagy and apoptosis that may accompany degenerative processes, as well as those responsible for the removal of damaged cells to deactivate inflammation and damage the entire organ, have been described (Rost-Roszkowska et al. 2019, 2021a, 2021b; Błaszczyk et al. 2023). The midgut of millipedes, including species belonging to Julidae, is lined with a simple pseudostratified columnar or simple columnar epithelium (Fontanetti and Camargo-Mathias 1997; Camargo-Mathias et al. 2004; Sosinka et al. 2014; Fontanetti et al. 2015; Rost-Roszkowska et al. 2018a, 2021; Błaszczyk et al. 2023). The type of epithelium verifies the arrangement of organelles in their cytoplasm (Cioffi 1984). In the analyzed Julidae species, all midgut epithelium cells have a multilayered appearance (secretory and regenerative cells do not reach the midgut lumen). Hence, this epithelium can be considered as the simple pseudostratified type. The main cells forming the epithelium of the millipede midgut are digestive cells (the principal cells), the cytoplasm of which shows clear regionalization in the distribution of organelles, which is related to the functions of these cells, i.e. secretion, absorption, and synthesis (Fontanetti and Camargo-Mathias 1997; Fantazzini et al. 2002; Camargo-Mathais et al. 2004; De Godoy and Fontanetti 2010; Souza and Fontanetti 2011; Sosinka et al. 2014; Fontanetti et al. 2015; Moreira-de-Sousa et al. 2017; Rost-Roszkowska et al. 2021b). In species belonging to Julidae, apart from clear regionalization of the cytoplasm, the occurrence of specific organelles in particular regions of the cytoplasm was observed. Occasional differences (e.g., the occurrence of multivesicular bodies or increased autophagy) may result from the physiological state of the cells at the time of analysis (Rost-Roszkowska et al. 2019). Spherites described in various regions of the cytoplasm of all Julidae species are associated with the accumulation of numerous xenobiotics, especially metals from the external environment, which enter the body along with the consumed food (Hubert 1979; Köhler and Alberti 1992; Köhler 2002; Fantazzini et al. 2002; Fontanetti et al. 2006; Moreira-de-Sousa et al. 2017). These structures have been described in many millipede species (Hubert 1979; Hopkin and Read 1992; Fantazzini et al. 2002; Fontanetti et al. 2006, 2015; Nogarol and Fontanetti 2011; Sosinka et al. 2014; Rost-Roszkowska et al. 2018a, 2021b). A process that plays an important role in cell detoxification is autophagy (Klionsky et al. 2021). During this process, damaged cellular organelles, metals, or other xenobiotics will be neutralized so as not to induce cell death. This process appears to be a common occurrence in the epithelium of the midgut of millipedes (Rost-Roszkowska et al. 2019). Thus, both the occurrence of spherites and the presence of autophagy are typical of animals living in the soil, litter, or under stones, i.e., in environments where metals can accumulate. Specialized intercellular junctions have been described between adjacent digestive cells: smooth septate junctions (sSJs) and gap junctions (GJs). These connections are characteristic for transporting epithelia, where they enable the transport of small molecules or even ions (Green et al. 1980; Goodenough and Paul 2009). sSJs and GJs were also detected between adjacent digestive cells in the midgut epithelia of different millipede species, including Julidae (Sosinka et al. 2014; Rost-Roszkowska et al. 2018a, 2021b). Thus, the overall structure and ultrastructure of digestive cells in the midgut of Julidae show a distinct pattern likely to be characteristic of all millipede groups. These studies, however, require further analyses.

Differences in the structure of the midgut epithelium between the analyzed Julidae species appear in the case of materials collected in the cytoplasm of digestive cells. Reserve substances derived from the food consumed can be stored in the cytoplasm of digestive cells, so mainly lipids and polysaccharides (Rost-Roszkowska et al. 2018a), or proteins (Rost-Roszkowska et al. 2021b) can be accumulated. Thus, it is suggested that the type of stored reserve material in millipedes is related to the type of food consumed (Hopkin and Read 1992; Fantazzini et al. 2002; Deshmukh and Deshmukh 2011; Sosinka et al. 2014; Fontanetti et al. 2015; Rost-Roszkowska et al. 2018a, 2021b). Proteins would probably originate from digested animal material (Rost-Roszkowska et al. 2021b), algae and lichens (Sosinka et al. 2014), or plant material rich in proteins (Dangerfield and Telford 1996). So far, there have been no comparisons of closely related millipede species, i.e., belonging to the same family but living in slightly different environments or differing in the type of food they eat. In the studied Julidae species, lipids, and polysaccharides may be stored in the cytoplasm of digestive cells. All but one of the Julidae species examined here are saprophytophagous. They eat dead leaves and dead plant material, as well as wood. It is assumed that *L. longipes* filters or collects small organic particles from cave water or damp walls. In *L. gioi* and *L. longipes* midgut digestive cells, polysaccharides were not detected. The lack of polysaccharides in the spheres with reserve material in the digestive cells of cave-dwelling *L. gioi* and *L. longipes* is probably related to the fact that both species live in humid, dark environments with slightly lower temperatures. Thus, the accumulation of polysaccharides has been completely replaced by the accumulation of only lipids, the most energy-efficient storage substances (Olsen et al. 2021). The presence of proteins was not detected in any of the analyzed Julidae species. Similar research results were obtained for *Julus scandinavius* (Latzel, 1884) (Sosinka et al. 2014), while in *Unciger transsilvanicus* (Verhoeff, 1899) there are additional proteins in the cytoplasm of these cells. It was explained by their diet containing these substances (Rost-Roszkowska et al. 2021). Differences in the accumulation of reserve materials in different regions of the cytoplasm of digestive cells have also been observed. These are probably related to the amount of these materials in the cytoplasm and, therefore, to the intensive processes of their synthesis and absorption in some species. Certainly, the ability to accumulate reserve materials is a characteristic feature of the digestive cells of all Julidae species. Still, the nature of the materials will depend on the type of food consumed or the animal's living environment, necessitating increased energy reserves.

In millipedes, reserve materials also accumulate in the cytoplasm of hepatic cells surrounding the epithelium of the midgut. These cells do not form a distinct epithelial layer, there are no specialized intercellular junctions between them, and their long cytoplasmic processes extend into the epithelium of the midgut. Thanks to this, substances are transported to the cytoplasm of hepatic cells, where they are stored as glycogen granules (Hubert 1988; Godoy and Fontanetti 2010; Nogarol and Fontanetti 2011; Nardi et al. 2016; Rost-Roszkowska et al. 2018b). The cytoplasm of the hepatic cells in all Julidae millipedes as well as the other millipede groups (Rost-Roszkowska et al. 2018b) contains mitochondria and rough endoplasmic reticulum cisternae and accumulates mainly glycogen granules, which were not detected in the cytoplasm of digestive cells in the intestinal epithelium (Hubert 1978; Bozzatto and Fontanetti 2012; Rost-Roszkowska et al. 2018b). However, in some millipede species, the cytoplasm of these cells contains spheres of storage material (e.g., *Polydesmus angustus* Latzel, 1884, *J. scandinavius*). Histochemical analysis showed that these structures are proteins (Rost-Roszkowska et al. 2018b). Since numerous autophagic structures have also been described in *J. scandinavius*, which is a member of the Julidae, it can be assumed that the protein structures described previously (Rost-Roszkowska et al. 2018b) are autophagic structures and not storage materials. Autophagic structures are created to digest damaged cell structures or organelles, or to collect storage materials for use as an energy source (via lipophagy and glycophagy) (Singh and Cuervo 2011; Zirin et al. 2013; Congcong 2022). The induction of this process may depend on the level of energy required and the stored energy reserve from which it is derived, such as lipids or glycogen (Congcong 2022; Park et al. 2023). Thus, autophagy can degrade different types of nutrient stores (here: polysaccharides, mainly glycogen) and take part in maintaining energy homeostasis. We can conclude that in the examined Julidae species, glycogen is the only reserve material found in hepatic cells, and autophagy is the common process that enables the proper functioning of hepatic cells.

A similar ultrastructural pattern also occurs in secretory cells of Julidae. They are very rarely located individually between the basal regions of digestive cells and do not contact the midgut lumen (Hopkin and Read 1992; Camargo-Mathias et al. 2004; Sosinka et al. 2014; Fontanetti et al. 2015; Rost-Roszkowska et al. 2018a, 2021b). The arrangement of organelles, such as mitochondria, rough endoplasmic reticulum cisternae, and grains with different electron densities, characteristic of secretory cells, are features of these cells in the midgut epithelium in millipedes, including Julidae (Godoy and Fontanetti 2010; Fontanetti et al. 2015). The literature indicates that secretory cells are digestive cells that are at various physiological stages involved in secretion (Fontanetti et al. 2015). However, distinct cells differing in ultrastructure with characteristic granules of different electron densities have been described in millipedes (Sosinka et al. 2014; Rost-Roszkowska et al. 2018a, 2021b). Secretory cells of the midgut epithelium of invertebrates are considered separate cell types (Punin et al. 2000; Bonelli et al. 2019; Caccia et al. 2019), probably responsible for endocrine functions. Secretory cells are characterized in insects by two different types. Closed-type cells do not reach the midgut lumen, while open cells possessing elongated shapes contact the gut lumen (Caccia et al. 2019). The cells described in Julidae and other millipede species have a character of closed cells. These cells are believed to maintain the whole organism's homeostasis due to the ability to synthesize and secrete bioactive peptides (Song et al. 2014; Caccia et al. 2019). However, to determine the role of the cells described in the epithelium of the studied Julida species and other millipede species, it is necessary to perform appropriate immunohistochemical tests.

The next type of cells that form the midgut epithelium in millipedes, including Julidae species, is regenerative cells (midgut stem cells). They may occur singly in the Julidae midgut (Köhler and Alberti 1992; Fontanetti et al. 2001, 2015; Fantazzini et al. 2002; Camargo-Mathias et al. 2004; de Godoy and Fontanetti 2010; Nogarol and Fontanetti 2011; Sosinka et al. 2014; Fontanetti et al. 2015; Rost-Roszkowska et al. 2018a, 2019, 2021b) or may form regenerative nests (Kaufman 1960, 1961; Rost-Roszkowska et al. 2021b). In millipedes, including species belonging to Julidae, regenerative cells are responsible for self-renewal of the epithelium in the event of damage or wear of its cells (Godoy and Fontanetti 2010; Souza and Fontanetti 2011; Bozzatto and Fontanetti 2012; Christofoletti et al. 2012; Fontanetti et al. 2015; Rost-Roszkowska et al. 2018a, 2019). Hence, the cytoplasm of these cells is especially rich in mitochondria and cisternae of the rough endoplasmic reticulum, i.e. organelles providing energy and proteins necessary for cell proliferation and differentiation (Rost-Roszkowska et al. 2021b). In all the Julidae species we studied, we observed exactly the same set of cell organelles. However, we noted that in *L. sarajevensis* and *C. boleti*, in the cytoplasm of regenerative cells, there are spheres of storage material with different electron densities. In these species, the entire cytoplasm of digestive cells is rich in reserve materials, and they are especially intensively accumulated in the basal cytoplasm adjacent to regenerative cells. On the other hand, in *P. cattarensis*, *P. hungaricus*, and *L. gioi*, the cytoplasm of regenerative cells also has single vacuoles. Similar structures have been described in *J. scandinavius*. It is very likely that these vacuoles are remnants of storage materials degraded by lipophagy or lipolysis (Singh et al. 2009; Zechner et al. 2017; Rost-Roszkowska et al. 2022, 2023). However, this requires further research.

5. Conclusions

The present study included species from as many as half recognized tribes within the family Julidae, from "lower julids" to "higher julids" (see Enghoff et al. 2011, 2013). Our study revealed, in the midgut epithelium of Julidae, the general pattern of digestive, secretory, and regenerative cells, as well as hepatic cells surrounding the midgut. This structure does not depend on the environment in which the animal lives. The type of food consumed affects the type of accumulated reserve materials. We can conclude that the general structure and ultrastructure of selected Julidae species' midgut may represent the general pattern of the midgut epithelium in millipedes. However, it should be confirmed by further analysis of species belonging to other Julidae or even other millipede groups.

6. Declaration of competing interest

The authors declare that they have no competing financial or personal interests.

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