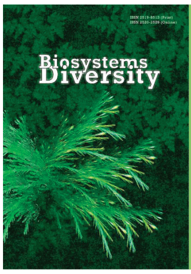

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Morphological variation of four species of *Strongyloides* (Nematoda, Rhabditida) parasitising various mammal species

Y. A. Gugosyan*, O. O. Boyko*, V. V. Brygadyrenko*, **

**Dnipro State Agrarian and Economic University, Dnipro, Ukraine*
***Oles Honchar Dnipro National University, Dnipro, Ukraine*

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Dnipro State Agrarian and Economic University, Sergiy Efremov st., 25, Dnipro, 49000, Ukraine. Tel.: +38-066-112-95-05. E-mail: y.gugosyan@gmail.com

Oles Honchar Dnipro National University, Gagarin av., 72, Dnipro, 49010, Ukraine. Tel.: +38-050-93-90-788. E-mail: brigad@ua.fm

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Study of the morphologic peculiarities of free-living stages of nematodes of the *Strongyloides* genus is important in differential diagnostics of pathogens. We studied the parasite of goats (*Capra aegagrus hircus* Linnaeus, 1758) – *Strongyloides papillosus* (Wedl, 1856); the parasite of horses (*Equus ferus caballus* Linnaeus, 1758) – *S. westeri* Ihle, 1917; the parasite of swine (*Sus scrofa* Linnaeus, 1758) – *S. ransomi* Schwartz & Alicata, 1930; the parasite of dogs (*Canis lupus familiaris* Linnaeus, 1758) – *S. stercoralis* (Bavay, 1876). Rhabditiform larvae (L1, L2), filarial larvae (L3), mature males (M) and free-living females (F) were analyzed for each of the four species by five morphological parameters: body length (Lb), total maximum body width (Sb), length of the esophagus (Lo), length of the intestine (Le), length of the tail end (Lc); for females, we additionally examined length from the head end to the vulva (Lv) and the number of formed eggs in the uterus cavity (E), and for males – length of spicules (Ls). First stage larvae of *S. papillosus* and *S. stercoralis* significantly differed in all parameters, and first stage larvae of *S. westeri* and *S. stercoralis* significantly differed in four out of five parameters. By indices of ratios of total maximum body width (Sb) to body length (Lb), length of the esophagus (Lo) to length of the intestine (Le), length of the tail end (Lc) to body length (Lb), length of the intestine (Le) to body length (Lb), a reliable difference was recorded between L_1 of *S. papillosus* and *S. ransomi*, L_3 of *S. papillosus* and *S. westeri*, *S. westeri* and *S. ransomi*, between males of *S. papillosus* and *S. westeri*, *S. westeri* and *S. stercoralis*, between females of *S. papillosus* and *S. westeri*, *S. papillosus* and *S. stercoralis*. All four examined species were observed to have reliable differences of ratio of length of esophagus to length of intestine in third stage larvae.

Keywords: morphometric parameters; *Strongyloides papillosus*; *S. westeri*; *S. ransomi*; *S. stercoralis*.

Introduction

Nematodes of the *Strongyloides* genus parasitize the small intestine of many species of wild and domestic mammals. *Strongyloides* species inhabiting Ukraine include *Strongyloides papillosus* Wedl, 1856, parasite of ruminants, rabbits and guinea pigs; *S. ransomi* Schwartz & Alicata, 1930, parasite of swine; *S. westeri* Ihle, 1917, parasite of horses; *S. stercoralis* (Bavay, 1876), parasite of carnivores and humans. In conditions of low intensity of the invasion, parasitization by nematodes of the *Strongyloides* genus does not lead to emergence of manifested clinical signs and the course of the disease is accompanied with no symptoms. However, high parameters of intensity of *Strongyloides* infestation can in most cases cause disorders of metabolism in the organism, functions of the gastrointestinal tract, organs of the respiratory system, and also reduction of animals' productivity. As a result, farms contaminated with strongyloidiases suffer significant economic losses.

According to Roesel et al. (2016), in the territory of East Africa, swine-breeding complexes infested with helminthiases, suffer economic losses as a result of reduction of the output volumes, and also increase in production costs. In most farms of East Africa, swine are recorded to be infested with nematodes of the Strongylida order, parasites of the gastrointestinal tract, *Metastrongylus* spp., *Ascaris suum* Goeze, 1782, *S. ransomi*, and also *Trichuris suis* Schrank, 1788. In Indonesia, swine-breeding in rural areas is an important part of livestock rearing. However, the high level of infestation and mortality of swine obstructs the development of the production in the country. Studies by Nugroho et al. (2015) indicate the spread of the following parasites among swine: nematodes of the Strongylida order, *T. suis*, *A. suum*, *S. ransomi*, and also coccidians. In Tanzania, swine are also ubiquitously recorded to host helminths of the gastointestinal tract (infection rate of helminthiases equaled 63.7%): *Oesophagostomum* spp., *Trichostrongylus* spp., *A. suum*, *T. suis* and *S. ransomi* with extensity of infestation equaling 57.4%, 17.5%, 5.3% and 1.1%, respectively (Kabululu et al., 2015). Nganga et al. (2007) studied abundance of different species of helminths among swine in Kenya. Nematodes were identified in 67.8% of swine, out of which 31.3% of animals had mixed infestations: 10 species of helminths were found: *Oesophagostomum dentatum* (39.1%), *T. suis* (32.2%), *A. suum* (28.7%), *Oesophagostomum quadrispinulatum* (14.8%), *Trichostrongylus colubriformis* (10.4%), *T. axei* (4.3%), *S. ransomi* (4.3%), *Hyostrongylus rubidus* (1.7%), *Ascarops strongylina* (1.7%) and *Physocephalus sexalutus* (0.9%). In farms in Kenya, where swine are kept free-range, nematode infestations are also often a serious problem for swine-breeding. On such farms, the extensity of infestation reaches 84.2%, and mean intensity of nematode infestation equals 2,355 eggs/g of feces. Kagira et al. (2011) found *Oesophagostomum* spp. in 75% of swine, and *S. ransomi* in 37.0%. Other species of swine nematodes recorded on free-range farms in Kanya are rarer; *A. suum* (18%), *Metastrongylus* spp. (11%), *T. suis* (7%) and *P. sexalatus* (3%). According to Tamboura et al. (2006), intensity of infestation of swine with gastrointestinal nematodes depends on the type of system of production of animals. The examination of swine in Burkina Faso revealed that out of 383 examined swine, 91% were infested with *A. suum* helminths (extensivity of the infestation was 40%; intensity of infestation – 100–1400 EPG (eggs per gram of feces)) – commonest species, other species were *S. ransomi* (21%; 100–4200 EPG), *Oesophagostomum* spp. (18%; 100–1000 EPG), *H. rubidus* (11%; 100–1800 EPG), *Globocephalus* spp. (10%; 100–400 EPG) and *T. suis* (1%; 100–200 EPG). The literature contains information on intensity of infestation and severity of the course of strongyloidiasis for parasitization by

S. papillosus in different species of hosts: depending on their age, geographic range, season and many other factors (Singh et al., 1997; Bekele, 2002; Agyei, 2003; Jäger et al., 2005; Eysker et al., 2005; Boyko et al., 2009). During the larva stage, *S. papillosus* infests the gastrointestinal tract, and the respiratory organs of mammals. In an experimental infestation of rabbits, Nakamura et al. (1994) observed decrease in body weight to 44% compared to the initial weight and consequent exhaustion of the animals. As a result of parasitization of *S. papillosus* in calves, Kváč et al. (2007) recorded mortality in 25% of animals. At autopsy, all the dead calves were observed to have pathological changes in the lungs, which were related to migration of larvae. Studies by Wymann et al. (2008) also indicate age peculiarities of vulnerability to this species of nematodes. Currently, new methods against *S. papillosus* and control of its abundance in animals and environment are being developed (Boyko & Brygadyrenko, 2016; Boyko et al., 2016).

Studies by Dewes et al. (1990) on percutaneous penetration of *S. westeri* indicate that animals become anxious, hyperactive, develop swelling of the lower part of their limbs and dermatitis on the skin of legs, stomach and snouts during 2–3 weeks. Through this path of infestation, broodmares can develop mastitis as a result of concentration of larvae in mammary gland during migration (Greiner et al., 1991). In the case of an extreme peroral infestation of animals with hundreds of thousands of invasive larvae of *S. westeri*, Greer et al. (1974) observed animals to have diarrhea, periodic cramps, anemia of mucus membranes. Changes in hematological parameters were characterized by increase in the number of leukocytes with increase in the percent of eosinophiles, neutrophils and lymphocytes, reduction of content of albumins and increase in β-globulins; the peak of changes occurred on the sixth week after the experiment started. In the duodenum, there were found moderate inflammation and hyperemia. Histological studies revealed atrophy of the villi of the intestine, and accumulation of lymphatic cells, neutrophils and eosinophils were found around the parasites. In Brazil, lethal cases of strongyloidiasis were described among colts. Pathological autopsy revealed subcutaneous edemas, ascites, hydrothorax, inflammation and hyperemia of the duodenum, and histological examination revealed depressions in the upper part of the villi of the intestine, filled with hermaphrodite females of *Strongyloides*. Numerous small concentrations of atelectases and blunted edges of diaphragm lobes were observed in all lung lobes and under the pleura (Lucena et al., 2012).

No less common is *S. stercoralis*. Parasitization by this nematode species can also lead to various disorders in the host organism. Carnivores suffering strongyloidiases were observed to have symptoms of acute watery diarrhea, pain during defecation, intermittent cough, vomiting and exhaustion (Umur et al., 2017). According to Jaleta et al. (2017) and Nagayasu et al. (2017), *S. stercoralis* of dogs has two populations. One is specific only to dogs, and the other population of *S. stercoralis* can also parasitize humans. Such studies indicate the high risk for humans who are in contact with dogs. According to Catalano et al. (2017), *S. stercoralis* colitis is a severe disease with a high level of mortality, but is easily curable. Strongyloidiasis in humans can remain for up to several decades and can lead to chronic colitis. Chronic colitis is related to heightened risk of development of colorectal cancer; quite possibly chronic colitis induced by strongyloidiasis poses a similar risk as well. Poveda et al. (2017) have also recorded colitis in patients diagnosed with strongyloidiasis. Studies by Politis (2017) indicate presence of diarrhea in people with *S. stercoralis*. People parasitized by this species of helminth have nocturnal dyspnea, sweatiness, productive cough, and also constrictive pericarditis (Lee et al., 2017). The study by Nabeya et al. (2017) described cases of manifestations in the lungs, including acute respiratory distress syndrome, bacterial pneumonia and lung bleeding.

Identification of larvae and mature specimens of *Strongyloides* genus by morphological parameters poses difficulties for parasitologists. Therefore, the objective of this paper was to determine variability of metric parameters and morphometric indices for four of the commonest species of this genus, which are in most frequent contact with pets and humans.

Materials and methods

The research was conducted in 2018 at the Department of Parasitology and Veterinary-Sanitary Examination of the Dnipro State Agrarian and Economic University. For the experiment, we selected animals infested with *Strongyloides* spp. pathogen. Diagnosis was based on finding eggs of *Strongyloides* using the McMaster method. Samples of the animals' feces were taken separately, preventing their contamination with soil nematodes. Cultivation of eggs and larvae was performed in a thermostat at temperature of 23–25 °C over 1–7 days. Obtaining cultures of larvae and free-living generations of *Strongyloides* spp. was made using the Baermann method, and identification – in accordance with notable morphological signs (Van Wyk et al., 2004; Van Wyk & Mayhew, 2013). During the experiment, we identified and examined the following species: *S. papillosus* (Wedl, 1856), *S. westeri* (Ihle, 1917), *S. ransomi* (Schwartz & Alicata, 1930), *S. stercoralis* (Bavay, 1876).

Larvae at different stages of the development and free-living generations of *Strongyloides* were differentiated by taking into account morphological peculiarities of structure of the head and tail ends, presence of widening of the esophagus. Metric parameters of postembryonic stages of the development of *Strongyloides* spp. were determined using an object-micrometer and a Sigeta CAM MD-300 3 Mpix digital camera (China). In all studied objects, we determined total length of body (Lb), maximum body width (Sb), length of the esophagus (Lo), length of the intestine (Le), length of the tail end (Lc), separately for free-living females we measured length from the head end to the vulva (Lv), number of developed eggs in the cavity of the womb (E), and separately for the males we measured length of the spicules (Ls). We calculated the indices of total maximum body width (Sb) to body length (Lb); length of esophagus (Lo) to length of intestine (Le); length of tail end (Lc) to body length (Lb); length of intestine (Le) to body length (Lb).

In total, 20 individuals of each species were analyzed for each parameter for each post-embryonic stage of the development for each of the four host animal species. Differences between the selections were considered statistically significant at $P < 0.05$. The data were compared using Tukey's test (with consideration of the Bonferroni correction). The data was analyzed in Statistica 8 (StatSoft Inc., USA). In the diagrams the small squares show the median, the large rectangles show the 25% and 75% quartiles, the vertical lines show 95% of the variation, the stars and circles show the outliers.

Results

The appearance and morphological features of larvae and mature nematodes are demonstrated in Figures 1, 3, 5, 7 and 9. The examination of body length of larvae of the first stage of the development of nematodes of *Strongyloides* genus from ruminants, horses, swine, and dogs (on average body length equals 210–310 μm) revealed reliable difference by the parameters between *S. papillosus* and *S. stercoralis*, *S. westeri* and *S. ransomi*, *S. westeri* and *S. stercoralis*, and also *S. ransomi* and *S. stercoralis* (Fig. 2a). Width of the body of first stage larva ranged within 12–19 μm. Parameter of total maximum body width reliably differed for *S. papillosus* and *S. ransomi*, *S. papillosus* and *S. stercoralis*. We observed no reliable difference in this parameter for *S. papillosus* and *S. westeri*, *S. westeri* and *S. ransomi*, *S. westeri* and *S. stercoralis*, and also *S. ransomi* and *S. stercoralis* (Fig. 2b).

Length of the esophagus significantly differed in first stage larvae of *S. papillosus* and *S. westeri*, *S. papillosus* and *S. ransomi*, *S. papillosus* and *S. stercoralis*. We also recorded reliable difference in this parameter for *S. westeri* and *S. ransomi*, *S. westeri* and *S. stercoralis*. Average value of this morphometric parameter equaled 60–119 μm (Fig. 2c). Parameters of length of the intestine in four species of nematodes of the *Strongyloides* genus ranged within 100–160 μm. No significant differences were determined in length of the intestine for three examined species of nematodes: *S. papillosus*, *S. westeri*, *S. ransomi*. Compared to other three species, length of the intestine significantly differed only in first stage larvae of *S. stercoralis* nematodes (Fig. 2d).

Length of the tail end of L_1 *S. westeri* differed from that of *S. ransomi* and *S. stercoralis*. For nematode larvae of the *Strongyloides* genus, this parameter ranged within 31–49 μm (Fig. 2e). Average body length of larvae of the second stage ranged within 325–475 μm. Significant difference in parameters of body length was recorded only for L_2 *S. stercoralis*. The rest of the studied species did not reliably differ one from another by this parameter (Fig. 4a). Measurements of body width showed reliable difference also for L_2 *S. stercoralis*. Insignificant difference in body width was observed only between L_2 *S. stercoralis* and *S. westeri*. L_2 *S. papillosus*, *S. westeri*, *S. ransomi* did not have significant difference in body width – 18–25 µm (Fig. 4b).

A similar picture was also observed during comparison of morphometric parameters in relation to length of the esophagus. L_2 *S. papillosus*, *S. westeri*, *S. ransomi* had also no reliable differences between one another. Length of the esophagus in L_2 *S. stercoralis* was significantly different compared to the other examined species of *Strongyloides* nematodes. On average, this parameter ranged within 85–120 µm (Fig. 4c). In the second stage *Strongyloides* larvae, length of the esophagus on average equalled 190–310 µm. The highest parameters were recorded in *S. westeri*, the lowest – in *S. stercoralis* (Fig. 4d). Reliable differences by this parameter were determined between *S. papillosus* and *S. stercoralis*, *S. papillosus* and *S. westeri*, *S. ransomi* and *S. stercoralis*, *S. westeri* and *S. stercoralis*.

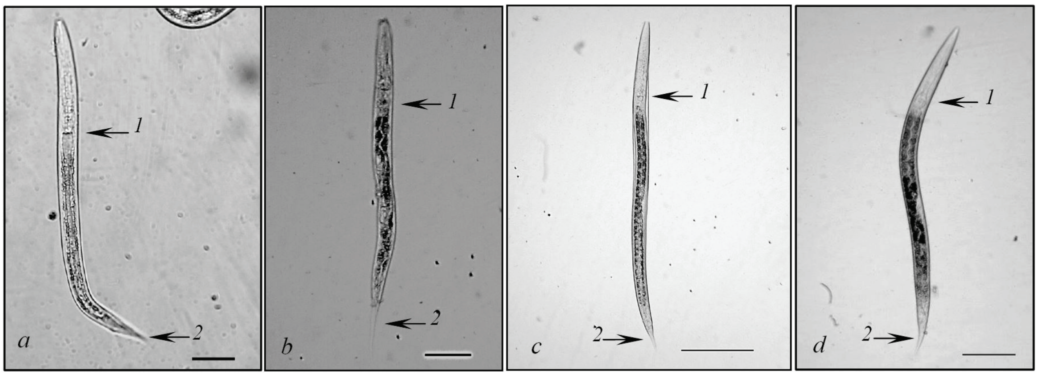

Fig. 1. Rhabditiform larvae (L_1): *a* – *S. papillosus*, *b* – *S. westeri*, *c* – *S. ransomi*, *d* – *S. stercoralis*; *1* – bulbus-like widening in the esophagus, *2* – the tail end; bar = 50 µm

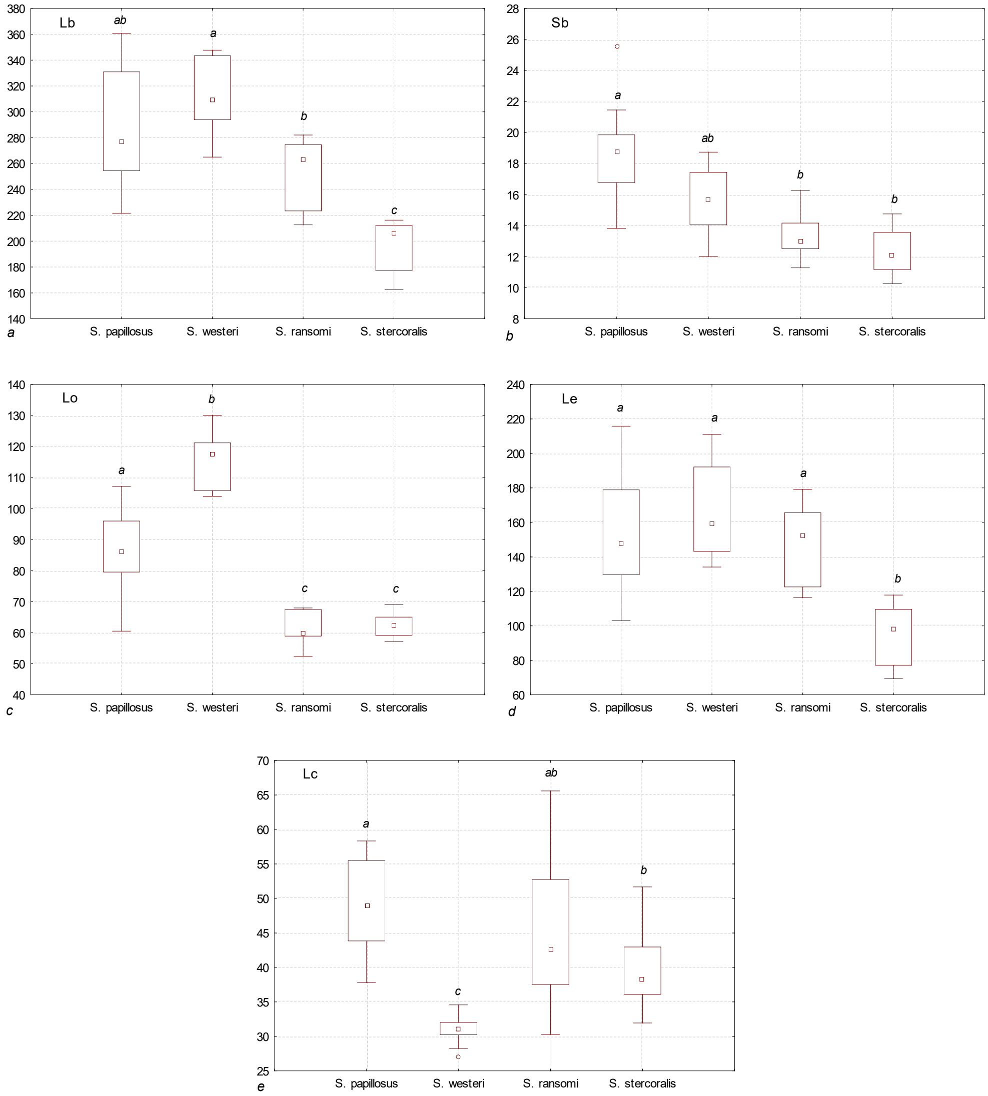

Fig. 2. Morphological variability of rhabditiform larvae (L_1) of *S. papillosus*, *S. westeri*, *S. ransomi* and *S. stercoralis*: *a* – body length (Lb), *b* – maximum body width (Sb), *c* – length of esophagus (Lo), *d* – length of intestine (Le), *e* – length of tail end (Lc)

Length of the tail end of second stage larvae ranged within 40–80 µm. The lowest parameters were recorded for L_2 *S. westeri*, the highest – for L_2 *S. papillosus*. Also a significant difference by this parameter was observed for L_2 *S. papillosus* and *S. westeri*, *S. papillosus* and *S. stercoralis*, *S. westeri* and *S. ransomi*, *S. ransomi* and *S. stercoralis* (Fig. 4e). Examination of morphometric parameters in third stage larvae revealed reliable differences in body length between *S. westeri* and *S. stercoralis*, *S. westeri* and *S. ransomi*. Body size of the larvae on average was 510–690 µm (Fig. 6a). The lowest parameters of total maximum body width were observed in L_3 *S. westeri*, the highest – in L_3 *S. stercoralis*. Reliable differences by this parameter were recorded for L_3 *S. westeri*. Other species did not reliably differ between one another in body width.

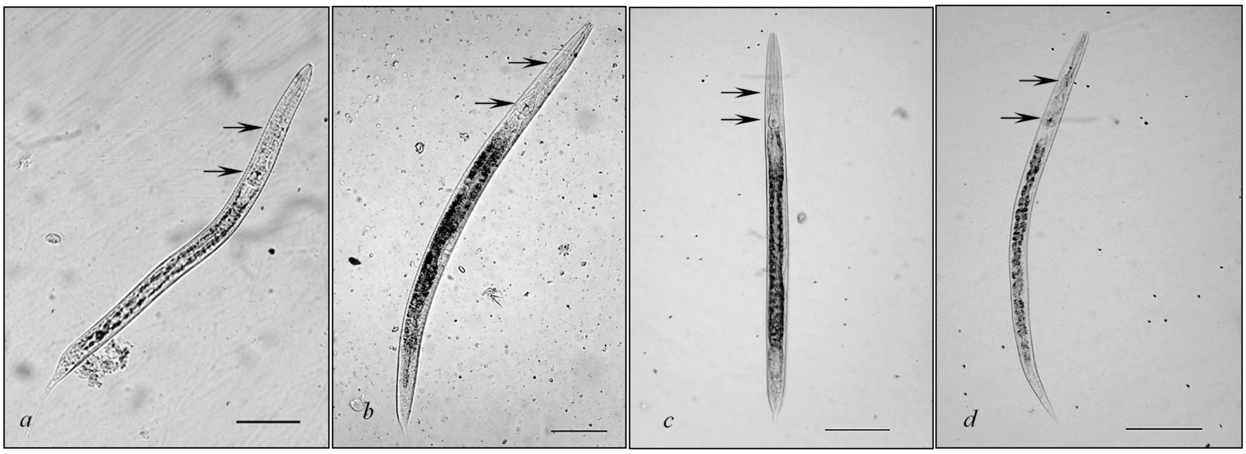

Fig. 3. Rhabditiform larvae (L_2): *a* – *S. papillosus*, *b* – *S. westeri*, *c* – *S. ransomi*, *d* – *S. stercoralis*; pointers indicate presence of two bulbuses in the esophagus; bar = 50 µm

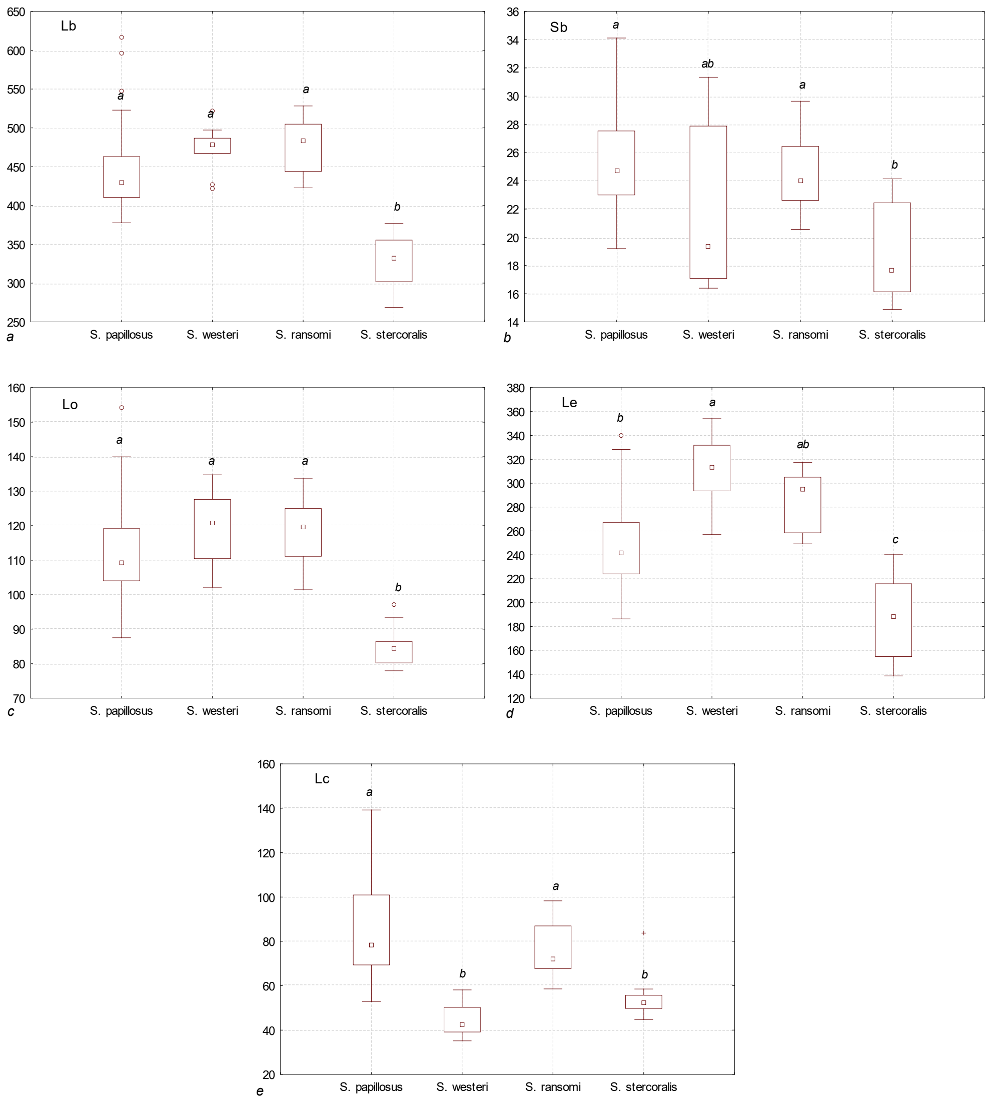

Fig. 4. Morphological variability of rhabditiform larvae (L_2) of *S. papillosus*, *S. westeri*, *S. ransomi* and *S. stercoralis*: *a* – body length (Lb), *b* – maximum body width (Sb), *c* – length of esophagus (Lo), *d* – length of intestine (Le), *e* – length of tail end (Lc)

The lowest length of the esophagus was determined for L_3 *S. papillosus*, which reliably distinguished it from the larvae of other studied species. By this parameter, L_3 *S. westeri*, *S. ransomi* and *S. stercoralis* had no reliable differences between one another. On average, length of the esophagus of the third stage larvae ranged within 180–270 µm (Fig. 6c). The lowest length of the esophagus was observed in L_3 *S. westeri*, which reliably distinguishes this species from the other nematode larvae we studied. L_3 *S. papillosus*, *S. ransomi* and *S. stercoralis* did not reliably differ from one another by this parameter (Fig. 6d). The longest tail end of third stage larvae was recorded in *S. papillosus*. Length of tail ends of L_3 *S. ransomi* and *S. stercoralis* and *S. westeri* did not reliably differ between one another and on average equaled about 100 µm. Difference by this parameter between L_3 *S. papillosus* and larvae of the remaining species equaled around 30 µm (Fig. 6e).

Measurements of morphometric parameters of males indicate absence of reliable differences by length of the body and the esophagus in the four studied species of nematodes. Average values of body length were within 700–790 µm, length of the esophagus – 140–170 µm (Fig. 8a, c). The lowest total maximum body width was recorded in *S. westeri*. This value reliably differed from *S. ransomi* and *S. stercoralis* (Fig. 8b).

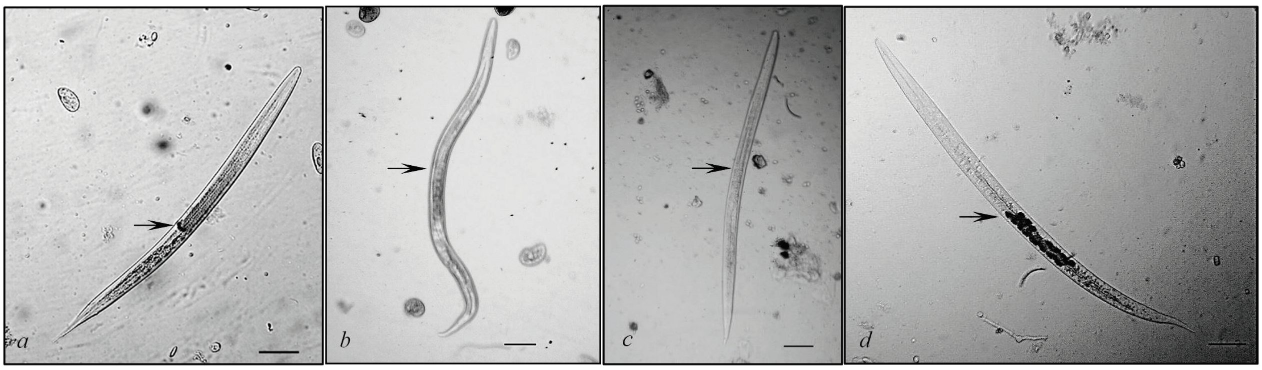

Fig. 5. Filariform larvae (L_3): *a* – *S. papillosus*, *b* – *S. westeri*, *c* – *S. ransomi*, *d* – *S. stercoralis*; pointers indicate the place where the esophagus turns into the intestine; bar = 50 µm

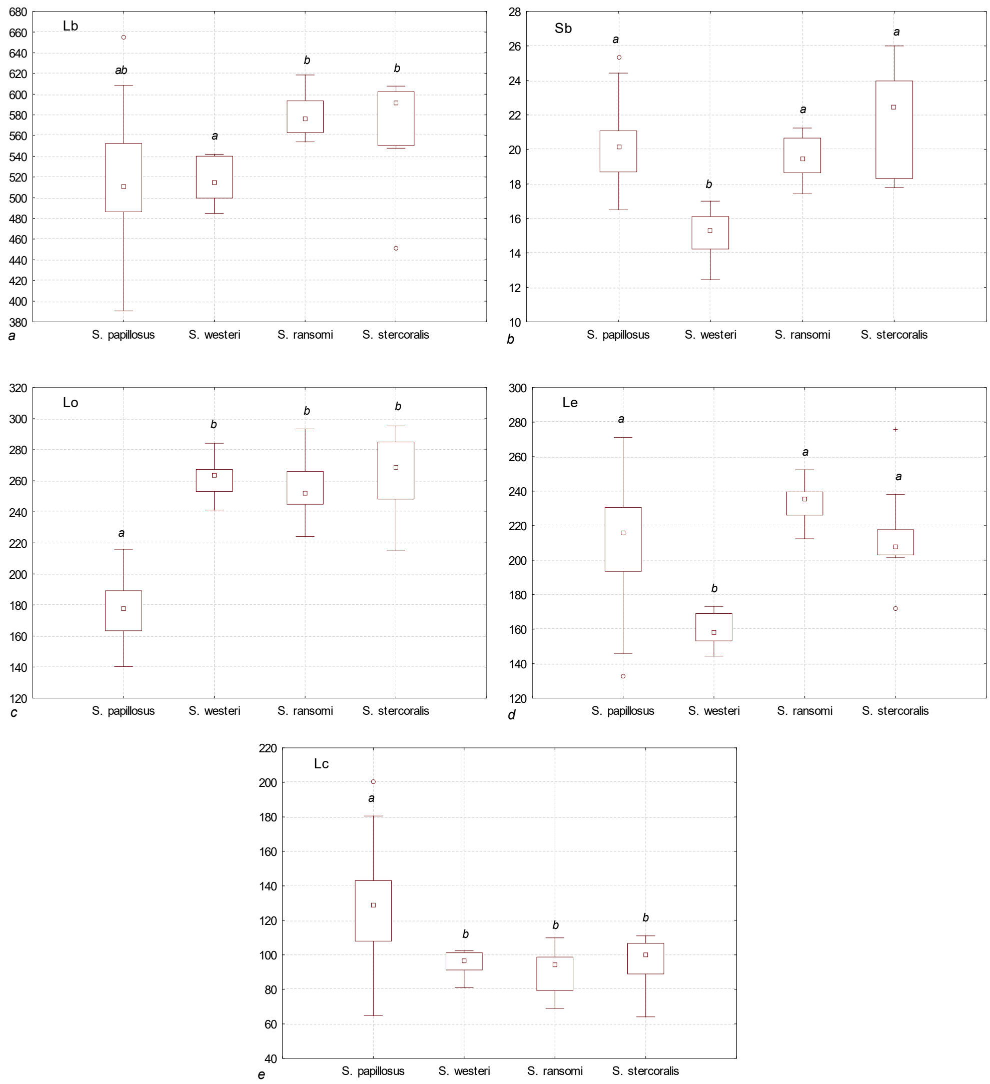

Fig. 6. Morphological variability of filariform larvae (L_3) of *S. papillosus*, *S. westeri*, *S. ransomi* and *S. stercoralis*: *a* – body length (Lb), *b* – maximum body width (Sb), *c* – length of esophagus (Lo), *d* – length of intestine (Le), *e* – length of tail end (Lc)

Fig. 7. Free-living male: *a*, *e* – *S. papillosus*; *b*, *f* – *S. westeri*; *c*, *g* – *S. ransomi*; *d*, *h* – *S. stercoralis*; pointers indicate the spicules; bar = 50 µm

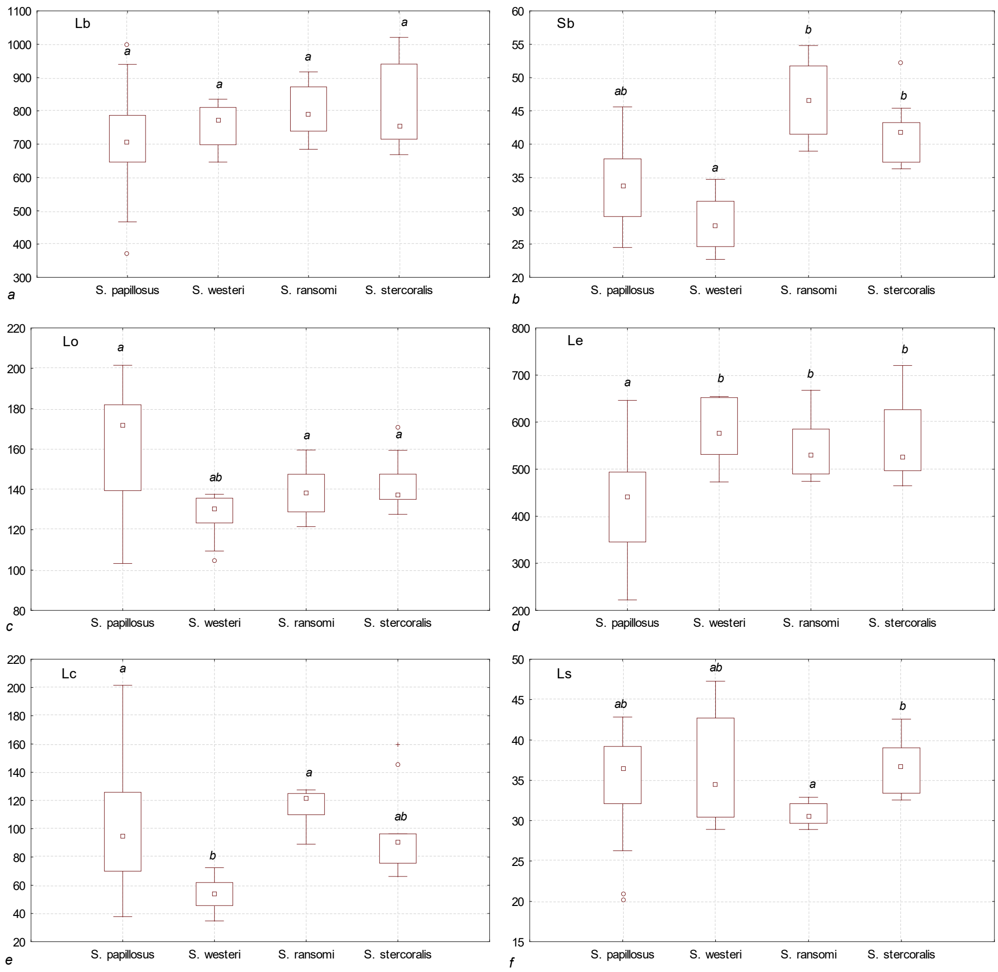

Fig. 8. Morphological variability of free-living male of *S. papillosus*, *S. westeri*, *S. ransomi* and *S. stercoralis*:
a – body length (Lb), *b* – maximum body width (Sb), *c* – length of esophagus (Lo),
d – length of intestine (Le), *e* – length of tail end (Lc), *f* – length of the spicules (Ls)

Length of the intestine much lower compared to the rest of the species was observed in *S. papillosus* (Fig. 8d). Length of the tail end of males reliably differed between *S. papillosus* and *S. westeri*, *S. westeri* and *S. ransomi*. Average value of this parameter ranged within 59–120 μm (Fig. 8e). Length of the spicules of four species of nematodes ranged within 31–37 μm. This parameter reliably differed only between *S. ransomi* and *S. stercoralis* (Fig. 8f).

Body length of females on average ranged within 850–950 μm. By this parameter, we found no reliable differences among the four species of nematodes (Fig. 10a). Similar results in morphometry were obtained also for length of the esophagus (Fig. 10c). Average values of this parameter were within 130–180 μm. Total maximum body width reliably differed in *S. papillosus* and *S. stercoralis*, *S. westeri* and *S. stercoralis*. This parameter was within 37–56 μm (Fig. 10b).

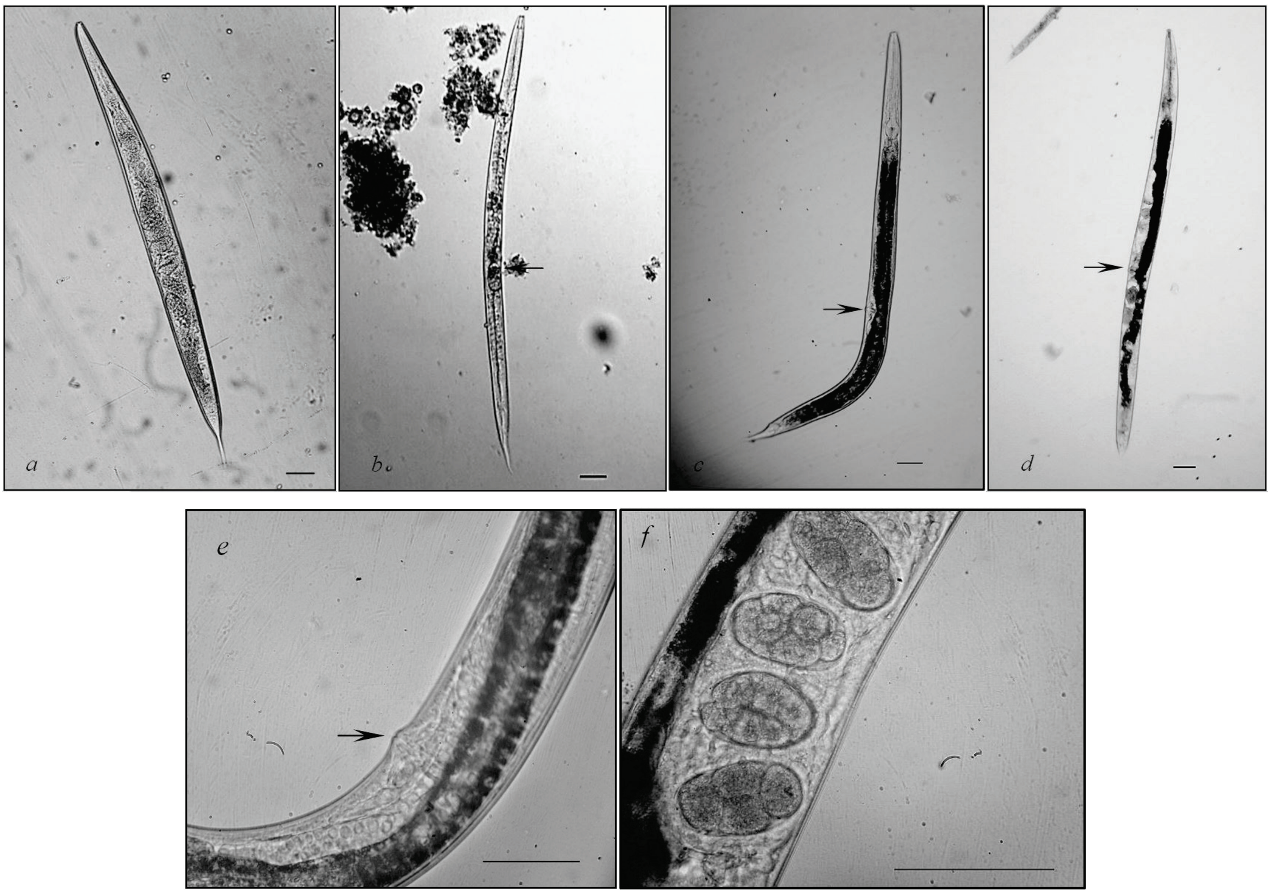

Fig. 9. Free-living female: *a* – *S. papillosus*, *b* – *S. westeri*, *c* – *S. ransomi*, *d* – *S. stercoralis*, *e* – area of the vulva, *f* – uterus with formed eggs, pointers indicate the vulva slit; bar = 50 μm

Table 1
The results of morphometric analysis of three larva stages, free-living males and females of different species of the genus Strongyloides

Stage of larva development, sex of adult nematode	Species	Total number of the parameters compared	The number of statistically reliably differing parameters	Characteristics by which species reliably differed from three other examined species			
				S. papillosus	*S. westeri*	*S. ransomi*	*S. stercoralis*
L_1	*S. papillosus*	5	5	–	Lo, Lc	Sb, Lo	Lb, Sb, Lo, Le, Lc
	S. westeri		4	–	–	Lo, Lc	Lb, Lo, Le, Lc
	S. ransomi		5	–	–	–	Lb, Le
	S. stercoralis		5	–	–	–	–
L_2	*S. papillosus*	5	5	–	Le, Lc	*	Lb, Sb, Lo, Le, Lc
	S. westeri		4	–	–	Lc	Lb, Lo, Le
	S. ransomi		5	–	–	–	Lb, Sb, Lo, Le, Lc
	S. stercoralis		5	–	–	–	–
L_3	*S. papillosus*	5	4	–	Sb, Lo, Le, Lc	Lo, Lc	Lo, Lc
	S. westeri		5	–	–	Lb, Sb, Le	Lb, Sb, Le
	S. ransomi		5	–	–	–	*
	S. stercoralis		5	–	–	–	–
Male	*S. papillosus*	6	2	–	Le, Lc	Le	Le
	S. westeri		3	–	–	Sb, Lc	Sb
	S. ransomi		3	–	–	–	Ls
	S. stercoralis		3	–	–	–	–
Female	*S. papillosus*	7	4	–	Le, Lv, E	E	Sb, Le, E
	S. westeri		5	–	–	Lc	Sb, E
	S. ransomi		2	–	–	–	*
	S. stercoralis		3	–	–	–	–

Note: * – no reliably differing characteristics.

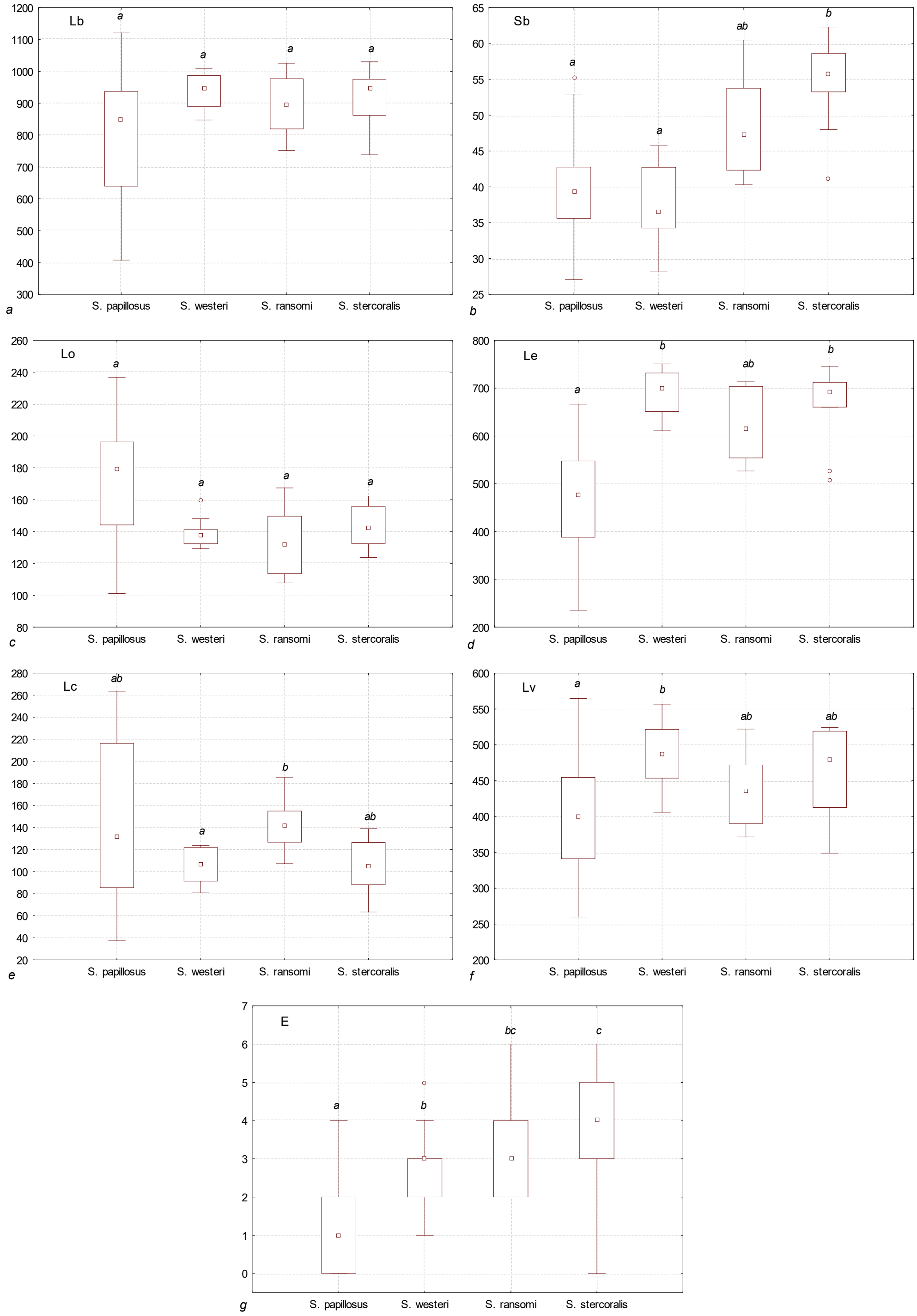

Fig. 10. Morphological variability of free-living female of *S. papillosus*, *S. westeri*, *S. ransomi* and *S. stercoralis*: *a* – body length (Lb), *b* – maximum body width (Sb), *c* – length of esophagus (Lo), *d* – length of intestine (Le), *e* – length of tail end (Lc), *f* – length from the head end to the vulva (Lv), *g* – number of developed eggs in the uterus cavity (E)

Measurement of the intestine revealed reliable difference between *S. papillosus* and *S. westeri*, *S. papillosus* and *S. stercoralis* (Fig. 10d). This parameter in the four species of nematodes ranged within 480–700 µm. Length of the tail end of females had reliable difference only between *S. westeri* and *S. ransomi* (Fig. 10e). On average, this parameter equaled 105–140 µm. Length from the head end to vulva reliably differed between females of *S. papillosus* and *S. westeri*. This parameter on average ranged within 400–480 µm (Fig. 10f). The number of eggs in the uterus ranged from one to four. Their lowest number was recorded in *S. papillosus*, the highest – in *S. stercoralis* (Fig. 10g). A reliable difference by this parameter was recorded between *S. papillosus* and *S. westeri*, *S. papillosus* and *S. stercoralis*, *S. papillosus* and *S. ransomi*, *S. westeri* and *S. stercoralis*.

Thus, first stage larvae reliably differed by all five parameters between *S. papillosus* and *S. stercoralis*, and by four out of five parameters between *S. westeri* and *S. stercoralis*. Second stage larvae also had reliable differences by all five parameters in *S. papillosus* and *S. stercoralis*. At this stage, only *S. ransomi* and *S. stercoralis* significantly differed in all parameters. Beginning from the third stage of the development, the number of reliable differences by morphometric parameters decreased (Table 1).

Using the results of our research, we calculated the indices of total maximum body width (Sb) to body length (Lb), length of esophagus (Lo) to length of intestine (Le), length of tail end (Lc) to body length (Lb), length of intestine (Le) to body length (Lb) for the four species of the *Strongyloides* genus (Fig. 11–15).

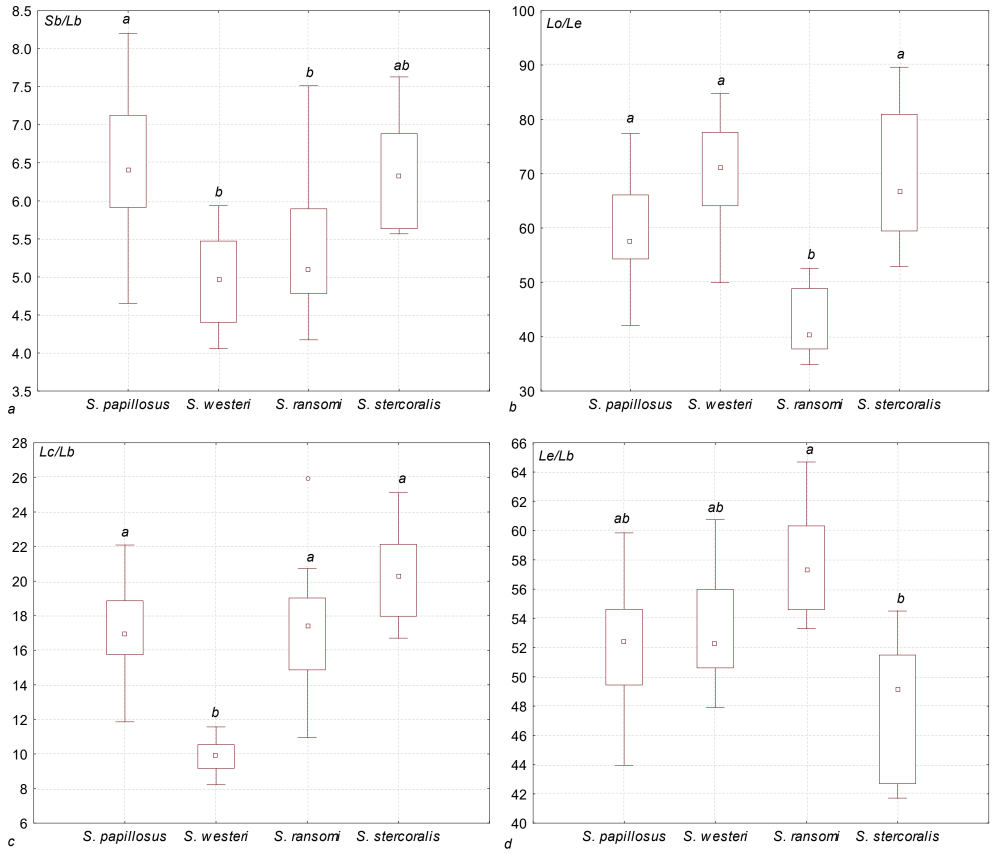

Fig. 11. Morphometric indices (%) of rhabditiform larvae (L_1) of four species of *Strongyloides* genus: *a* – ratio of total maximum body width (Sb) to body length (Lb), *b* – ratio of length of the esophagus (Lo) to length of intestine (Le), *c* – ratio of length of the tail end (Lc) to body length (Lb), *d* – ratio of length of the intestine (Le) to body length (Lb)

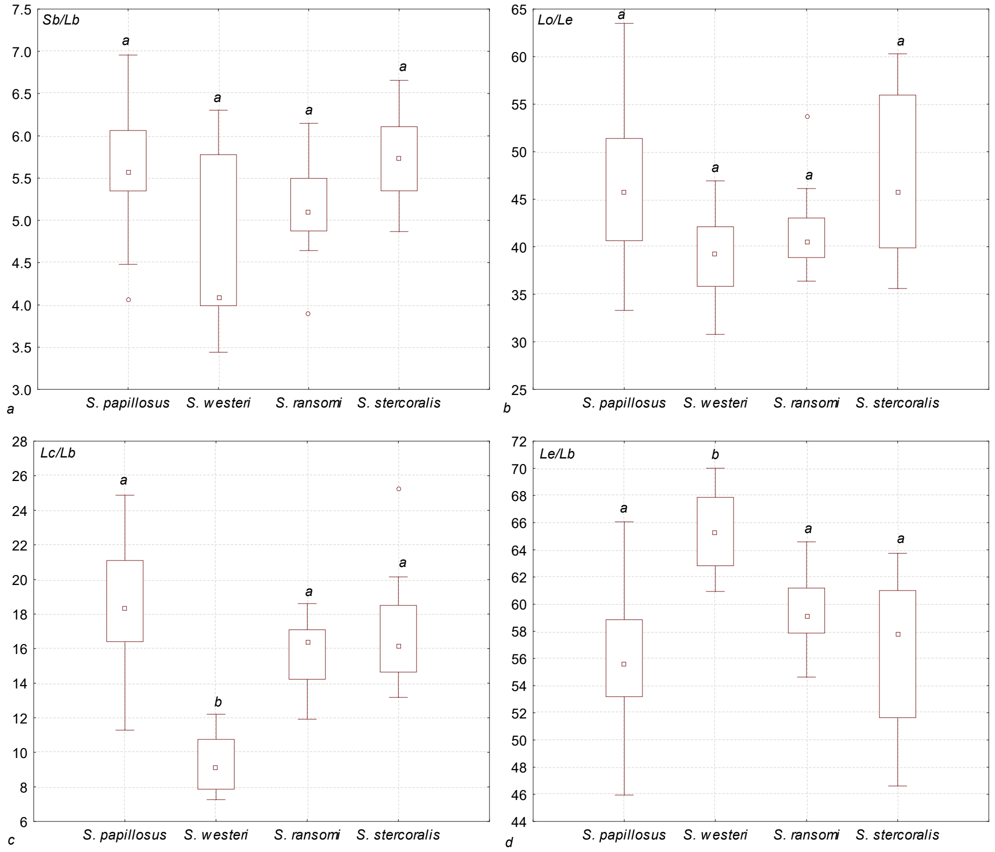

Fig. 12. Morphometric indices of rhabditiform larvae (L_2) of four species of *Strongyloides* genus: *a*–*d* – for explanations see Fig. 11

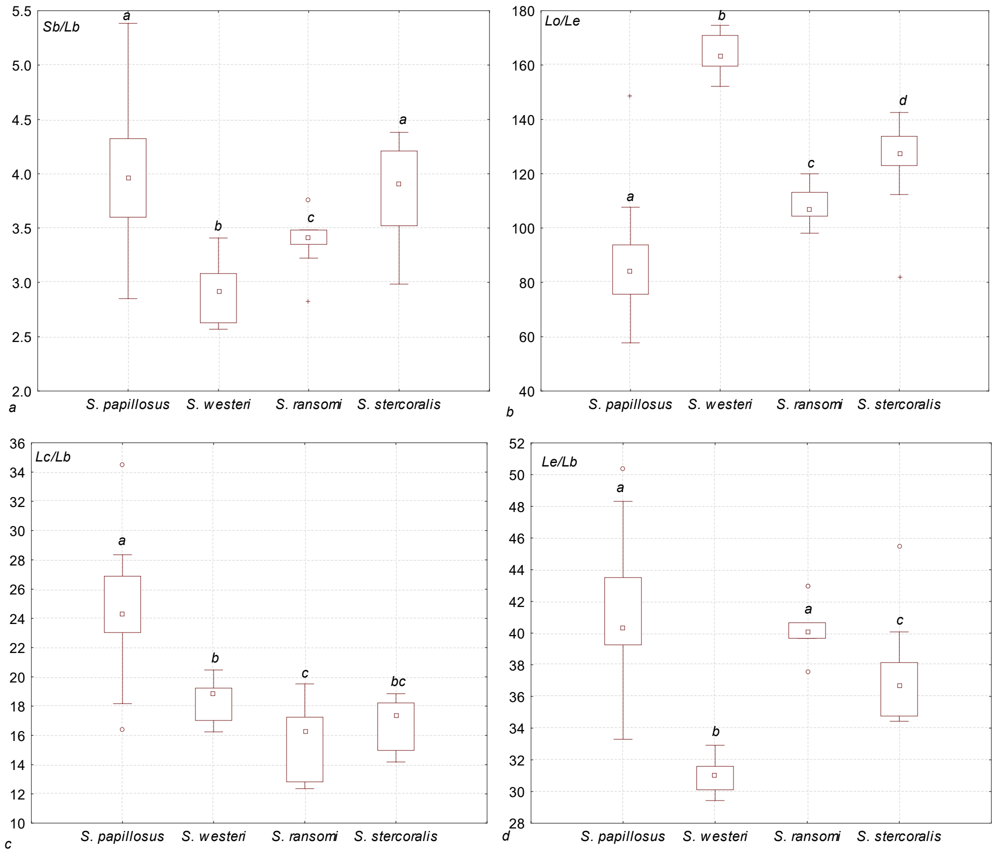

Fig. 13. Morphometric indices of filariform larvae (L_3) of four species of *Strongyloides*: *a–d* – for explanations see Fig. 11

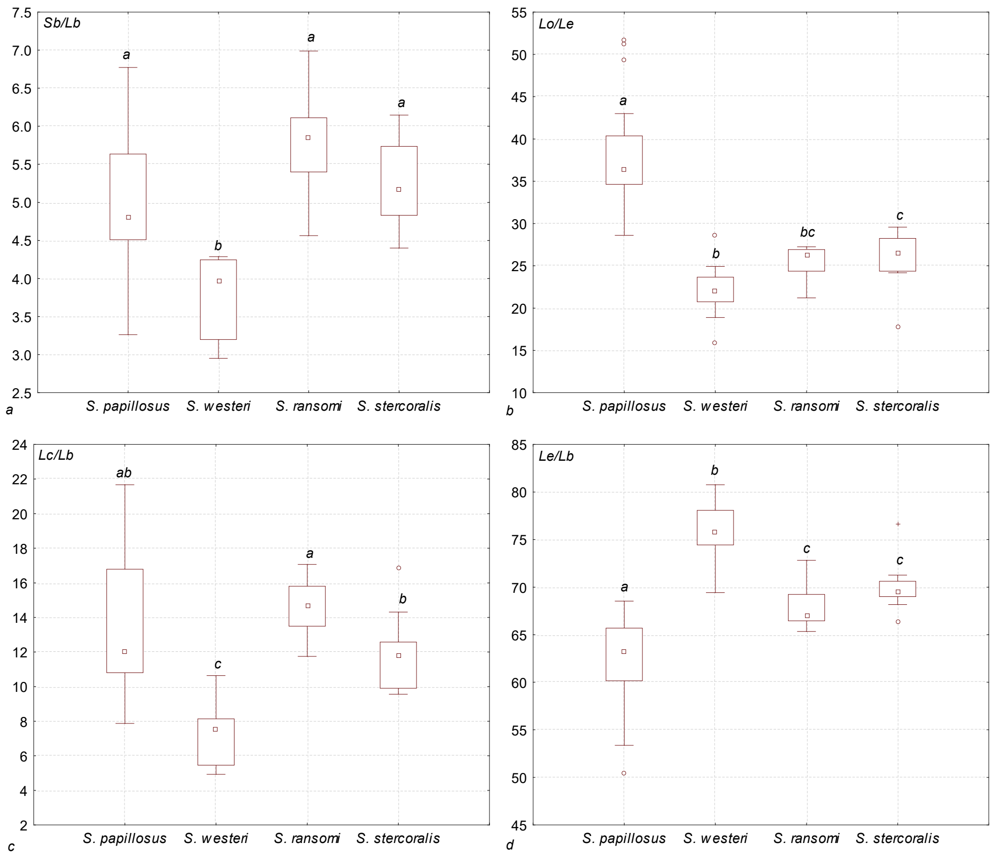

Fig. 14. Morphometric indices of free-living male of four species of *Strongyloides* genus: *a–d* – for explanations see Fig. 11

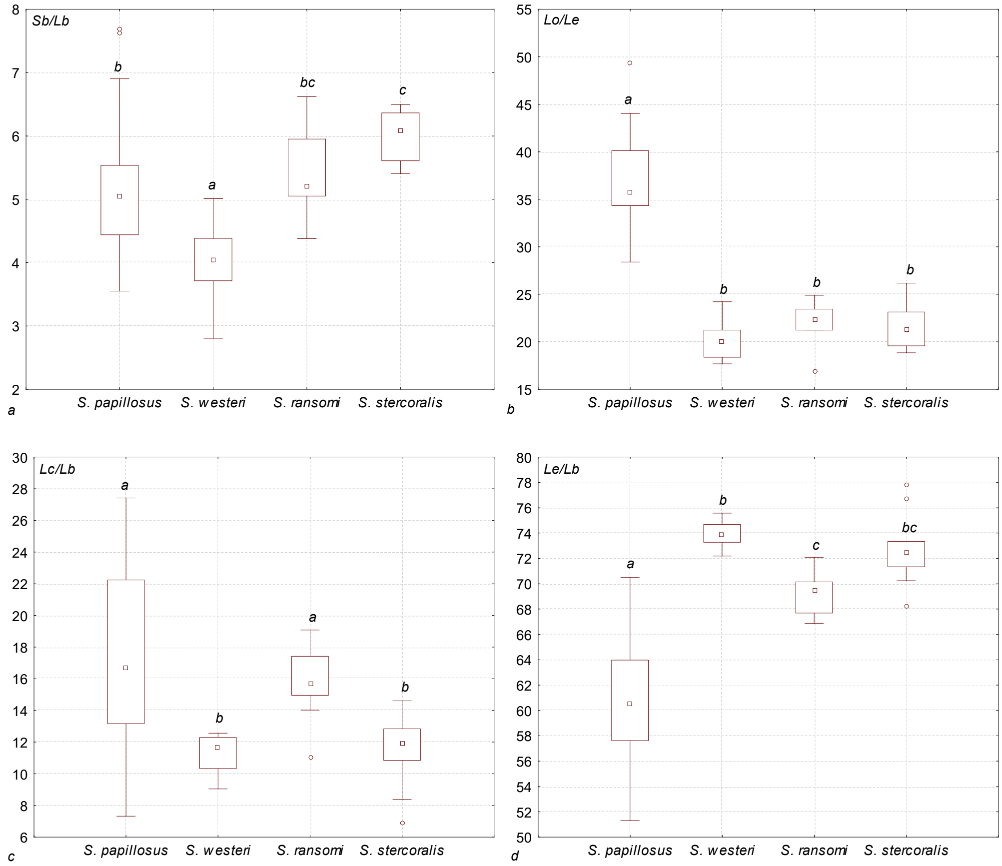

Fig. 15. Morphometric indices of free-living females of four species of *Strongyloides* genus: *a–d* – for explanations see Fig. 11

Among larvae of the first stage, reliable differences by the first index were observed between *S. papillosus* and *S. westeri*, and also between *S. papillosus* and *S. ransomi* (Fig. 11a). Index of ratio of length of esophagus to length of intestine statistically differed only in *S. ransomi* (Fig. 11b). No reliable differences by this index were observed in other species. The same was observed for ratio of length of tail end to body length (Fig. 11c). Significant differences were observed in *S. ransomi* and *S. stercoralis* by ratio of length of the intestine (Le) to body length (Lb) (Fig. 11d).

Second stage larvae of all four studied species of nematodes had no reliable differences by the first two indices (ratio of total maximum body width to body length, length of the esophagus to length of the intestine) (Fig. 12a, b). By the other two indices (ratio of length of the tail end to body length and length of the intestine to body length) statistically reliable difference was observed only for *S. westeri* (Fig. 12c, d).

Reliable difference for all four species was recorded for third stage larvae by index of length of the esophagus to length of the intestine (Fig. 13b). By ratios of total maximum body width to body length and length of tail end to body length, statistical difference was observed for *S. papillosus*, *S. westeri* and *S. ransomi* (Fig. 13a, c). By index of ratio of total maximum body width to body length, reliable differences were observed for *S. stercoralis* and *S. westeri*, and also *S. stercoralis* and *S. ransomi* (Fig. 13a). By index of length of the tail end to body length, we recorded reliable difference for *S. stercoralis* and *S. papillosus* (Fig. 13c). Difference in values of index of the intestine to body length in third stage larva were reliable between *S. papillosus* and *S. westeri*, *S. papillosus* and *S. stercoralis*, *S. westeri* and *S. stercoralis*, *S. ransomi* and *S. westeri*, *S. ransomi* and *S. stercoralis*. No differences by this index were observed in *S. papillosus* and *S. ransomi* (Fig. 13d).

In males, ratio of total maximum body width to body length unreliably differed for *S. papillosus*, *S. ransomi* and *S. stercoralis*. The only statistically reliable difference was observed for *S. westeri* compared to other species of the *Strongyloides* genus (Fig. 14a). Reliable difference in ratio of length of the esophagus to length of intestine was observed for *S. papillosus*, *S. westeri* and *S. stercoralis*, and also for *S. papillosus* and *S. ransomi* (Fig. 14b). For males of *S. papillosus* and *S. westeri*, we also found statistically reliable differences in ratio of length of tail end to body length. In males of *S. stercoralis*, *S. westeri* and *S. ransomi*, this index differed as well (Fig. 14c). Other results were obtained for comparing ratio of length of the intestine to body length. This index was reliably different was between *S. papillosus*, *S. westeri* and *S. ransomi*, and also between *S. papillosus* and *S. stercoralis*, *S. westeri* and *S. stercoralis* (Fig. 14d).

In females of the four species of nematodes of *Strongyloides* genus, reliable differences by total maximum body width to body length were observed in *S. papillosus*, *S. westeri* and *S. stercoralis*, and also *S. westeri* and *S. ransomi* (Fig. 15a). Index of length of esophagus to length of intestine reliably differed in *S. papillosus* (Fig. 15b). Also, females of *S. papillosus* differed from *S. westeri* and *S. stercoralis* by ratio of length of the tail end to body length. For females of *S. ransomi*, we also recorded reliable differences compared to *S. westeri* and *S. stercoralis* by this index (Fig. 15c). Females of *S. papillosus*, *S. westeri* and *S. ransomi*, and also *S. papillosus* and *S. stercoralis* had statistically significant differences in ratio of length of the intestine to body length (Fig. 15d).

Thus, by all four indices, we observed reliable difference in L_1 between *S. papillosus* and *S. ransomi*, in L_3 – *S. papillosus* and *S. westeri*, *S. westeri* and *S. ransomi*, in males – *S. papillosus* and *S. westeri*, *S. westeri* and *S. stercoralis*, in females of *S. papillosus* and *S. westeri*, *S. papillosus* and *S. stercoralis*. For four species of *Strongyloides* genus, the ratio of length of the esophagus to length of the intestine statistically differed in third stage larvae (Table 2).

Discussion

Studies accompanied by examination of metric parameters of the body of representatives of the Strongyloididae family are undertaken mostly for the purpose of description of new species (Dos Santos et al., 2010; Huang et al., 2016; Spratt, 2018). The data we presented are focused on morphology of common species of *Strongyloides* which parasitize domestic animals in Ukraine. In territory of our country, such studies have not been performed since the early XX century. In turn, we should mention presence of variability characteristic of all living organisms, including by their morphological and metric parameters. Peculiarities of adaptive and evolutionary changes of the development of nematodes of the *Strongyloides* genus help to improve the understanding of the processes of parasitism (Lok et al., 2017; Hunt et al., 2018).

In this article, we determined differential metric features of the structure of postembryonic stages of the development of *S. papillosus*, *S. westeri*, *S. ransomi*, *S. stercoralis*. The obtained data prove the changes of size of the body of larvae over the development and transition into invasive form or free-living generation. The results we obtained coincide with studies by different authors. As for comparison of metric parameters of *S. papillosus*, obtained over our studies, with the studies by Basir (1950), we should mention absence of differences in sizes of L_1, L_2 and free-living females. At the same time, average length of body of L_3, according to our data equaled 515 µm, which is insignificantly lower than what is shown by the data of Basir (575–640 µm); average length of body of free-living males was also lower by 25 µm.

Table 2
Morphometric indices of three larva stages, free-living males and females of different species of the genus *Strongyloides*

Stage of larva development, sex of adult nematode	Total number of the parameters compared	Species	The number of statistically reliably differing parameters	Index by which a species reliably differed from three other examined species			
				S. papillosus	*S. westeri*	*S. ransomi*	*S. stercoralis*
L_1	4	*S. papillosus*	3	–	Sb/Lb, Lc/Lb	Sb/Lb, Lo/Le	*
		S. westeri	3	–	–	Lo/Le, Lc/Lb	Lc/Lb
		S. ransomi	4	–	–	–	Lo/Le, Le/Lb
		S. stercoralis	3	–	–	–	–
L_2	4	*S. papillosus*	2	–	Lc/Lb, Le/Lb	*	*
		S. westeri	2	–	–	Lc/Lb, Le/Lb	Lc/Lb, Le/Lb
		S. ransomi	2	–	–	–	*
		S. stercoralis	2	–	–	–	–
L_3	4	*S. papillosus*	4	–	Sb/Lb, Lo/Le, Lc/Lb, Le/Lb	Sb/Lb, Lo/Le, Lc/Lb	Lo/Le, Lc/Lb, Le/Lb
		S. westeri	4	–	–	Sb/Lb, Lo/Le, Lc/Lb, Le/Lb	Sb/Lb, Lo/Le, Le/Lb
		S. ransomi	4	–	–	–	Lo/Le, Le/Lb
		S. stercoralis	4	–	–	–	–
Male	4	*S. papillosus*	4	–	Sb/Lb, Lo/Le, Lc/Lb, Le/Lb	Lo/Le, Le/Lb	Lo/Le, Le/Lb
		S. westeri	4	–	–	Sb/Lb, Lc/Lb, Le/Lb	Sb/Lb, Lo/Le, Lc/Lb, Le/Lb
		S. ransomi	4	–	–	–	Lc/Lb
		S. stercoralis	4	–	–	–	–
Female	4	*S. papillosus*	4	–	Sb/Lb, Lo/Le, Lc/Lb, Le/Lb	Lo/Le, Le/Lb	Sb/Lb, Lo/Le, Lc/Lb, Le/Lb
		S. westeri	4	–	–	Sb/Lb, Lc/Lb, Le/Lb	Sb/Lb
		S. ransomi	4	–	–	–	Lc/Lb
		S. stercoralis	4	–	–	–	–

Note: * – no reliably differing characteristics.

Comparing sizes of *S. westeri* with the studies by Schuurmans-Stekhoven (1930), we found support for our data. Differences were found in sizes of rhabditiform larvae and we consider this related to the fact that the authors had not divided the larvae into L_1 and L_2. Our previous studies proved that metric parameters of embryonic stages of the development of *S. westeri* have significant differences and depend on the stage of the development of helminth. At the same time, regulation of the formation of filarial larvae and free-living generations of males and females can be controlled using changes in temperatures during their cultivation (Gugosyan et al., 2018).

Schwartz & Alicata (1930) indicate a possibility of parasitism of different species of *Strongyloides* genus in swine. The main differential features are metric parameters of the body of helminths. After we had analyzed results of these studies, we determined that the body length of free-living males of *S. ransomi* according to our studies is lower. At the same time, sizes of rhabditiform and filarial larvae significantly did not differ. Huong Giang et al. (2017) continued the study of parasitism of *Strongyloides* in swine, comparing morphological and molecular characteristics of *S. ransomi*, obtained from the territory of different countries of Asia. They determined that compared to other species of *Strongyloides* genus, *S. ransomi* is morphologically similar to *S. papillosus*, but at molecular analysis of sequence of DNA, it was close to *S. venezuelensis*.

Eberhardt et al. (2008) indicate presence of two species of the *Strongyloides* genus which parasitize agricultural ruminants. The helminths they isolated belonged to certain genetically isolated populations. Based on the results of molecular studies, these authors suggest using name *S. papillosus* for *Strongyloides* of sheep, and *S. vituli* for *Strongyloides* of cattle. Currently, in Ukraine, there are no data on parasitism of different species of *Strongyloides* in ruminants, and the name *S. papillosus* is generally accepted. Differential diagnosis of different species of *Strongyloides* is also possible on the basis of morphological differences of the head ends of parasitic females (Sato et al., 2007).

The data we obtained for length of body of free-living males and females of *S. stercoralis* were lower than the same parameters presented by Little (1966). Variability of sizes is especially characteristic of free-living males of *Strongyloides*, though length of the spicules of these helminths remains relatively constant. Diagnosis and differentiation of *Strongyloides* is often complicated, at the same time parasitization can be lethal (Eydal & Skírnisson, 2016). For identification and isolation of *S. stercoralis*, researchers (Jongwutiwes et al., 1999; Khanna et al., 2015) recommend using agar-plate culture. Lopez et al. (2000) suggested a method of differentiation of rhabditiform L_1 and L_2 larvae using count of cells in this primordial organ over their development. Our studies can help conducting efficient differentiation of larvae and free-living generations of *Strongyloides* using metric parameters and by comparing morphometric indices.

Conclusions

Metric parameters of postembryonic stages of the development of *Strongyloides* have characteristic differences and depend on the species and stage of the development of the helminth. In our study, we demonstrated possibility of differential diagnosing of species on the basis of determining morphometric indices. We obtained new metric data on the structure of *S. papillosus*, *S. westeri*, *S. ransomi* and *S. stercoralis*, which parasitize domestic animals.

We measured body length (Lb), total maximum body width (Sb), length of the esophagus (Lo), length of the intestine (Le), length of the tail end (Lc); additionally for females we measured length from the head end to vulva (Lv) and the number of formed eggs in the uterus cavity (E), and additionally for males we measured length of spicules (Ls). According to morphometric parameters, there are significant differences for L_1, L_2 *S. papillosus* and *S. stercoralis*, and also L_2 *S. ransomi* and *S. stercoralis*. We analyzed ratio of total maximum body width (Sb) to body length (Lb), length of the esophagus (Lo) to length of intestine (Le), length of tail end (Lc) to body length (Lb), length of intestine (Le) to body length (Lb) and determined a reliable difference by these indices in L_1 of *S. papillosus* and *S. ransomi*, L_3 – *S. papillosus* and *S. westeri*, *S. westeri* and *S. ransomi*, in males – *S. papillosus* and *S. westeri*, *S. westeri* and *S. stercoralis*, in females of *S. papillosus* and *S. westeri*, *S. papillosus* and *S. stercoralis*. Larvae of all four examined species had reliable differences by index of ratio of length of the esophagus to length of the intestine.

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