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LYSOSOMAL ENZYMES IN ADAPTIVE RESPONSES OF CESTODES OF THE GENUS *TRIAENOPHORUS*

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The activity of seven acid hydrolases (acid phosphatase, DNase, RNase, β-glucosidase, β-galactosidase, cathepsin B, cathepsin D) and tissue protein content were comparatively studied in two cestode species of the genus *Triaenophorus* (*T. crassus* and *T. nodulosus*) sampled from pike (*Esox lucius*) from Lake Kamennoye (northern Karelia). Differences between the lysosomal enzyme profiles of these species were identified. *Triaenophorus crassus* demonstrated higher activities of acid phosphatase and β-galactosidase. The activities of β-glucosidase, cathepsin B and DNase were reliably lower than in *T. nodulosus*. The lower ecological plasticity of *T. crassus* and the differences detected in the biochemical reactions in the two helminth species are indicative of a more strenuous relationships of *T. crassus* with its definitive host, pike, in comparing with *T. nodulosus*.

Keywords: *Triaenophorus*, *Esox lucius*, host specificity, lysosomal enzymes

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The cestode genus *Triaenophorus* Rudolphi, 1793 is chiefly represented in freshwater bodies in Northern Europe, Siberia and North America by two species: *Triaenophorus nodulosus* Pallas, 1781 and *Triaenophorus crassus* Forel, 1868 (Kuperman, 1973). Both cestodes change three hosts over their complex life cycle. The first intermediate hosts for larval stages of both parasites are Copepoda. The range of second intermediate hosts of *T. nodulosus* is extensive, encompassing 57 fish species of 17 families. Plerocercoids of this helminth are most often found in the liver of perch and ruffe. The diversity of second intermediate hosts for *T. crassus*is much narrower, represented by 16 species of Salmonidae and the related Osmeridae and Thymallidae (Kuperman, 1973). The definitive host for the cestodes is the Northern pike *Esox lucius* L., in whose intestines the parasites mature and complete their development (Kuperman, 1973).

Tapeworms possess some unique features they have acquired while adapting to the parasitic lifestyle (Dubinina, 1974). Morphofunctionally and biochemically, they are very well adapted to their host (Shishova-Kasatochkina, Leutskaya, 1979; Sidorov et al., 1989). The digestive system being reduced in cestodes, their tegument performs the essential secretory, excretory, digestion and absorption functions. The helminth tegument is involved in many physiological and biochemical processes that balance the host-parasite relationship (Davydov, Mikryakov, 1988; Kuperman, 1988; Kuz'mina, 2005). The host organism responds to helminth invasion by launching versatile protective mechanisms to minimize the damage inflicted by the parasite (Izvekova, 2001; Sajid, McKerrow, 2002; Vysotskaya et al., 2003; Dzik, 2006; Dezfuli et al., 2014; Nikishin, 2016).

Adaptations in intestinal cestodes are rendered more complex by the dual environment of endoparasites, which have to adapt to the host (1st order environment) as well as respond to changes in the host's external environment (2nd order environment). Changes in the environment disrupt the host's food chains, wherefore facultative hosts get involved, resulting in the formation of "nonspecific parasitism" (Kuklin, Kuklina, 2005; Ieshko et al., 2012).

Over time, adaptation to new hosts results in speciation and emergence of new parasitic systems (Kuperman, 1973). The mechanisms of the organism's adaptation to the environment at the cellular level are built upon biochemical changes, including the reactions for supplying the organism with matter and energy, metabolic regulation, and protection against adverse impacts. An important role in the adaptive and protective responses of aquatic organisms belongs to lysosomal enzymes – special intracellular organelles containing several dozens of acid hydrolases (Vysotskaya, Nemova, 2008). Information about the activity of these enzymes in closely related species of the genus *Triaenophorus* and their participation in the process of adapting to the host is in deficit.

The aim was to study in a comparative manner the activity of lysosomal enzymes in tissues of adult cestodes *Triaenophorus nodulosus* and *Triaenophorus crassus* from pike intestines.

MATERIAL AND METHODS

Material for the study was sampled from northern Karelia, from Lake Kamennoye in the Kostomukshsky Strict Nature Reserve (Kem River catchment, White Sea) in June, 2011. The 18 pike specimens with body length (AC) ranged from 33 to 86 cm (62 ± 3) were investigated. The fish aged 2 – 14 years (7.6 ± 0.7) with body mass 328-5000 g (2184 ± 285).

The captured pikes were examined by partial helminthological dissection, with the prevalence (E) and intensity (M) of infection with the cestodes *T. nodulosus* and *T. crassus* determined as suggested by Bush et al. (1997). The fish were examined in June; all the retrieved cestodes were mature; data on *Triaenophorus* infection rates are given in Table 1.

Pike liver was used for comparisons of biochemical indices in the parasitic systems, since this lysosome-rich organ is actively involved in the host's adaptive responses. Whole cestodes were taken for the analyses. Tissue aliquots were rendered to 10% homogenates in 0.25 M sucrose solution with EDTA and 0.1% Triton X-100 non-ionic detergent, which destroys intracellular organelle membranes releasing the enzymes contained therein. The samples were centrifuged at 10 000 g in centrifuges with cooling. The supernatant fluid was analysed for the activity of seven lysosomal enzymes (acid phosphatase, DNase, RNase, β-glucosidase, β-galactosidase, cathepsin B, cathepsin D) and for protein content.

Analytical studies were done using equipment of the Core Facility of the Karelian Research Centre of the Russian Academy of Sciences (Tissue Lyser LT homogenizer, Qiagen, Germany; Allegra 64R centrifuge, Beckman Coulter, USA; spectrophotometer SF-2000, OKB-Spektr, Russia).

The substrate in determinations of the activity of acid phosphatase (EC 3.1.3.2) was sodium β-glycerophosphate (Barrett, Heath, 1980). The enzyme activity was expressed in micrograms of hydrolytically generated inorganic phosphorus, whose quantity was calculated based on its reaction with chromogenic reagent (Kahovkova, Odavic, 1969). The activity of acid nucleases – DNase (EC3.1.22.1) and RNase (EC3.1.4.23) – was determined as suggested by Pokrovskii and Archakov (1968) and Levitskii et al. (1973), respectively. The substrates were deoxyribonucleic acid (pH 5) and ribonucleic acid (pH 5.2) solutions in acetate buffer. Hydrolytic reaction products were quantified by spectrophotometry at 260 nm. The activity of the enzymes was expressed in relative units ${}_{\Delta}D_{260}$. Determination of the activity of acid β-glucosidase (EC 3.2.1.21) was based on photometric determination of the *para*-nitrophenol amount released by the reaction (Pokrovskii et al., 1971). The substrate was a p-nitrophenyl-β-D-glucopyranoside solution in a citrate buffer (pH 5). The activity of β-galactosidase (EC 3.2.1.23) was measured as suggested by Barrett and Heath (1980). The substrate was sodium p-nitrophenyl-β-D-galactopyranoside (pH 4). The activity of both glycosidases was expressed in micromoles of p-nitrophenol per unit time per mg protein. The activity of acid proteases was determined by modified spectrophotometric techniques: for cathepsin B (EC 3.4.22.1) – based on break-up of 0.065 M Na-benzoyl-L-arginine ethyl ester solution in acetate buffer (pH 5), for cathepsin D (EC 3.4.23.5) – based on the hydrolysis of 1% bovine haemoglobin in acetate buffer at pH 3.6 (Alekseenko, 1968). Protease activity was expressed in relative units of change in optical density (${}_{\Delta}D$) per mg protein: cathepsin B – at 525 nm, cathepsin D – at 280 nm. Protein content in the samples was determined according to the techniques suggested by Bradford (1976).

Data on cestode infection rates in pike were processed and analysed using Past software (Hammer et al., 2001), differences between biochemical parameters were tested for reliability using the Mann-Whitney U-test (Gubler, Genkin, 1969). Differences were considered significant with $p \leq 0.05$.

RESULTS

All the examined pikes from Lake Kamennoye were quite intensively infected with the cestodes *Triaenophorus crassus* and *T. nodulosus* (Table 1). The intensity of the *T. nodulosus* (1–73) infection was much lower than the *T. crassus* (25–175) infection rates.

Table 1. Summary statistics of infection with cestodes of the genus *Triaenophorus* in pike from Lake Kamennoye

Index	*T. nodulosus*	*T. crassus*
Number of examined pikes	18	18
Infection prevalence, %	100	100
Min intensity	1	25
Max intensity	73	175
Mean intensity	21.57	64
SE	4.89	13.23
Variance	334.88	2451.53
SD	18.30	49.51
Median	15.5	42
Variance/mean s2/M	15.52	38.31

The results of the biochemical study of the cestodes are shown in Figures 1-4. It follows from the reported data that the activity of lysosomal enzymes in parasite tissues was commensurate with the respective indices in the host's liver. This is indicated by the activity of the lysosomal marker enzyme – acid phosphatase (Fig. 1). One should remark that the activity of this enzyme in *T. crassus* was notably higher than in the other cestode.

The difference between *T. nodulosus* and *T. crassus* in tissue acid RNase activity was not significant (Fig. 2), whereas the other nuclease – DNase, was significantly lower in *T. crassus*.

The most significant differences between the cestodes concerned the activity of glycosidases (Fig. 3). Firstly, the absolute values of β-galactosidase activity in both worms were significantly higher than those of β-glucosidase. Secondly, galactosidase activity in *T. crassus* was higher and glucosidase activity was lower than in *T. nodulosus*.

The same was true for the activity of both proteases (Fig. 4). Their levels in *T. crassus* were lower than in *T. nodulosus*. Note also that cathepsin B activity in cestodes was 2–3 times higher than in the host's liver (1.02±0.04 relative units – ΔD_{525}/mg protein per hour). On the contrary, the cathepsin D activity of cestodes was 4 times lower than in the pike's liver (0.91±0.05 relative units - ΔD_{280} /mg protein per hour). The variation of soluble protein content in the samples was not so significant: this index in *T. nodulosus* tissues was 74.5 ± 3.7, in *T. crassus* – 77.5 ± 3.2, and in pike liver – 62.7 ± 4.4 mg/g dry mass.

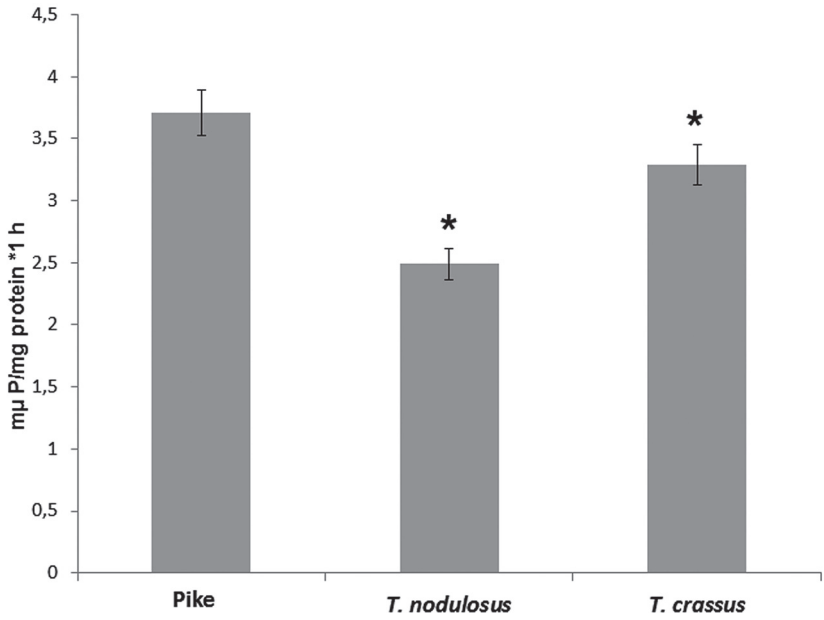

Figure 1. Acid phosphatase activity in tissues of adult cestodes of the genus *Triaenophorus* and the liver of their host – pike. $n = 5$.
*Differences between variants are significant at $p \leq 0.05$.

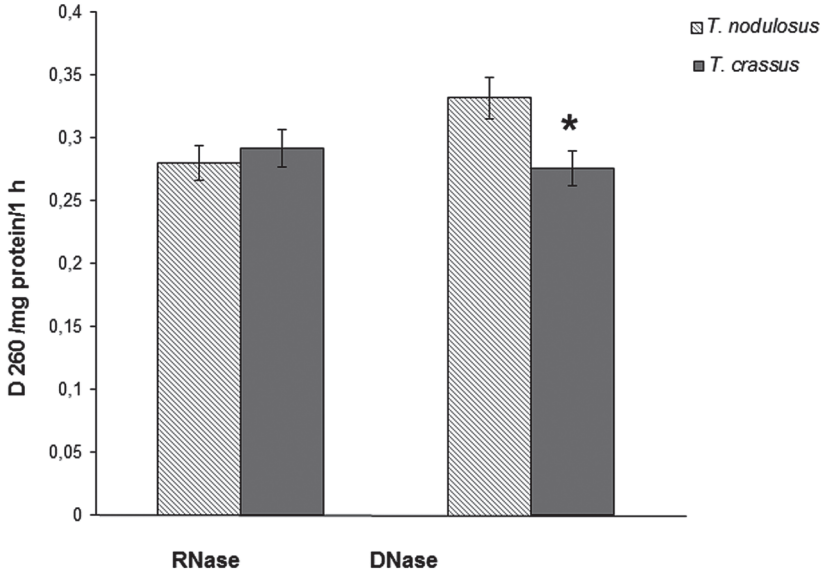

Figure 2. Nuclease activity in tissues of adult cestodes of the genus *Triaenophorus*. $n = 5$. *Differences between variants are significant at $p \leq 0.05$.

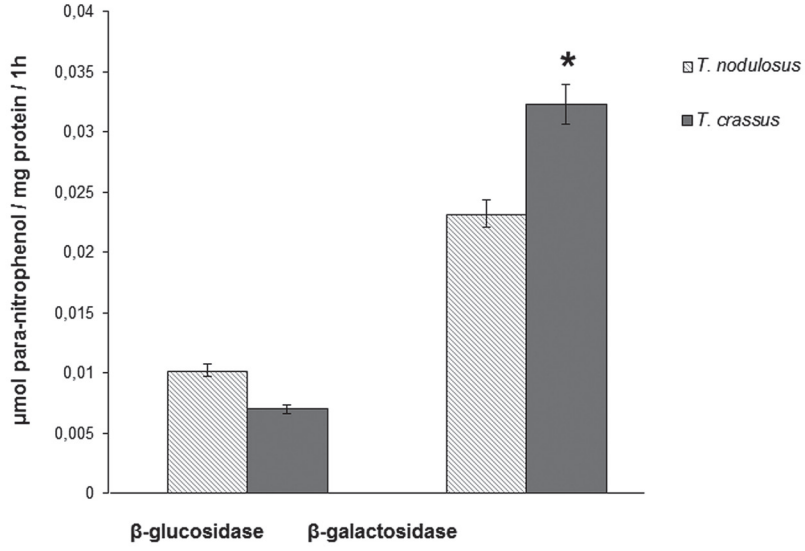

Figure 3. Glycosidase activity in tissues of adult cestodes of the genus *Triaenophorus*. $n = 5$. *Differences between variants are significant at $p \leq 0.05$.

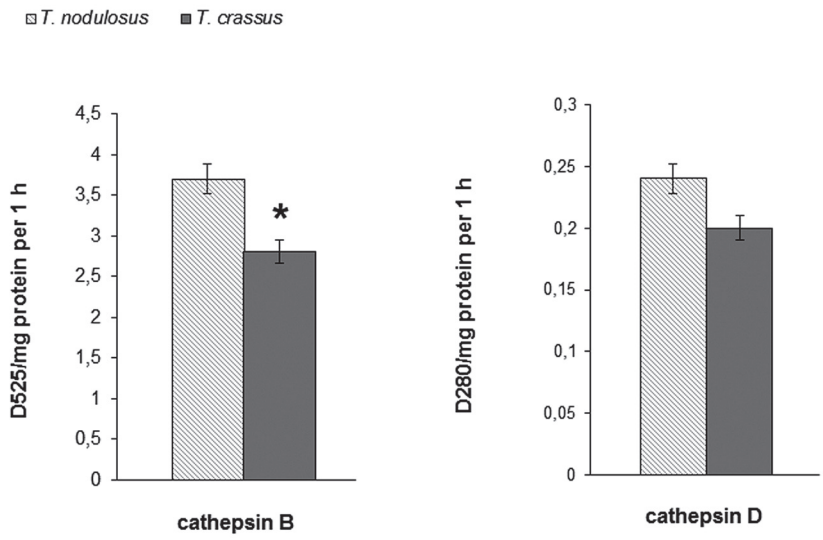

Figure 4. Protease activity in tissues of adult cestodes of the genus *Triaenophorus*. $n = 5$.
*Differences between variants are significant at $p \leq 0.05$.

DISCUSSION

It seems a highly aggregated distribution, indicated by the s^2/M ratio, was demonstrated by *T. crassus* (Table 1), suggesting pike was more susceptible to infestation by this species as compared to *T. nodulosus*.

Cestodes of the genus *Triaenophorus* are systematically close species. The ranges of distribution of both *T. nodulosus* and its host of the genus *Esox* are almost the same. The distribution area of *T. crassus* is somewhat narrower. It occupies the northern part of pike's range and covers circumpolar Holarctic regions. The definitive and the first intermediate hosts are the same for both helminth species. The most significant difference between them is the localisation of plerocercoids in the second intermediate host: muscles of salmoniform fishes for *T. crassus*, and usually liver of Percidae for *T. nodulosus*. Adaption to the environment inside their respective second intermediate hosts has been the key factor for the divergence of these cestode species (Kuperman, 1973). The differences detected in the adaptive responses of the helminths in our study also suggest that *T. crassus* is a stricter definitive host specialist than *T. nodulosus*. The leading role in the species' adaptations belongs to biochemical changes, including changes in the lysosomal enzyme complex activity. These enzymes are involved in membrane and cellular digestion processes (Vysotskaya, Nemova, 2008). Cestode tegument is rich in structures participating in lysosome formation (Kuperman, 1988). A higher activity of acid phosphatase in *T. crassus* tissues compared to *T. nodulosus* indicates that the former generates more lysosomes and that the costs of its adaptation to

the host are higher. Acid phosphatase is known as a broad-spectrum phosphoric monoester hydrolase, which has an important role in the metabolism of carbohydrates, lipids, nucleic acids and phosphorus compounds and, hence, in supplying the organism with energy.

Another enzyme whose activity was significantly higher in *T. crassus* than in the other cestode was β-galactosidase. The level of this glycosidase can be elevated when the parasite's adaptive reactions involve galactose-containing lipids and proteoglycans, which act as metabolic regulators (Vdovichenko, Vysotskaya, 2013). Also, considering that carbohydrate metabolism is the principal source of energy for helminths, when the stores of energy substrates have mostly been exhausted, alternative mechanisms can be launched to support tissue bioenergy, and then the role of lysosomal glycosidases, including β-galactosidase, will grow (Vysotskaya, Nemova, 2008).

We have previously demonstrated that the activity of the lysosomal protease cathepsin B in tissues of *T. nodulosus* cestodes is several times higher than in pike organs (Vysotskaya et al., 2015). The lysosomal proteolytic system is the main player in protein metabolism. On top of cleaving proteins to peptides and amino acids, lysosomal proteases perform a number of specific functions for renewal of proteins, activation of precursors of biologically active proteins and peptides, including hormones (Turk et al., 2001; Buhling et al., 2004; Nemova, Bondareva, 2005). Cathepsin B participates in the degradation of many intra- and extracellular proteins (Brix et al., 2008; Arampatzidou et al., 2011; Yadati et al., 2020). Cathepsin B was shown to take part in apoptosis and immunoregulation processes (Turk, Turk, 2009). The high activity of cathepsin B we observed in the tissues of both cestodes suggests that this enzyme is actively involved in the parasites' protective response to impact from the host. Probably that activity of cathepsin B in *T. crassus* was significantly lower than in *T. nodulosus* due to the effect of the peptide antibiotics the host produces to protect itself against various infection agents, including invasion by helminths (Dezfuli et al., 2014). Besides, proteases, as well as other acid hydrolases, can be inhibited by own proteins produced by the parasite to protect against the host's proteolytic enzymes and excreted at host-helminth contact sites (Holt et al., 2006; Chen et al., 2017; Izvekova, Frolova, 2019; Vidak et al., 2019). The assumption that the cestodes in question can respond differently to the same impact from the host is supported by the recently obtained data on qualitative and quantitative differences in the protein composition of these species (Kochneva et al., 2018).

Thus, according to the biochemical aspects of host-parasite relationships, as well as data on the distribution, life cycles, and host affiliations, *T. crassus* appears to be a stricter specialist than *T. nodulosus*. It is adapted to living in cold oligotrophic waters. Its first intermediate hosts are northern copepodite species. The parasite's distribution in water bodies is mainly associated with vendace – a very common species in northern lakes (Potapova, 1978; Valtonen et al., 1989). The other species – *T. nodulosus* has a broader distribution and a much wider range of second intermediate hosts, including salmoniform fishes. The key role in maintaining *T. nodulosus* abundance belongs to perch and ruffe – the main items in pike's diet (Kuperman, 1973). Differences in ecological valence and specialisation between *Triaenophorus* species are the reasons for the different resilience of their parasitic systems through the natural succession in water bodies and under human impact. To wit,

Lake Kostomukshskoye, contaminated by wastes from iron-ore mine and mill, exhibits a poorer species composition of the biota, including a drastic reduction of the fish fauna. Vanishing of vendace, the main intermediate host for *T. crassus,* from the lake entails the extinction of the parasite, in spite of the presence of other aquatic organisms involved in its life cycle. In this situation, the decline of aquatic animal diversity similarly leads to changes in the structure of the *T. nodulosus* parasitic system in line with changes in the host's trophic links, since the main intermediate host (perch) is also absent from the lake. A typical intermediate host is recruited into the parasite's life cycle (Ieshko et al., 2012). Research into the biochemical aspects of relationships in the *T. nodulosus*–pike parasitic system in a water body altered by human activities has demonstrated that the main contributor to the adaptive response to the adverse environmental impact is the host. The parasite, on the other hand, also contributes to overall homeostasis in the system by adjusting its metabolism to the host's condition (Vysotskaya et al., 2015). It is there for ease to say that the host-parasite relationship in the *T. nodulosus*–pike system is highly balanced at the fine biochemistry level. The fact that of the two cestode species of the genus *Triaenophorus* only *T. nodulosus* occurred in the technogenic suppressed lake suggests that this parasitic system has a higher adaptive potential than that of *T. crassus.*

Our studies revealed differences between the biochemical and population parameters of the two cestode species, which evidence a more strenuous process of adaptation to the host in *T. crassus*. This, together with a narrower range of second intermediate hosts and a lower ecological plasticity, corroborates the assumption about a later speciation of *T. crassus* compared to *T. nodulosus*. Of the two ancient and steady parasitic systems, the original one is the *T. nodulosus* – pike *Esox lucius* L. system.

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ЛИЗОСОМАЛЬНЫЕ ФЕРМЕНТЫ В АДАПТИВНЫХ РЕАКЦИЯХ ЦЕСТОД РОДА *TRIAENOPHORUS*

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Ключевые слова: *Triaenophorus*, *Esox lucius*, гостальная специфичность, лизосомальные ферменты

РЕЗЮМЕ

Проведено сравнительное изучение активности семи кислых гидролаз (кислой фосфатазы, ДНКазы, РНКазы, β-глюкозидазы, β-галактозидазы, катепсина B, катепсина D) и содержания белка в тканях двух видов цестод рода *Triaenophorus* (*T. crassus* и *T. nodulosus*) из щуки озера Каменного (Северная Карелия). Установлены различия в ферментных профилях лизосом у изученных паразитов. Для *Triaenophorus crassus* характерны более высокие значения активности кислой фосфатазы и β-галактозидазы, активность же β-глюкозидазы, катепсина B и ДНКазы была более низкой, чем у *T. nodulosus*. Выявленные различия в показателях заражения и параметрах распределения численности цестод в популяции хозяина (*Esox lucius* Linnaeus, 1758) свидетельствуют о более напряженном приспособительном процессе к хозяину у *T. crassus*, что наряду с более узким кругом вторых промежуточных хозяев и меньшей экологической пластичностью подтверждает более позднее происхождение этого вида по сравнению с *T. nodulosus*.