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Fauna of the Endobiotic Ciliates from the Rumen of the Red Deer *Cervus elaphus* Linnaeus, 1758

O. A. Kornilova[a], A. V. Radaev[b], I. V. Seryodkin[c], and L. V. Chistyakova[d, *]

[a] *Herzen State Pedagogical University of Russia, St. Petersburg, 191186 Russia*
[b] *Saint Petersburg State University, St. Petersburg, 199034 Russia*
[c] *Pacific Geographical Institute, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, 690041 Russia*
[d] *Zoological Institute, Russian Academy of Sciences, St. Petersburg, 199034 Russia*
**e-mail: Ludmila.Chistyakova@zin.ru*

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Abstract—Fauna of endobiotic ciliates of the red deer *Cervus elaphus xanthopygus* and of the Altai wapiti *Cervus elaphus sibiricus* in Asia was studied for the first time. In total, 14 species and five forms of ciliates belonging to five genera of Ophryoscolecidae and Isotrichidae were found. The species composition of endobiotic ciliates in all studied individuals of deer appeared to be rather similar. Most of the samples contained *Entodinium wapiti*, previously considered specific to the North American wapiti *Cervus canadensis*. The influence of different factors on the formation of a certain structure of communities of ciliates, endobionts of the rumen of the red deer *Cervus elaphus*, is discussed.

Keywords: endobiotic ciliates, *Cervus elaphus*, Ophryoscolecidae, Isotrichidae
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INTRODUCTION

Endobiotic ciliates are one of the components of a complex ecosystem formed in the rumen of ruminants (Newbold et al., 2015). As an important component of the rumen microbiome, ciliates take part in the host's digestion processes, including the breakdown of plant fibers. The fauna of endobiotic ciliates in the rumen of cattle and other domesticated ruminant species has been studied in sufficient detail; a significant number of publications are devoted to the study of the species diversity of ciliates, their interactions with various groups of microorganisms inhabiting the rumen, and rumen biochemistry, primarily the processes of methanogenesis (Kornilova, 2004a; Hall, 2011; Denton et al., 2015; Tapio et al., 2017; Park and Yu, 2018). However, endobiotic ciliates from the digestive tract of wild ruminant species have not been studied in such detail. As a rule, there are isolated publications on the species diversity of endobionts in the rumen of a particular host species; for a number of ruminant species, there are no data at all. At the same time, the study of ciliate communities from the rumen of ruminants that differ in their biological and ecological features (e.g., diet and herd size) is of undoubted interest. The results of such studies make it possible to assess the influence of various factors on the formation of endobiont communities, to identify differences in the species structure of such communities between individual populations and host animal species, and to determine the level of specificity of interactions between partners in a symbiotic association. In this work, the fauna of endobiotic ciliates of the red deer *Cervus elaphus* in Asia was studied for the first time.

MATERIALS AND METHODS

The study was conducted on the material of ciliates from the rumen of red deer—the subspecies of red deer *Cervus elaphus xanthopygus* Milne-Edwards, 1867 (Terneisky and Olginsky districts, Primorsky krai) and the subspecies of maral *C. e. sibiricus* Severtzov, 1873 (Ondugai district, Altai Republic) (Table 1).

The material was collected in different seasons of the year from 2015 to 2021. The contents of the rumen with a volume of 30 mL were collected in its posterior section (at a distance from the connection with the esophagus and reticulum) near the inner wall using a sterile scalpel and tweezers and placed in a sterile test tube with a volume of 100 mL. The samples were fixed in 7% formalin solution at a ratio of 2 : 1 to rumen contents; the samples were stored at 4°C before fixation.

Light microscopic studies and microphotography were performed using an MBI-11 microscope (LOMO, Russia), Altami-Invert-3 (Altami, Russia) microscope with a photo attachment, and Leica DM2500 microscope (Leica-Microsystems, Germany) equipped with differential interference contrast and a Leica DFC495 digital camera (8.0 MP).

Table 1. Conditions for the collection of samples of rumen contents of the red deer *Cervus elaphus xanthopygus* Milne-Edwards, 1867 from Primorsky krai (samples 1–10) and *C. elaphus sibiricus* Severtzov, 1873 from the Altai Republic (sample 11)

Indices	Samples										
	1	2	3	4	5	6	7	8	9	10	11
Collecion date	May 28, 2015	July 11, 2016	March 22, 2019	December 2, 2019	December 2, 2019	July 3, 2020	September 17, 2020	September 24, 2020	December 15, 2020	December 26, 2020	April 22, 2021
Age/sex of deers	Male, 1 y.o.	Female, adult	Male, 2 y.o.	Female adult	Female fawn	Female, 2 y.o.	Female adult	Male, adult	Male, 3 y.o.	Male fawn	
Conditions of the material storage	Several hours	5–6 h	24-hour cooling	20-hour cooling	20-hour cooling	4-hour cooling	Several hours	2–3 h	1 h	12 h	12-hour cooling
Collection site	Terneysky district	Terneysky district	Terneysky district	Terneysky district	Terneysky district	Terneysky district	Terneysky district	Olginsky district	Terneysky district	Terneysky district	Ondugai district

When studying cell morphology, a 0.1% methyl green solution in 1% acetic acid solution was used to detect the macronucleus. The number of ciliates in 1 mL of rumen contents was determined using the "calibrated drop" method (Kornilova, 2004b). To determine the species of ciliates, the works of Dogiel (1929), Williams and Coleman (1992), Dehority (1993), and Kornilova (2010) were used.

RESULTS AND DISCUSSION

In the samples of red deer rumen contents, we identified a total of 14 species and five forms of ciliates belonging to five genera of the Ophryoscolecidae and Isotrichidae families (Table 2; Figs. 1, 2). The total number of ciliates in 1 mL of rumen contents ranged from 122290 in red deer no. 3 to 420380 in red deer no. 4. *Epidinium caudatum* and *E. ecaudatum* were found in all samples without exception, with *E. ecaudatum* always occupying a dominant position in terms of numbers. *Eudiplodinium maggii* was identified in the overwhelming majority of samples (with the exception of sample no. 2). We also found ciliates in the rumen contents of all deer that, according to a set of identifying features, can be classified into three forms of the species *Eudiplodinium neglectum* (Dogiel, 1929) (Table 2).

At the same time, *E. neglectum* f. *bovis* and *E. neglectum* f. *spectabile* differ mainly in the shape of the cell and macronucleus; the main difference between *E. neglectum* f. *impalae* and the previous two forms is the location of the micronucleus at the anterior edge of the macronucleus (Fig. 1). Currently, these forms are often considered as separate species, but many authors, following Dogiel, note the exceptional similarity of the species *E. bovis*, *E. spectabile*, and *E. impalae*, which casts doubt on their validity (Kofoid and MacLennan, 1932; Hungate, 1942; Williams and Coleman, 1992). We prefer to consider the studied ciliates as forms of the species *E. neglectum*, in accordance with the identification guide by Dogiel (1929).

In the rumen of deer, we found nine species and forms of the genus *Entodinium*, with three species—*E. caudatum*, *E. dubardi*, and *E. exiguum*—occurring in all the individuals studied (Fig. 2). The remaining species of *Entodinium* (except *E. longinucleatum* and *E. furca* f. *furca*) were found in more than half of the samples. In the overwhelming majority of red deer, as well as in the maral, ciliates of *Entodinium wapiti* were found in the rumen (Fig. 2). This species was described from the rumen of a deer from North America—wapiti *Cervus canadensis* Erxleben, 1777—and was considered specific to this host (Dehority, 1995). Table 3 shows comparative morphometric data on *E. wapiti* from red deer (no. 7), maral (no. 11), and wapiti (according to Dehority, 1995). The range of variability of ciliates from the rumen of red deer and wapiti is similar, whereas in the rumen of the maral predominantly large ciliates are found. A wide range of variability of morphometric features is very typical for endobiotic ciliates; such a unique feature as a triangular outgrowth on the cell surface allows unambiguous identification of *E. wapiti*.

The species composition of endobiotic ciliates in all red deer from the Terney and Olginsky districts of Primorye, as well as maral from the Altai Republic, demonstrates a significant degree of similarity (Chekanovsky-Sorensen index of 0.9). At the same time, the species *Enoploplastron triloricatum* was found only in the rumen of the maral. It is also interesting to note that the isotrichid ciliates *Dasytricha ruminantium* were found in the maral and only two red deer—a mother and daughter from the Terneysky district of

Table 2. Species and forms of endobiotic ciliates found in the rumen of the Asian subspecies of the red deer *Cervus elaphus* Linnaeus, 1758—red deer *C. elaphus xanthopygus* Milne-Edwards, 1867 from Primorsky krai (samples 1–10) and *C. elaphus sibiricus* Severtzov, 1873 from the Altai Republic (sample 11)

Genus, species, form	Samples										
	1	2	3	4	5	6	7	8	9	10	11
***Entodinium* Stein, 1859**											
E. caudatum Stein, 1859	+++	+++	++	++	++	+	+	+	++	+ +	++
E. dubardi Buisson, 1923	++	++	++	++	++	++	++	+	++	++	++
E. exiguum Dogiel, 1925	+	+	++	++	+	+	+	+	++	+	++
E. furca Cunha, 1914	–	+	+	+	+	+	+	+	+	+	–
E. furca f. *dilobum* Dogiel, 1927	–	+	+	++	++	++	+	+	+	+	–
E. furca f. *furca* Dogiel, 1927	–	–	+	–	–	–	–	–	–	+	–
E. longinucleatum Dogiel, 1925	–	+	–	–	–	+	–	+	+	–	–
E. nanellum Dogiel, 1922	+	–	+	++	+	++	++	+	++	–	++
E. simplex Dogiel, 1927	++	+	+	–	–	++	++	+++	–	++	++
E. wapiti Dehority, 1995	–	+	++	++	++	+	+++	–	+	+	++
***Eudiplodinium* Dogiel, 1927**											
E. maggii (Fiorentini, 1889)	–	+	++	+	+	+	++	+	++	+	++
E. neglectum (Dogiel, 1925)	+	+	+	+	+	+	+	+	+	+	+
E. neglectum f. *bovis* (Dogiel, 1925)	+	++	++	–	–	++	+	++	++	–	++
E. neglectum f. *impalae* (Dogiel, 1925)	–	++	–	++	++	+	++	++	–	–	++
E. neglectum f. *spectabile* (Dogiel, 1925)	+	+	++	++	++	+	++	+	++	+	++
***Enoploplastron* Kofoid & MacLennan, 1932**											
E. triloricatum (Dogiel, 1925)	–	–	–	–	–	–	–	–	–	–	++
***Epidinium* Crawley, 1923**	+	+	+	+	+	+	+	+	+	+	+
E. ecaudatum (Fiorentini, 1889)	+++	+++	+++	++	+++	+++	++	++	+++	+++	+++
E. caudatum (Fiorentini, 1889)	+	++	+	+	+	++	–	+	+	+	++
***Dasytricha* Schuberg, 1888**											
D. ruminantium Schuberg, 1888	–	–	–	+	+	–	–	–	–	–	++
The number of ciliates in 1 mL of rumen contents	137580	420380	122290	160510	145220	359230	290440	129940	267510	198730	191080

Number of ciliates in 1 mL of sample: + single cells, ++ more than 100 cells, +++ more than 1000 cells, dash—ciliates of this species were not detected.

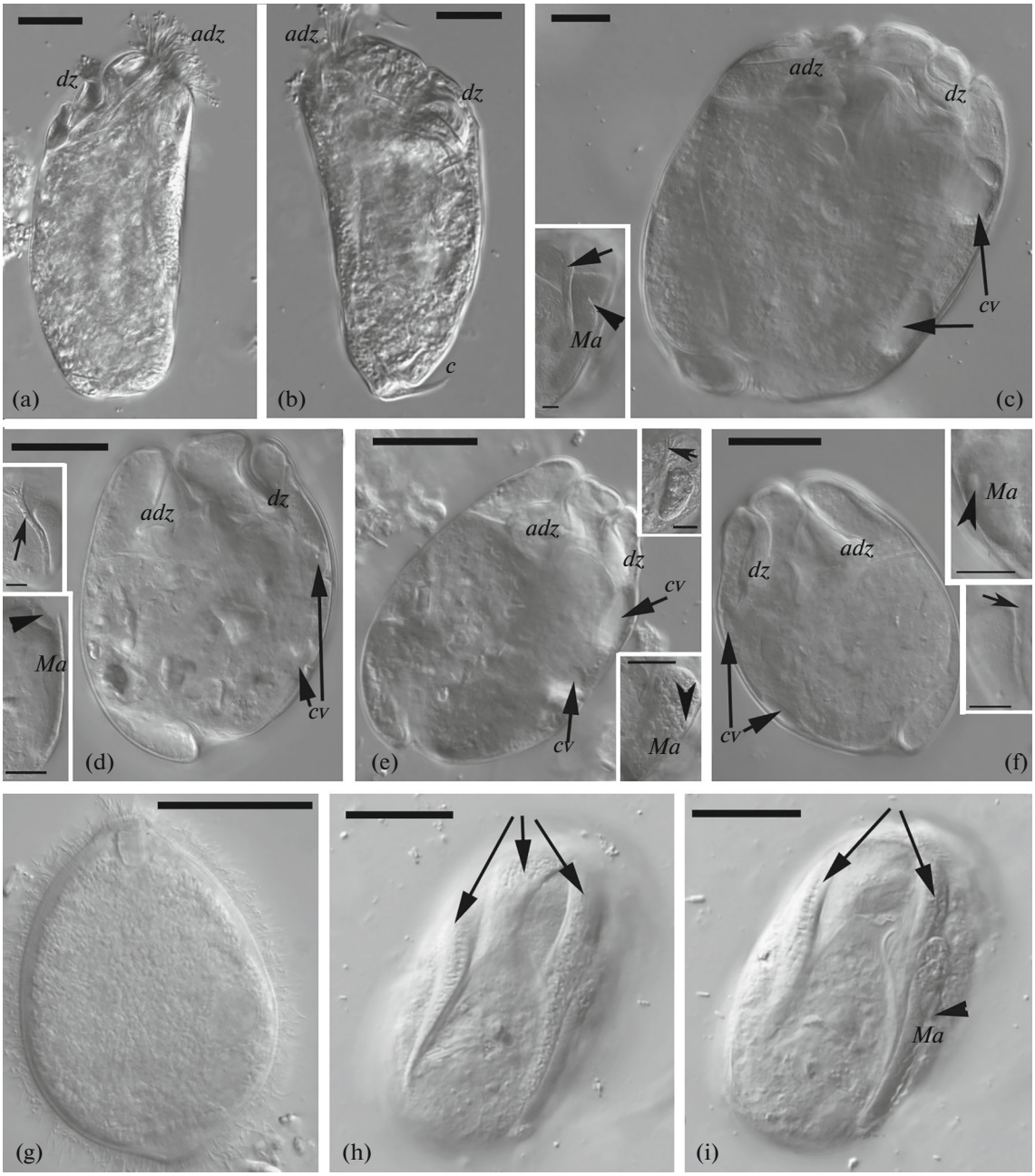

Fig. 1. Endobiotic ciliates from the rumen of the red deer *Cervus elaphus*: (a) *Epidinium ecaudatum*; (b) *E. caudatum*; (c) *Eudiplodinium maggii*; (d) *E. neglectum* f. *impalae*; (e) *E. neglectum* f. *bovis*; (f) *E. neglectum* f. *spectabile*; (g) *Dasytricha ruminantium*; (h, i) *Enoploplastron triloricatum*. *dz*—dorsal zone of membranellae, *adz*—adoral zone of membranellae, *c*—caudal spine, *cv*—contractile vacuole, *Ma*—macronucleus, arrowhead—micronucleus, arrow—skeletal plate. Light microscopy, DIC. Scale bar 20 μm; in insets, 10 μm.

Primorye. Moreover, the species composition of the endobiotic ciliates in these two individuals turned out to be identical, which is explained by the peculiarities of the transmission of endobionts in a series of generations of ruminants (Kornilova, 2004a).

The fauna of endobiotic ciliates of the rumen of red deer in Asia has not been studied before. Studies on ciliates from deer of this species from other geographic regions have been previously conducted in several European countries and in New Zealand and Australia (Dehority, 1997). There is also a single publication devoted to the study of the endobiont fauna of wapiti (Dehority, 1995). This deer has long been considered a subspecies of red deer and only relatively recently was it identified as a separate species *Cervus canadensis* (Ludt et al., 2004; Mizzi et al., 2017). The results of the

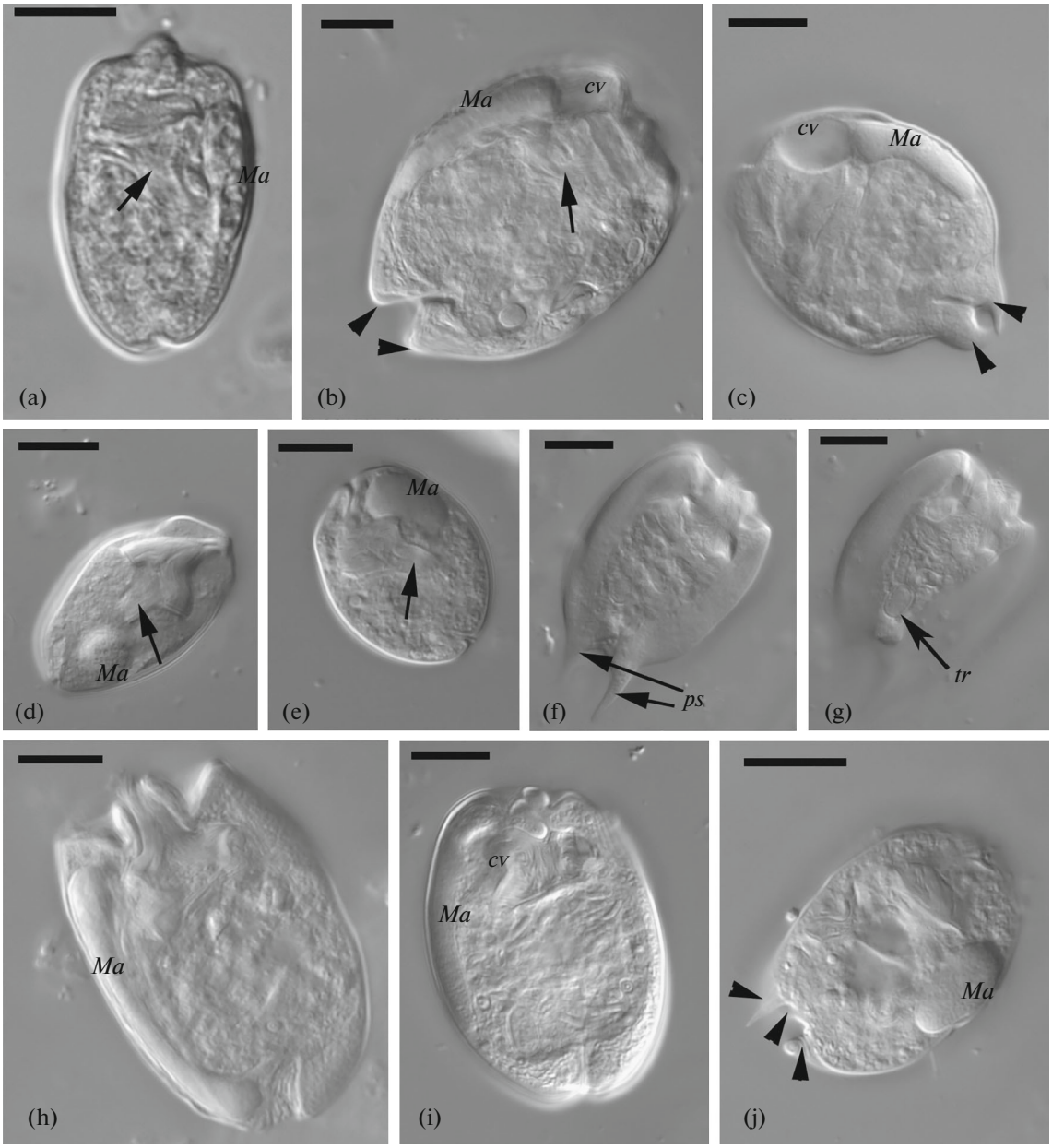

Fig. 2. *Entodinium* ciliates from the rumen of the red deer *Cervus elaphus*: (a) *Entodinium simplex*; (b) *E. furca* f. *dilobum*; (c) *E. furca* f. *furca*; (d) *E. exiguum*; (e) *E. nanellum*; (f, g) *E. wapiti*; (h) *E. longinucleatum*; (i) *E. dubardi*; (j) *E. caudatum*. *Ma*—macronucleus, *cv*—contractile vacuole, *tr*—triangular rib on the cell surface, *ps*—posterior spines, arrow—cytopharynx, arrowhead—posterior lobes. Light microscopy, DIC. Scale bar 10 μm.

latest studies suggest that the red deer and maral are close to the wapiti, possibly combining them into *C. canadensis* (Mackiewicz et al., 2022), but further research in this area is needed to conduct a full taxonomic revision of the genus *Elaphus*. In this regard, in our work, we consider the red deer and maral as subspecies of the red deer *C. elaphus*. Table 4 provides summary data on the occurrence of ciliates of different genera in the rumen of deer from different geographic regions.

According to current concepts, the structure of endobiotic ciliates communities in the vertebrate digestive tract is determined by the combined effect of several factors (Newbold et al., 2015). Endobiont ciliates are characterized by a certain specificity in relation to the host, which arose as a result of coevolution of partners in the symbiotic system. At the same time, the species composition of endobionts is somewhat influenced by the feeding and lifestyle characteristics of the host, including the level of herd behavior. And, finally, horizontal nonspecific transfer of endobionts

Table 3. Morphometry of *Entodinium wapiti* (without taking into account caudal projections) from the rumen of (1) red deer, (2) Altai maral, and (3) wapiti

Host animal	Length (min–max, μm)	Mean length, μm	SD	CV, %	Width, (min–max, μm)	Mean width, μm	SD	CV, %	Length to width ratio (min–max)	Length to width ratio (mean)	SD	CV, %
1	25.0–40.0	34.4	2.6	7.5	20.0–30.5	24.1	2.1	8.7	1.20–1.60	1.42	0.24	16.9
2	34.0–37.5	35.8	0.9	2.5	27.5–32.5	29.2	1.1	3.8	1.10–1.30	1.22	0.09	7.4
3	21.0–34.0	28.2	3.6	12.8	21.0–28.0	25.0	2.3	9.2	1.00–1.28	1.13	0.11	9.7

1—red deer no. 7; 2—maral no. 11; 3—wapiti (according to Dehority, 1995). The number of measured cells in red deer and maral—25 each; in wapiti—10.

between different host species is possible in close contact. The composition of the endobiont fauna of Asian subspecies of red deer (by ciliate genera) is more similar to that of wapiti, which may indicate their fairly close relationship. It should be emphasized once again that, according to the available data, the ciliate species *E. wapiti* was found only in these two host species. The similarity in the species composition of ciliate communities in deer living in the same area may be associated, among other things, with the possibility of close interaction between individual family groups of hosts. Marals in the Altai are characterized by seasonal migrations of up to 50 km in length, associated with the change of winter and summer pastures (Sobansky, 2008). In Primorsky krai, both sedentary and migratory individuals are found among the red deer. The winter habitats of migratory deer are located 10–45 km from the summer ones (Myslenkov and Mikvel, 2003). In all three sampling areas, red deer visit natural salt licks for most of the year, especially in summer (Panichev et al., 2018, 2022). The salt licks are characterized by a concentration of red deer, with up to 15 individuals present at a time. They actively communicate with each other, taking turns licking the soil from the same "licks"—depressions eaten out in the areas most attractive for lithophagy. On the salt licks, red deer contact not only each other but also other deer species: elk *Alces alces* (Linnaeus, 1758) and Siberian roe deer *Capreolus pygargus* (Pallas, 1771), as well as sika deer *Cervus nippon* Temminck, 1838 for the Olginsky district of Primorsky krai (Seryodkin and Panichev, 2022). The prevalence of species of the genus *Entodinium* in endobiont communities and a rather low level of species diversity of ciliates have been noted for many species of wild ruminants, which is usually associated with the dietary characteristics or lifestyle of the host (including low gregariousness) (Williams and Coleman, 1992; Clauss et al., 2011; Kornilova et al., 2021). Thus, it has been suggested that such a structure of ciliate communities is characteristic of hosts that feed mainly on twigs, although no direct relationship between the host diet and the species composition of endobionts has been shown (Clauss et al., 2011). In this regard, it should be noted that both the red deer and the maral feed mainly on herbaceous vegetation and leaves of tree species in the summer and switch to woody-twig food in the winter (Bromley and Kucherenko, 1983; Sobansky, 2008). In the fall, the red deer often consumes oak acorns and Korean pine nuts (Sheremetyev and Prokopenko, 2005).

According to the assumption of Dogiel (1946) about the phylogeny of ruminant ciliates, the evolutionary formation of the *Epidinium–Eudiplodinium* branches occurred in the common ancestor of deer and bovids. At the same time, such genera as *Ostracodinium*, *Polyplastron*, and *Ophryoscolex* were formed later in bovid hosts. In this regard, it is interesting to note that domesticated deer, compared to wild individuals, generally have a greater diversity of endobiont ciliates (Table 4). It is possible that the fauna of endobiotic ciliates of European and Australian deer was enriched owing to closer and more frequent contacts with local species of bovids and their domesticated forms.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

Table 4. Occurrence of representatives of various genera of endobiotic ciliates in the rumen of the red deer *Cervus elaphus* from different locations

No.	Genus	Region			
		1	2	3	4
1	*Entodinium* Stein, 1859	100	88	100	100
2	*Diplodinium* Schuberg, 1888	–	75	58	–
3	*Eudiplodinium* Dogiel, 1927	100	88	100	100
4	*Ostracodinium* Dogiel, 1927	–	13	–	–
5	*Metadinium* Awerinzew & Mutafowa, 1914	–	13	33	50
6	*Enoploplastron* Kofoid & MacLennan, 1932	9	13	–	50
7	*Elytroplastron* Kofoid & MacLennan, 1932	–	25	33	–
8	*Epidinium* Crawley, 1923	100	75	25	50
9	*Ophryoscolex* Stein, 1859	–	13	–	–
10	*Isotricha* Stein, 1859	–	50	67	–
11	*Dasytricha* Schuberg, 1888	27	38	–	–

1—subspecies of red deer (red deer and maral) from Asia, 2—wild and domesticated red deer from Europe (according to Dehority, 1997), 3—red deer (domesticated) from Australia (Dehority, 1997), 4—wapiti from Canada (Dehority, 1995). Shown is the ratio (%) of positive samples to the total number of samples; dash—representatives of the given genus of infusorians were not detected.

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