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Local Epizootics Caused by Teleomorphic Cordycipitoid Fungi (*Ascomycota*: *Hypocreales*) in Populations of Forest Lepidopterans and Sawflies of the Summer–Autumn Complex in Siberia

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Abstract—Unique epizootic loci were revealed in the summer–autumn complex of the multispecies communities of forest lepidopterans and sawflies in two regions of Novosibirsk oblast and in the Baikal region at the border of the Buryat Republic and Irkutsk oblast. Mass insect mortality was caused by two species of cordycipitoid fungi: *Cordyceps militaris* and *Cordyceps* sp. At least 30 species from 7 families of millers (*Macroheterocera*) and sawflies from the family *Cimbicidae* were found to be *C. militaris* hosts. Lepidopterans from the family *Thyatiridae* are the hosts of the second species, *Cordyceps* sp. Total mortality was noted for the condition close to optimal for pupation, i.e., in places of mass pupa accumulation. It may be assumed on the basis of the results of the laboratory experiments that, under natural conditions, host insects may be infected by ascospores and conidia at the anamorphic stage.

Keywords: entomoparasitic cordycipitoid fungi, *Cordyceps militaris*, *Cordyceps* sp., multispecies communities of lepidopterans and sawflies, Siberia.

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Wide application of molecular genetic methods in the taxonomy of fungi makes it possible to find relationships within the phylogenetic tree of ascomycetes (the division Ascomycota) between many anamorphic species, which have completely lost the sexual stage (teleomorph) in its cycle of development, and the species forming it. The former opposition between the ascomycetous and anamorphic fungi (class *Deuteromycetes* ⟶ division *Deuteromycota* ⟶ the formal macrotaxon Anamorphic Fungi) is therefore presently considered almost as a vestige of the past from the point of view of cladistic mycosystematics. However, there is a different plane of analysis, the synecological one, in which this opposition inevitably suggests itself.

Ascomycetous cordycipitoid fungi are one of the interesting groups where many examples occur confirming this opinion. As a result of the recent revision with the use of the molecular genetic methods, the large former genus *Cordyceps* was divided into four genera, which are now classified within three different families of the order *Hypocreales*: *Metacordyceps* (the family *Clavicipitaceae*), *Ophiocordyceps, Elaphocordyceps* (*Ophiocordycipitaceae*), and *Cordyceps* (*Cordycipitaceae*) [1]. This is the reason why, for brevity's sake, the authors use for these fungi the designation "cordycipitoid," similar to the widely used terms agaricoid, aphyllophoroid fungi, etc. About 400 species of these fungi are parasites (pathogens) of phytophagous invertebrates, mainly insects. Importantly, in the endless flow of publications worldwide on the findings of different species of these fungi, cases of mass formation of sexual structures on dead hosts during the outbreaks of fungal epizootics in the host populations are very rarely reported, even under the optimum conditions of tropical rainforests and/or mountainous regions where teleomorph formation is a far more frequent phenomenon than on flatlands in the temperate zone [2, 3]. In contrast, the precedents of a significant reduction in the population of invertebrates as a result of epizootic infection by the anamorphs of many species with the formation of conidial infections on host cadavers have been described in the literature since the 19th century. It is due to the observation of these impressive facts that some representatives of this group of fungi have been long studied from the applied point of view as potential agents of biocontrol of phytophagous invertebrates. They can be exemplified by the cosmopolite anamorphic species such as *Beauveria bassiana* (Bals.-Criv.) Vuill., *B. brongniartii* (Sacc.) Petch, *Isaria farinosa* (Holmsk.) Fr., *Lecani-*

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cillium lecanii (Zimm.) Zare et W. Gams, *Metarhizium anisopliae* (Metschn.) Sorokin, and *Pochonia chlamydosporia* (Goddard) Zare et W. Gams. However, at present these designations are increasingly more often used in the taxonomy literature as synonyms, whereas priority is given to the teleomorph names. The latter are known merely by single findings in some local points (mainly in mountainous regions in the south of China, in Japan, in the tropical forests of Ecuador, and other exotic parts of the planet). Thus, it is reasonable to speak, first, about the endemicity of the teleomorphs of these species (and many others) and, second, about their teleomorph formation as an atavistic process. There is no denying that, objectively, there exists a tendency for the role of the anamorphs in the trophic chains and in containing the population of phytophagous invertebrates to be ever increasing.

It is curious that, among the representatives of all the genera and families of cordycipitoid fungi, there are also many species that, on the contrary, occur on hosts only or mainly in the teleomorphic stage [4]. There are no grounds to think that these species (at least those having vast areas), contrary to the species indicated above, are becoming extinct. However, there is insufficient evidence available in the literature to form at least a vague notion of their epizootic significance. This may probably be explained by the absence of interest in the population aspects of the interrelationships between these parasites and their invertebrate hosts both in applied specialists (since such fungal species are often isolated into a culture with more difficulty, and if they are, they appear to be nontechnological) and in taxonomists who are interested in the search for taxa and their description, for which purpose it is sufficient to collect a series of specimens disregarding the extent of affection.

Importantly, the overwhelming majority of the works with descriptions of cordycipitoid fungi are characterized by vague information concerning host invertebrates, for example, found on a small spider, dead *Coleoptera* larvae, etc. While such data are certainly not very informative for generalizations, more importantly, incorrect definitions of the hosts may result in taxonomic errors, for there are many twin species with a narrow trophic specialization that are difficult to differentiate by appearance [4, 5].

It should be said that, from the authors' experience, even when specimens are found in soil or litter on half-destroyed cadavers of larvae or pupae, in many cases exact species identification of the hosts proves difficult and painstaking, but, nevertheless, possible.

The aforesaid can vividly be illustrated by *C. militaris* (L. : Fr.) Fr., the type species of the genus *Cordyceps* (the family *Cordycipitaceae*), which is widespread in many regions of the world, including Russia. Its asexual sporulation never occurs in nature on its own; conidia can only be found on poorly developed mycelium in the intersegmental folds of the insect cuticle and at the base of the stromata [4].

Despite the abundance of works in which *C. militaris* is mentioned, specific data on the trophic relations of the fungus are usually absent from them. Most often the information is limited to generalities: it occurs on caterpillars and/or pupae of *Lepidoptera* [4, 6–12, and many other works].

More specific evidence of the insects infected by *C. militaris* can only be found in separate publications. Thus, in Japan, moth caterpillars and pupae from the family of owlet moths (*Noctuidae*), sphinx moths (*Sphingidae*), geometer moths (*Geometridae*), and notodontid moths (*Notodontidae*) are known among its hosts [13–15]. Mass death of sphinx moth pupae from *C. militarus* was recorded in the forest ecosystems in the south of Primorskii krai [5]. Evlakhova and Shvetsova [16] cite the caterpillars of the poplar hawk moth *Laothoe populi* L. (*Sphingidae*) and two species from the family *Lasiocampidae*, the fox moth *Macrothylacia rubi* L. and the pine moth *Dendrolimus pini* L., as the fungus hosts in the former Soviet Union (with no indication of the sites of collection of the materials). Cases of mass infection of *D. pini* caterpillars by this fungus were also noted in Poland [17]. The epizootic character of the occurrence of *C. militaris* on the caterpillars of the siberian moth *Dendrolimus sibiricus* Tschetv. in Irkutsk oblast is indicated in [18]; however, the authors did not present any specific data. In addition, on the territory of Siberia, the fungus was noted on the pupae of the redbacked cutworm *Euxoa ochrogaster* Guenee (*Noctuidae*) [19], the white satin moth *Leucoma salicis* L. (*Lymantriidae*) [18], the lime hawk moth *Mimas tiliae* L. (*Sphingidae*), and the buff-tip *Phalera bucephala* L. (*Notodontidae*) [20]. In Japan, this fungus is indicated as one of the main biotic factors containing the population of the notodontid moth *Syntypistis punctatella* Motsch. (*Notodontidae*), which is a mass defoliant of beech (*Fagus crenata*) [14, 15]. It is important to note that, in all the global data, these two works seem to be the only ones in which the epizootics caused by *M. militaris* are described in detail.

Several works have reported rare cases in which the fungus was found on the insects from other orders. Thus, in Japan, the parasitism of *C. militaris* was noted on the larvae of a sawfly from the genus *Cimbex* (*Hymenoptera: Cimbicidae*) [13]; in Germany, on the larvae of the crane fly *Tipula paludosa* Mg. (*Diptera: Tipulidae*) [21]. In the United States, the fungus was discovered on the pupae of unidentified beetles (*Coleoptera*) [7]; in Russia, in the south of Tomsk oblast on the adult of the six-toothed bark beetle *Ips sexdentatus* Boerner (*Scolytidae: Ipinae*) [22].

When in 1999–2006 the authors carried out a targeted search for the causative agents of insect mycoses in the forests in the south of Siberia, as well as in northeastern and central Altai, none of the entomoparasitic cordycipitoid fungi at the teleomorphic stage was found at all, while, among the anamorphic cordycipitoid fungi, only the usual cosmopolite species such as *B. bassiana, M. anisopliae, I. farinosa*, and *I. fumosorosea* infecting predominantly different representatives of the orders *Coleoptera, Lepidoptera, Hemiptera*, and *Diptera* were noted. Mass death of insects due to mycoses was not observed even during the outbreaks of the summer–autumn group of lepidopterans in the forest–steppe Trans-Urals region in 1999–2001.

It is interesting to note that many researchers studied entomoparsitic fungi in different regions of Siberia, but, apart from *C. militaris*, only two species of cordycipitoid fungi at the teleomorphic stage have been found on its vast territory over long years. These are *Ophiocordyceps acicularis* (Ravenel) Petch (=*Cordyceps acicularis*), on the adult of the large pine weevil *Hylobius abietis* L. (*Coleoptera: Curculionidae*) [18] and *O. unilateralis* (Tul. et C. Tul.) Petch (=*C. unilateralis*), and on ants (*Hymenoptera: Formicoidea*) [4].

Fungal epizootics in western Siberia and in Baikal region were first recorded in 2007–2008. The first reconnaissance observations made it clear that exceptionally interesting loci of mycotic infections are found in nature. First, simultaneously, the mass death of the regular comembers of one consortium, lepidopterans and sawflies of the summer–autumn ecological group, but not simply different species of phytophagous dissociated in their ecological niches, occurred. Second, simultaneously, two teleomorphic species, *C. militaris* with typical orange-red stromata (Fig. 1; 1–4) and *'Cordyceps'* sp. with a straw-colored or light yellow tint of the fruit-bearing part of the stromata, on average, slightly smaller (Fig. 1; 5–8), appeared to be the causative agents of the epizootic—but to which of the families and which genus this species should be assigned according to the most recent system of cordycipitoid fungi [1] remains to be clarified (further molecular genetic studies are expected to be carried out).

In connection with the discovery of such a nontrivial material (similar evidence from the literature is not known to the authors), the following tasks were set: (1) to determine, based on the study of the remnants of infected insects, their species identity in order to reveal the trophic specialization of both pathogens; (2) to reveal the specific features of localization of parasitic fungi in the epizootic loci and to trace their temporal dynamics; and (3) to isolate the pathogens into culture and to study the pathogenic properties of the isolates in relation to several species of the test insects.

MATERIALS AND METHODS

Field studies were carried out in August to September 2007 and in July to October 2008–2009 in Novosibirsk oblast, as well as in July 2008 on the border of the Buryat Republic and Irkutsk oblast near Baikal Lake. Methods generally accepted in forest entomology [23] were used to determine the density of insect populations and their being affected by the fungi.

Lepidopteran pupae were identified using manuals and atlases [24–26]. Pupa determinations were collated with the collections of the Zoological Museum of the Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences, Novosibirsk.

In order to isolate the fungi into culture, their fruit bodies were homogenized in sterile water; the initial suspensions were then diluted serially and applied (0.5 ml) to the surface of agarized Waksman and Sabouraud media [27] supplemented with lactic acid (0.4%). The suspension was uniformly spread over the surface with a spatula and incubated in a thermostat at 24 ± 1°C for 15–20 days.

The pathogenic properties of the isolates were studied on caterpillars of the greater wax moth *Galleria mellonella* L. (*Galleriidae*) and the apple ermine moth *Yponomeuta malinellus* Zell. (*Yponomeutidae*). The insects were treated with suspensions of three types of fungal spores: ascospores, conidia (phyaloconidia), and blastospores [28–30]. For these experiments, separate ascospore cells were removed from the stromata found in nature by homogenization in water. The fungal conidia were obtained in vitro on agarized Waksman medium or on autoclaved millet after 30 days of cultivation at 24 ± 1°C and blastospores by means of submerged cultivation in liquid Czapek medium with peptone (0.4%) on a rotor shaker (110 rpm, 20 ± 1°C, 6 days). The initial suspensions were then diluted with water to 1×10^7 spores/ml. Each variant in these experiments was staged at least in three repeats of ten caterpillars each, which were maintained with feed in glass petri dishes at 27 ± 1°C. The method of injecting the blastospores into the pupa hemocoel with a microinjector was also used (0.006 ml with a titer of 5×10^7 spores/ml), with their subsequent maintenance in moistened peat moss [31].

RESULTS

Field studies. The death of lepidopterans and sawflies simultaneously from *C. militaris* and *Cordyceps* sp. was recorded in the following three localities in the surveyed areas on the territory of Siberia.

(1) The vicinity of the town of Bolotnoe, Novosibirsk oblast, 55°41′ N, 84°22′ E, 2007–2009; birch–poplar–pine forest. The area where the fungal pathogens were discovered was approximately 30 ha. The first findings of fungi were made here at the beginning of the third decade of July; the last ones, in the first decade of October.

In 2007, *C. militaris* predominated (more than 90%). The number of insects infected by the fungus in the period of mass appearance of stromata (from the third decade of July to the end of August) was, according to the data of spot check enumeration in the woodland area, an average of 1.5 specimens/m^2, but, in

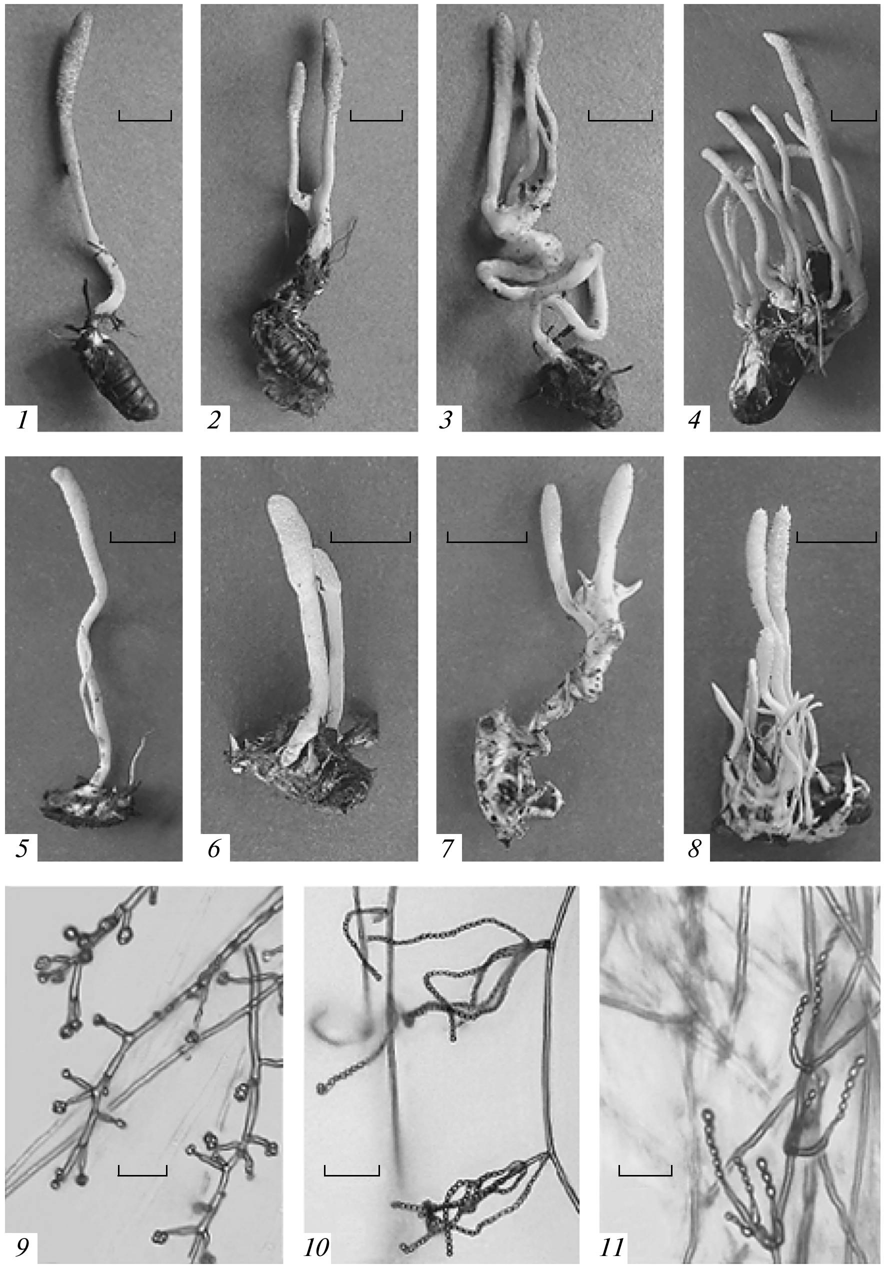

Fig. 1. Entomopathogenic fungi *C. militaris* and *Cordyceps* sp. from western Siberia (Novosibirsk oblast): *C. militaris* stromata (*1–4*), *Cordyceps* sp. stromata (*5–8*), *Lecanicillium* sp. (from *C. militaris* stromata) (*9*), *Isaria farinosa* (from *C. militaris* stromata) (*10*), and the *Paecilomyces*-like anamorph isolated from the *Cordyceps* sp. stromata (11). Scale bar: (*1–8*), 1 cm; (*9–11*), 20 μm.

some places, was as high as 20 specimens/m^2. Such aggregations were observed in places with the predominance of pendulous birch (*Betula pendula*) on the border of the forest and cleaning cutting in fallen trees overgrown with raspberry (*Rubus*) and nettle (*Urtica*), as well as at the mossy bases of the tree butts and near old stumps. In the areas with predominance of Scotch pines (*Pinus silvestris*) and poplars (*Populus* sp.), no such mass aggregations were found.

In 2008, both species of the fungus occurred at a ratio of 1 : 1, but the number of dead insects decreased to an average value of 0.1–0.2 specimens/m^2 and the maximal number was 5 specimens/m^2.

In 2009, the number of insects that died of mycoses decreased to 0.01 specimens/m^2 and the ratio of the species of the parasitic fungi was 3.5 : 1.

It is important to point out that, first, over several years, the population of both species of parasitic fungi was noted to decrease simultaneously with reduction in the number of caterpillars in the birch crowns and decrease in the level of defoliation of the stand of trees. Second, no live host pupae were found at all after thor-

Table 1. Changes in the number of entomoparasitic fungi, their host insects, and the level of defoliation of *Betula pendula* in the epizootic locus in the vicinity of the town of Bolotnoe

Observation years	Number of infected pupae in the litter, specimens/m^2*		Average density of live larvae at the top of the birches, specimens**	Defoliation of tress, %***	Number of live pupae in the litter, specimens/m^2****
	Average	Maximal			
2007	1.5	20	5	15–25	0
2008	0.15	5	1.5	5–10	0
2009	0.01	1	0	5	0

Notes: * Assessment in the period of mass appearance of stromata (August).
** Assessment in the period of the peak population (the end of July to August)
*** Assessment in the period of nutrition of older age larvae (the end of August).
**** Assessment of the wintering stock (September to October).

ough unearthing of the litter on the trial sites in September to October 2007–2009 (Table 1). These facts may be indicative of the highly considerable elimination of host insects by teleomorphic fungi.

(2) The vicinity of the Krinitsa railway station, Toguchinskii raion, Novosibirsk oblast; 55°04′ N, 83°32′ E, 2008–2009; willow–birch forest. The locus area was at least 5 ha, the findings of fungi were single, and the *C. militaris* to *'Cordyceps'* sp. abundance ratio was approximately 1 : 1.

(3) The vicinity of the town of Vydrino, Kabanskii raion, Buryat Republic; 51°26′ N, 104°38′ E, 2008; coniferous small-leaved forest with predominance of fir (*Abies*), spruce (*Picea*), Scotch pine (*Pinus sylvestris*), alder (*Alnus*), and birch in the valley of the Snezhnaya River on the border with Irkutsk oblast. The locus area was at least 25 ha, the average density of the insects killed by fungal infection was 0.5 specimens/m^2, and the maximal density was 5 specimens/m^2. In this locus, *C. militaris* overwhelmed *Cordyceps* sp. (the abundance ratio was approximately 99 : 1).

It is important to note that, in all the points indicated, both fungus species occurred in the same microhabitats; not infrequently, they were found nearby, at a very close distance of 20 cm. However, after the species identification of the infected pupae, their trophic relations were found to be different.

In Novosibirsk oblast, at least 30 species of higher heteroceriid lepidopterans (*Macroheterocera*) from 7 families were *C. militaris* hosts (Table 2). The overwhelming majority of these species belonged to the summer–autumn complex of phyllophagous, which are birch and willow (*Salicaceae*) consorts. The predominant infected lepidopteran species were the white prominent *Leucodonta bicoloria* D. et S. (a mass species eating out the birch foliage) and the geometrid moth *Semiothisa notata* L. (the caterpillars feed on birches and willows).

The second species, *'Cordyceps'* sp., was mainly found ($n = 104$) on the pupas of three *Thyatiridae* species the caterpillars of which feed on birth and poplar leaves *Tetheella fluctuosa* Hbn. (56%), *Ochropacha duplaris* L. (38%), and *Tethea or* D. et S. (4%)—and, very rarely, on the pupae of other lepidopterans (2%) we failed to identify.

At the larva and adult stages, the mycoses-caused mortality was recorded only in two specimens (one caterpillar in a cocoon and one moth in a cocoon).

Interestingly, half of the insects killed by *C. militaris* in the locus discovered in 2008 in the Baikal region appeared to be prepupae of the sawflies (*Hymenoptera: Cimbicidae*) (Table 3). The second fungal species, *Cordyceps* sp., was found in this woodland only in two specimens on the lepidopteran pupae, which were impossible to identify due to their severe destruction.

Laboratory investigation of the fungal cultures. When the agarized nutrient media were inoculated with the ascospores from the *C. miltaris* samples collected in Novosibirsk oblast and in the Baikal region, ten anamorph isolates with morphological characteristics completely identical to those indicated in the literature [4, 32–34] were isolated in culture. Interestingly, plating of the stromas of this fungus, along with the typical anamorph (Fig. 1; 9), often revealed also another anamorph whose characteristics clearly fit in with the diagnosis of the species *Isaria farinosa* (Fig. 1; 10). However, it is known that the latter has a *Cordyceps memorabilis* Cesati teleomorph, which rarely occurs in nature [40]. It should be noted that no unanimity of opinion exists about the generic identity of this fungus: in some sources it is referred to as *Lecanicillium* sp. [33, 34]; in others, as a representative of the genus *Paecilomyces* [35–37]. Some of the species of the latter genus having teleomorphs in the genus *Cordyceps* have recently been assigned to the genus *Isaria*, but the *C. militaris* anamorph has not been included in it [38, 39]. Thus, the *I. farinosa*–*C. militaris* association remains not quite clear; this phenomenon has long been noted by different researchers [41].

The microscopic study of the colonies of the *Cordyceps* sp. anamorph forming short conidial chains on the phyalides swollen in the basal part (Fig. 1; 11)

Table 2. Species of lepidopterans infected by *C. militaris* in Novosibirsk oblast in 2007–2008 ($n = 217$)

Taxa	% of individuals	Taxa	% of individuals
Family *Geometridae*	**32.6**	Family *Thyatiridae*	**11.1**
Semiothisa notata L.	10.0	*Tethea or* D. et S.	3.6
Parectropis similaria Hfn.	5.6	*Tetheella fluctuosa* Hbn.	3.3
Cabera pusaria L.	1.9	*Ochropacha duplaris* L.	2.4
Biston betularius L.	1.8	*Tethea ocularis* L.	1.8
Cyclophora albipunctaria Hufn.	1.4	Family *Noctuidae*	**6.8**
Lomaspilis marginata L.	1.4	*Melanchra persicariae* L.	3.2
Lycia hirtaria Clerck	1.4	*Lacanobia thalassina* Hufn.	0.5
Semiothisa alternata D. et S.	0.9	*Acronicta leporina* L.	0.5
Ectropis crepuscularia D. et S.	0.9	*Acronicta sp.*	0.5
Eupithecia sp.	0.9	Unidentified species from the subfamily *Hadeninae*	2.3
Ematurga atomaria L.	0.5		
Hypomecis punctinalis Scop.	0.5	Family *Arctiidae*	**0.5**
Unidentified species from the tribe *Cleorini*	2.7	Unidentified species	0.5
Unidentified species	2.8	Family *Sphingidae*	**0.5**
Family *Notodontidae*	**32.0**	*Mimas tiliae* L.	0.5
Leucodonta bicoloria D. et S.	25.5	Family *Lasiocampidae*	**0.5**
Ptilodon capucina L.	4.1	Unidentified species	0.5
Pheosia sp.	1.4	Unidentified *Lepidoptera*	**16.1**
Notodonta torva Hbn.	0.5		
Phalera bucephala L.	0.5		

suggests its classification as a *Paecilomyces*-like fungus in the former wide sense of this genus [42]. However, this species differs in the complex of diagnostic characteristics from those cited in this work and described later in other publications, mainly in China [43]. It is important to note that the anamorph was not observed in nature, but was only obtained in culture.

Since the population of live host insects in gradation decaying loci was very low (evidently as a result of severe fungal infection), the virulent properties of the isolates had to be studied on caterpillars of other available and convenient species of lepidopterans: the apple ermine moth (natural population) and the greater wax moth (a laboratory line), which proved to be susceptible to both fungal species.

After the apple ermine moth caterpillars were infected with *C. militaris* anamorph conidia, the mortality was 95% after 10 days. Only in 10% of the caterpillars were the bodies mummified after death and overgrown in the humid chamber with the mycelium of fungus. The rest of the cadavers were decomposed as if infected by viruses or bacteria.

The growth of the greater wax moth caterpillars infected with the ascospores and blastospores of both fungal species was insignificantly stunted, and the mortality did not exceed 20%. However, when they were treated with *C. militaris* conidia, the delay of the caterpillar growth and pupation was markedly pronounced (Fig. 1; 12). Pupation was delayed 15–25 days, the total mortality attained 45%, and the share of cadavers the surfaces of which were overgrown with mycelium in the humid chamber was 1%. When ten pupae killed as result of conidial infection were placed into moist soil, one *C. militaris* stroma with perithecia was formed one and a half months later.

Infection of the greater wax moth pupae by injecting *C. militaris* blastospores into the hemocoel caused 90% mortality of the specimens (10% of the controls were killed after the injection of sterile water). Stromata began to appear on all the dead pupae ($n = 40$) 10 days after they were placed into moistened peat moss, and 25 days later perithecia began to form on them. When two other anamorphs (*I. farinosa* associated with *C. militaris* and *Paecilomyces* sp. from the second species) were infected with blastospores, only the synnemata of these fungi formed on the dead insects.

DISCUSSION

In Siberia and in the Urals, the phyllophagous insects of the summer–autumn ecological group are of great economic importance. They have therefore served as subjects of studies of entomologists and routine monitoring of forest pathology for over 40 years.

Table 3. Insects infected with *C. militaris* in the Baikal region in 2008 ($n = 30$)

Taxa	% of specimens
Order *Hymenoptera*	**50**
Family *Cimbicidae*	**50**
Unidentified species	50
Order *Lepidoptera*	**50**
Family *Geometridae*	**23**
Hypomecis punctinalis Scop.	10
Opistograptis luteolata L.	3
Unidentified species from the tribe *Cleorini*	7
Unidentified species	3
Family *Noctuidae*	**17**
Calocasia coryli L.	10
Acronicta sp.	7
Family *Notodontidae*	**4**
Leucodonta bicoloria D. et S.	4
Family *Lymantriidae*	**3**
Unidentified species	3
Unidentified *Lepidoptera*	**3**

Interestingly, until now, viral and bacterial diseases, as well as entomophagous insects, have been indicated as the main factors restricting the populations of these insects [25, 26, 44–46]. Only in one case, in the trans-Ural region, were 25–30% of the *Ptilodon capucina* L. and *Pseudoips prasinana* L. pupae recorded as infected by the anamorphic fungus *B. bassiana* [47].

The unique nature of the loci of fungal infections revealed in Novosibirsk oblast and in the Baikal region consists in the phenomenon of simultaneous mass death of a large complex of species of phyllophagous insects (from different families and two orders) having been observed there for the first time, the death being caused simultaneously by two teleomorphic ascomycetous fungi. Above, we have already emphasized that, during the epizootics of fungal infections, it is usually possible to find cadavers of insects with anamorphs.

The larvae of the lepidopterans and sawflies of the summer–autumn group develop from July to September (predominantly on plants of the families *Betulaceae* and *Salicaceae*). The pupation of most of the larvae occurs at the end of August to the first half of September (although it usually begins early in August) in forest litter, soil, or dead fallen wood. It is here where the pupae winter, and the moths fly out already in the following June and July [25, 48].

Considering this specific feature of their biology shared by the insects of this group, their infection by the fungi most probably occurs at the end of summer and at the beginning of autumn, precisely when the larvae enter the pupation stage, and the stromata are formed after the pupa death, i.e., during the next summer period. This is evidenced by the fact that, during the mass appearance of stromata in nature (July to August), the younger- and medium-instar larvae of this group predominated in the tree crowns. Moreover, many of the collected dead pupae with stromata did not look fresh: they were dark, dull, half empty inside,

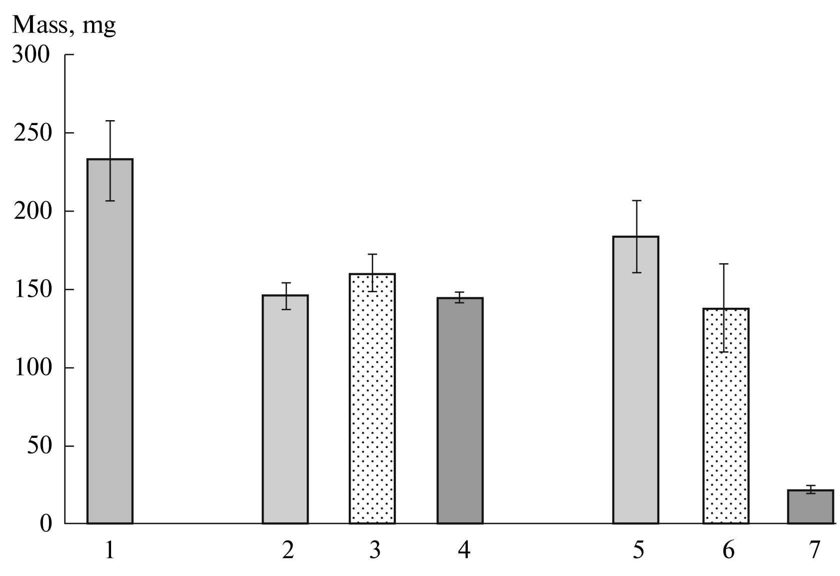

Fig. 2. Mass of the *Galleria mellonella* larvae 10 days after infection with different spores of the two species of cordycipitoid fungi. (1) control; (2–4); “*Cordyceps”* sp.: (2) ascospores, (3) blastospores, (4) conidia, (5–7), *Cordyceps militaris*: (5) ascospores, (6) blastospores, (7) conidia.

and brittle when pressed lightly. It is also known that a long life cycle with stromata formation only after wintering is typical, for example, of the fungus *Ophiocordyceps sinensis* (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones et Spatafora (the family *Ophiocordycipitaceae*; in the vast literature, this species is better known under the obsolete name *Cordyceps sinensis*) parasitizing on the larvae of swift moths (Hepialidae) [49].

What is important is that, having completed the period of feeding on the foliage, the larvae falling from the trees do not start pupating immediately, but search for the most suitable places for this purpose, where their aggregations can usually be found. It is in such microhabitats that the highest density of infected pupae (up to 20 specimens/m^2) was noted. Thus, mass death caused by mycoses occurred in places where the hosts found optimum conditions. A similar phenomenon was observed earlier in Krasnodar krai in relation to the fungus *Ophiocordyceps clavulata* (Schwein.) Petch (=*Cordyceps clavulata*) parasitizing on *Parthenolecanium corni* Bouche (*Homoptera: Coccinea*) [3].

Unfortunately, the authors failed to observe the onset of the development of fungal epizootics in the populations of the insects studied. In all probability, the peak of the phytophagous population in the vicinity of the town of Bolotnoe was in 2005 or 2006, which was evidenced by a rather high pupae density in 2007. However, they were all infected by the cordycipitoid fungi. In the subsequent years, both the lepidopterans and their pathogens decreased in number. Similar data were obtained in Japan: in the populations of the notodontid moth *Syntypistis punctatella*, the surge of the infection caused by *C. militaris* was observed at the population peak and in the period of its decreasing phase [14, 15].

Laboratory research on infecting the caterpillars of the two species of lepidopterans showed that the infection may be mediated by both ascospores and conidia. Blastospores were also found to possess a certain infectivity. However, in nature, they are only formed in the hemolymph of infected insects (in culture, only under the submerged cultivation conditions in the mass of the constantly mixed and aerated liquid media); therefore, their involvement in natural infection seems to be doubtful.

Thus, in the taiga and northern forest–steppe landscapes of Siberia, the entomoparasitic fungi *C. militaris* and *Cordyceps* sp. may act as an important factor containing the number of lepidopterans and sawflies of the summer–autumn complex. Such situations are probably not rare; however, they are of local character. Thus, according to the data of Lednev et al. (2007) and personal communications of Chernyshev (Institute of Systematics and Ecology of Animals, Russian Academy of Sciences) and Belyaev (Novosibirsk State Agrarian University), the appearance of numerous stromata of *C. militaris* was repeatedly noted in the forests of the northeastern part of Novosibirsk oblast (Moshkov and Novosibirsk raions) in the 1990s and 2000s.

In the epizootic loci, *C. militaris* is characterized by a relatively broad range of insects. Its hosts are heteroceriid lepidopterans from different families, as well as sawflies. The range of "*Cordyceps*" sp. hosts is, in all probability, limited to the lepidopterans of the family *Thyatiridae*.

The possibility of the larvae being infected by *C. militaris* conidia, which are easily formed on artificial nutrient media in a surface culture, indicates that the fungus may be of interest as a potential producer of bioinsecticides for controlling the population of lepidopterans.

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