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BEETLES (COLEOPTERA) ASSOCIATED WITH THE TINDER FUNGUS, *FOMES FOMENTARIUS* (L.) FR. (POLYPORALES: POLYPORACEAE) IN UKRAINE

Дрогваленко, О. М. Твердокрилі (Coleoptera), пов'язані з трутовиком справжнім *Fomes fomentarius* (L.) Fr. (Polyporales: Polyporaceae) в Україні. *Вісті Харківського ентомологічного товариства*. 2023. Т. XXXI, вип. 2. С. 39–48. DOI: 10.36016/KhESG-2023-31-2-4.
Трутовик *Fomes fomentarius* — один з найпоширеніших видів ксилотрофних грибів, трапляється як у природних біотопах, так і в антропогенних. Гриби мають багаторічні плодові тіла зі щільними, але не дуже твердими текстурами «тканин», вони є центром сталого комплексу міцетофільних комах, переважно жуків. Дослідження в Україні виявило на/в карпофорах 110 видів жуків із 26 родин, з яких 72 види виявилися міцетобіонтами. З'ясовано, що незалежно від місця дослідження специфічний комплекс видів залишається незмінним: Tenebrionidae — Ciidae (*Cis* spp. з групи *castaneus*) — Ciidae (*Ropalodontus* spp.) — Ptinidae (*Dorcatoma* spp.). 2 рис., 1 табл., 23 назв.
Ключові слова: міцетобіонти, міцетофаги, трутовикові гриби, плодове тіло.

Drogvalenko, O. M. Beetles (Coleoptera) associated with the tinder fungus, *Fomes fomentarius* (L.) Fr. (Polyporales: Polyporaceae) in Ukraine. *The Kharkov Entomological Society Gazette*. 2023. Vol. XXXI, iss. 2. P. 39–48. DOI: 10.36016/KhESG-2023-31-2-4.
The tinder fungus *Fomes fomentarius* is one of the most common species of xylotrophic fungi, found both in natural and anthropogenic biotopes. The fungi have perennial fruiting bodies with dense but not very hard textured 'tissues' and are the center of a stable complex of mycetophilous insects, mainly beetles. A study in Ukraine found 110 species of beetles from 26 families on/in carpophores, of which 72 species turned out to be mycetobionts. It was found that, regardless of the location of the study, the specialist species complex remains constant: Tenebrionidae — Ciidae (*Cis* spp. from the *castaneus* species group) — Ciidae (*Ropalodontus* spp.) — Ptinidae (*Dorcatoma* spp.). 2 figs, 1 tab., 23 refs.
Keywords: mycetobionts, mycetophages, bracket fungi, fruiting body.

Дрогваленко, А. Н. Жесткокрылые (Coleoptera), связанные с трутовиком настоящим *Fomes fomentarius* (L.) Fr. (Polyporales: Polyporaceae) в Украине. *Известия Харьковского энтомологического общества*. 2023. Т. XXXI, вып. 2. С. 39–48. DOI: 10.36016/KhESG-2023-31-2-4.
Трутовик *Fomes fomentarius* — один из самых распространённых видов ксилотрофных грибов, встречается как в природных биотопах, так и в антропогенных. Грибы имеют многолетние плодовые тела с плотными, но не очень жёсткими текстурами «тканей» и являются центром устойчивого комплекса мицетофильных насекомых, преимущественно жуков. Исследование в Украине выявило на/в карпофорах 110 видов жуков из 26 семейств, из которых 72 вида оказались мицетобионтами. Выяснено, что независимо от места исследования специфичный комплекс видов остаётся неизменным: Tenebrionidae — Ciidae (*Cis* spp. из группы *castaneus*) — Ciidae (*Ropalodontus* spp.) — Ptinidae (*Dorcatoma* spp.). 2 рис., 1 табл., 23 назв.
Ключевые слова: мицетобионты, мицетофаги, трутовые грибы, плодовое тело.

I n t r o d u c t i o n . Tinder fungi are an important and integral part of the forest biocenoses. In the natural forests, they play a primary role in the destruction of dead wood, returning the elements to the cycle. They can parasitize living trees, providing the habitat and food for many animals, mostly insects. Complexes of mycetobiont insects, found on carpophores of macromycetes, play an important role in the chain of reductants of forest ecosystems, mechanically destroying basidiomes and dispersing fungal spores. Most of the inhabitants of fruiting bodies are mycetophagous. The rest of the mycetobionts are predators. Random visitors — mycetoxenes, — also regularly occur on the fruiting bodies. Tinder fungi from the various systematic groups have different species compositions of mycetobiont complexes due to differences in the chemical composition of fruiting bodies, the density of 'tissues' of carpophores, the term of existence, etc. In several countries, many researchers have paid attention to these specific insects as well as to the insect complexes in general (Jonsell, Nordlander, 1995; Rukke, 2002; Schigel, 2002, 2009, 2011a, 2011b; Tatarinova, Nikitsky, Dolgin, 2008; Jonsell *et al.*, 2016; Andrési, Tuba, 2018; Sazhnev, Mironova, 2019). Some studies of these complexes were also conducted in Ukraine (Drogvalenko, 1997a, 1997b, 2007, 2016; Mateleshko, 2005; Mateleshko, Lovas, 2010; Diedus *et al.*, 2022). Our current study of Ukrainian mycetobionts has lasted since 1991.

One of the most common species of xylotrophic fungi in Ukraine is the tinder fungus, *Fomes fomentarius* (L.) Fr. This species of fungi belongs to the class Agaricomycetes, order Polyporales, and has a Holarctic distribution. Its fruiting bodies are perennial, sessile, first rounded and then characteristically hoof-

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shaped. The stipe is absent; the carpophore is attached to the tree trunk mainly by its upper central part. The tissues of the carpophore are dense, soft, resembling a cork, covered with a thick and very dense crust on the top. The presence of such a crust distinguishes this species from sometimes similar carpophores of tinders from the genera *Fomitopsis*, *Inonotus*, *Phellinus*, and *Ganoderma*. The tubes of hymenophore are quite narrow. Basidioms can be very large: up to 40 cm in diameter and 20 cm thick. It inhabits many deciduous tree species. The fungus is mainly a saprophyte but on the weakened trees it can also be a parasite at first.

Materials and methods. The data were obtained as part of a comprehensive of the mycetophilous fauna of Ukraine through original research and collaboration with colleagues. Over 10,000 specimens were predominantly collected in Ukraine in Kharkiv, Donetsk, Luhansk, Lviv, Zakarpattia, Ternopil, Chernihiv, Chernivtsi regions, and Autonomous Republic of Crimea in the period from 1992–2020 during field seasons from April to October (Fig. 1). The study did not involve the use of traps. Additional data on common species were gathered from UkrBIN (2023) and iNaturalist (2023) communities. For the Supplementary dataset see Drogvalenko (2023).

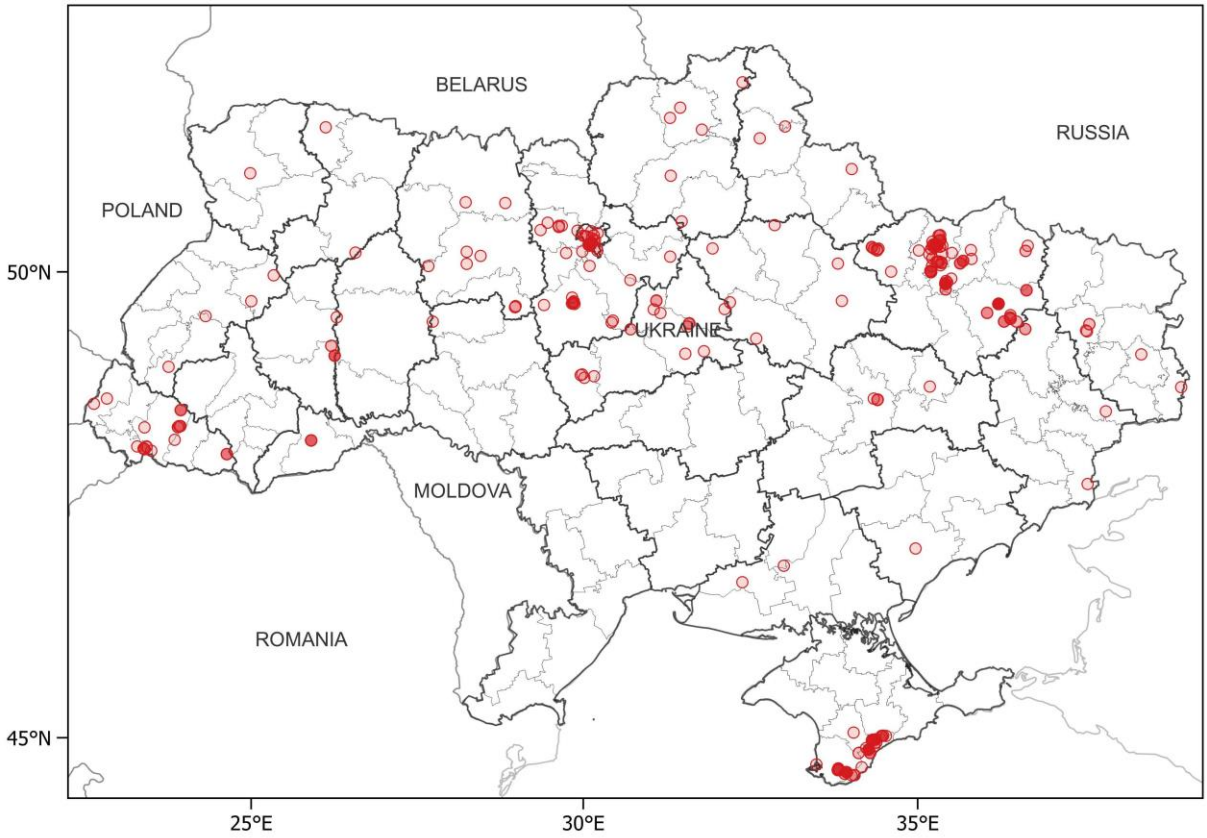

Fig. 1. Occurrences of beetles associated with *F. fomentarius* (data are based on specimen collections and photo observations from UkrBIN.com and iNaturalist.org): pink dots indicate location where beetles have been found; overlapping dots gives a brighter color — this means more finds in a given location.

The beetles and their larvae were collected both directly from fruiting bodies *in situ* and extracted from the inner tissues of carpophores after their destruction in the laboratory. The adults of some species were reared from larvae for secure identification. The vast majority of collected material is stored in the collection of the Museum of Nature of the V. N. Karazin Kharkiv National University (KUMN). The term ‘tissues’ of the fruiting body of the fungus refers to the non-genuine tissue of which the carpophores are composed, and this term will not be used in quotation marks hereafter.

Terminology and abbreviations: We delineated the following categories for this study regarding mycetobiont species based on their abundance and frequency:

Rare species: fewer than 10 specimens collected on tinder fungus per field season.

Common species: 10 to 20 specimens collected on tinder fungus per field season.

Dominant species: over 20 specimens collected on tinder fungus per field season.

Regarding the delimitation of specificity to the tinder fungus, the following categories were established:

Accidental visitor (AM): a species that lacks trophic relationships with both the tinder fungus and other mycetobionts. These insects do not utilize carpophores as a medium for larval development.

Facultative mycetobiont (FM): a species that lacks obligatory trophic relationships with both the tinder fungus and other mycetobionts. Their larvae often develop in alternative conditions.

Obligate mycetobiont (OM): a species that has obligatory trophic relationships with the tinder fungus or other mycetobionts and utilizes carpophores as a medium for larval development, *e. g.* under the bark of dead trees, in fermented tree sap, *etc*.

Results and discussions. 110 species of Coleoptera from 26 families are registered on the fruiting bodies of *F. fomentarius*. A substantial part of them were accidental visitors. The association with carpophores was established for 92 species of mycetobiont beetles: 42 species of obligate mycetobionts (45.6%) and 50 facultative mycetobionts (54.3%). 80 of them were the obligate mycetophages (include myxomycetophages) (86.9%), 6 — facultative mycetophages (6.5%), 5 — predators (5.4%), and 1 were saprophages (1.1%). The data about species composition of Coleoptera complexes from the fruiting bodies of *F. fomentarius*, their trophic relationships, and finding frequencies are given in Table 1 and Fig. 2.

Table 1. Ecological and faunal characteristics of mycetobiont beetles from carpophores *F. fomentarius*

Species	Connection with carpophores *F. fomentarius*	Trophic specialization	Relative abundance
Biphyllidae			
Biphyllus lunatus (Fabricius, 1787)	facultative mycetobiont	mycetophage	+
Diplocoelus fagi (Chevrolat, 1837)	facultative mycetobiont	mycetophage	+
Bothrideridae			
Bothrideres bipunctatus (Gmelin, 1790)	accidental visitor	mycetophage?	+
Carabidae			
Agonum viridicupreum (Goeze, 1777)	accidental visitor	predator	+
Cerylonidae			
Cerylon histeroides (Fabricius, 1792)	facultative mycetobiont	myxomycetophage	+
Ciidae			
Cis bidentatus (Olivier, 1790)	obligate mycetobiont	mycetophage	+
Cis castaneus (Herbst, 1793)	obligate mycetobiont	mycetophage	+++
Cis comptus Gyllenhal, 1827	facultative mycetobiont	mycetophage	++
Cis fagi Waltl, 1839	facultative mycetobiont	mycetophage	+
Cis fusciclavis Nyholm, 1953	obligate mycetobiont	mycetophage	++
Cis glabratus Mellié, 1849	facultative mycetobiont	mycetophage	+
Cis jacquemartii Mellié, 1849	obligate mycetobiont	mycetophage	+++
Cis lineatocribratus Mellié, 1849	obligate mycetobiont	mycetophage	+
Cis matchanus Reitter, 1915	obligate mycetobiont	mycetophage	+
Cis micans (Fabricius, 1792)	facultative mycetobiont	mycetophage	+
Cis submicans Abeille de Perrin, 1874	facultative mycetobiont	mycetophage	+
Ennearthron cornutum (Gyllenhal, 1827)	obligate mycetobiont	mycetophage	+++
Ennearthron palmi Lohse, 1966	facultative mycetobiont	mycetophage	+
Octotemnus glabriculus (Gyllenhal, 1827)	facultative mycetobiont	mycetophage	+
Octotemnus rugosopunctatus Drogvalenko, 2002*	facultative mycetobiont	mycetophage	+
Orthocis alni (Gyllenhal, 1813)	accidental visitor	mycetophage	+
Ropalodontus baudueri (Abeille de Perrin, 1874)	obligate mycetobiont	mycetophage	+++
Ropalodontus perforatus (Gyllenhal, 1813)	obligate mycetobiont	mycetophage	+++
Ropalodontus strandi Lohse, 1969	obligate mycetobiont	mycetophage	+++
Sulcacis fronticornis (Panzer, 1805)	obligate mycetobiont	mycetophage	+
Xylographus bostrichoides (Dufour, 1843)	obligate mycetobiont	mycetophage	++
Coccinellidae			
Halyzia sedecimguttata (Linnaeus, 1758)	accidental visitor	predator, mycetophage	+
Corylophidae			
Arthrolips obscura (C. R. Sahlberg, 1833)	obligate mycetobiont	mycetophage	+++
Orthoperus corticalis (Redtenbacher, 1849)	facultative mycetobiont	mycetophage	++
Cryptophagidae			
Atomaria elongatula Erichson, 1846	facultative mycetobiont	mycetophage	+
Atomaria umbrina (Gyllenhal, 1827)	facultative mycetobiont	mycetophage	+
Cryptophagus labilis Erichson, 1846	facultative mycetobiont	mycetophage	+
Micrambe bimaculatus (Panzer, 1798)	facultative mycetobiont	mycetophage	+
Pteryngium crenatum (Fabricius, 1798)	facultative mycetobiont	mycetophage	+

Continuation of Table 1

Species	Connection with carpophores *F. fomentarius*	Trophic specialization	Relative abundance
Erotylidae			
Dacne bipustulata (Thunberg, 1781)	obligate mycetobiont	mycetophage	+++
Triplax russica (Linnaeus, 1758)	obligate mycetobiont	mycetophage	++
Geotrupidae			
Geotrupes stercorarius (Linnaeus, 1758)	accidental visitor	saprophage	+
Histeridae			
Acritus minutus (Herbst, 1791)	accidental visitor	predator, saprophage	+
Paromalus flavicornis (Herbst, 1791)	accidental visitor	predator, saprophage	+
Hydrophilidae			
Cercyon lateralis (Marsham, 1802)	accidental visitor	saprophage	+
Laemophloeidae			
Cryptolestes pusillus (Schoenherr, 1817)	accidental visitor	mycetophage	+
Placonotus testaceus (Fabricius, 1787)	accidental visitor	mycetophage	+
Latridiidae			
Corticaria lapponica (Zetterstedt, 1838)	facultative mycetobiont	mycetophage	++
Corticaria serrata (Paykull, 1798)	facultative mycetobiont	mycetophage	++
Corticarina minuta (Fabricius, 1792)	accidental visitor	mycetophage	+
Enicmus brevicornis (Mannerheim, 1844)	obligate mycetobiont	mycetophage	+++
Enicmus rugosus (Herbst, 1793)	obligate mycetobiont	mycetophage, myxomycetophage	+++
Enicmus varendorffi Reitter, 1903*	obligate mycetobiont	mycetophage	++
Latridius brevicollis (C. G. Thomson, 1868)	obligate mycetobiont	mycetophage	+++
Latridius consimilis (Mannerheim, 1844)	facultative mycetobiont	mycetophage	+
Latridius hirtus Gyllenhal, 1827	facultative mycetobiont	mycetophage	++
Latridius minutus (Linnaeus, 1767)	facultative mycetobiont	mycetophage	++
Latridius porcatus (Herbst, 1793)	facultative mycetobiont	mycetophage	+
Melanophthalma suturalis (Mannerheim, 1844)	accidental visitor	mycetophage	+
Stephostethus caucasicus (Mannerheim, 1844)	accidental visitor	mycetophage	+
Leiodidae			
Agathidium rotundatum (Gyllenhal, 1827)	facultative mycetobiont	myxomycetophage	+
Agathidium varians Beck, 1817	facultative mycetobiont	myxomycetophage	+
Anisotoma axillaris Gyllenhal, 1810	facultative mycetobiont	myxomycetophage	+
Anisotoma humeralis (Herbst, 1791)	obligate mycetobiont	mycetophage, myxomycetophage	++
Anisotoma orbicularis (Herbst, 1791)	facultative mycetobiont	myxomycetophage	+
Catops fuliginosus Erichson, 1837	accidental visitor	necrophage	+
Lophocateridae			
Grynocharis oblonga (Linnaeus, 1758)	facultative mycetobiont	facultative mycetophage	+
Grynocharis pubescens Erichson, 1844*	facultative mycetobiont	facultative mycetophage	+
Monotomidae			
Rhizophagus bipustulatus (Fabricius, 1792)	facultative mycetobiont	facultative mycetophage	+
Mycetaeidae			
Mycetaea subterranea (Fabricius, 1801)	facultative mycetobiont	mycetophage	+
Mycetophagidae			
Litargus balteatus LeConte, 1856	facultative mycetobiont	mycetophage	+
Litargus connexus (Geoffroy, 1785)	obligate mycetobiont	mycetophage	++
Mycetophagus ciscaucasicus (Semenov, 1899)*	obligate mycetobiont	mycetophage	++
Mycetophagus multipunctatus Fabricius, 1792	facultative mycetobiont	mycetophage	+
Mycetophagus piceus (Fabricius, 1777)	obligate mycetobiont	mycetophage	+++
Mycetophagus quadriguttatus Ph. W. Müller, 1821	facultative mycetobiont	mycetophage	+
Triphyllus bicolor (Fabricius, 1777)	facultative mycetobiont	mycetophage	+
Nitidulidae			
Epuraea biguttata (Thunberg, 1784)	facultative mycetobiont	facultative mycetophage	+
Epuraea terminalis (Mannerheim, 1843)	facultative mycetobiont	facultative mycetophage	+
Ptinidae			
Dorcatoma dresdensis Herbst, 1792	obligate mycetobiont	mycetophage	+++
Dorcatoma minor Zahradník, 1993	obligate mycetobiont	mycetophage	+
Dorcatoma robusta A. Strand, 1938	obligate mycetobiont	mycetophage	+++
Ptinomorphus imperialis (Linnaeus, 1767)	accidental visitor	xylophage	+
Salpingidae			
Salpingus planirostris (Fabricius, 1787)	facultative mycetobiont	mycetophage	+

Continuation of Table 1

Species	Connection with carpophores *F. fomentarius*	Trophic specialization	Relative abundance
Silvanidae			
Ahasverus advena (Waltl, 1834)	accidental visitor	mycetophage	+
Silvanus unidentatus (Olivier, 1790)	accidental visitor	mycetophage	+
Uleiota planatus (Linnaeus, 1761)	accidental visitor	mycetophage	+
Sphindidae			
Aspidiphorus lareyniei Jacquelin du Val, 1859	obligate mycetobiont	mycetophage, myxomycetophage	+++
Aspidiphorus orbiculatus (Gyllenhal, 1808)	obligate mycetobiont	mycetophage, myxomycetophage	+++
Staphylinidae			
Anthobium atrocephalum (Gyllenhal, 1827)	accidental visitor	predator	+
Atheta gagatina (Baudi di Selve, 1848)	facultative mycetobiont	predator	++
Atheta liturata (Stephens, 1832)	facultative mycetobiont	predator	+++
Bolitochara pulchra (Gravenhorst, 1806)	facultative mycetobiont	predator	+++
Dinaraea aequata (Erichson, 1837)	accidental visitor	predator	+
Gyrophaena affinis Mannerheim, 1830	obligate mycetobiont	mycetophage	+++
Gyrophaena joyi Wendeler, 1924	obligate mycetobiont	mycetophage	+++
Gyrophaena manca Erichson, 1839	obligate mycetobiont	mycetophage	+++
Gyrophaena strictula Erichson, 1839	obligate mycetobiont	mycetophage	+++
Lordithon thoracicus (Fabricius,1777)	obligate mycetobiont	predator	++
Scaphisoma agaricinum (Linnaeus, 1758)	obligate mycetobiont	mycetophage	+++
Scaphisoma balcanicum Tamanini, 1954	obligate mycetobiont	mycetophage	+
Scaphisoma boleti (Panzer, 1793)	obligate mycetobiont	mycetophage	+++
Scaphisoma boreale Lundblad, 1952	obligate mycetobiont	mycetophage	+
Scaphisoma inopinatum Löbl, 1967	obligate mycetobiont	mycetophage	++
Scaphisoma subalpinum Reitter, 1880	obligate mycetobiont	mycetophage	+
Sepedophilus bipustulatus (Gravenhorst, 1802)	obligate mycetobiont	predator	+
Sepedophilus immaculatus (Stephens, 1832)	accidental visitor	predator	+
Tenebrionidae			
Alphitophagus bifasciatus (Say, 1824)	facultative mycetobiont	saprophage, mycetophage	+
Bolitophagus reticulatus (Linnaeus, 1767)	obligate mycetobiont	mycetophage	+++
Corticeus bicolor (Olivier, 1790)	facultative mycetobiont	facultative mycetophage	+
Diaperis boleti (Linnaeus, 1758)	facultative mycetobiont	mycetophage	++
Neomida haemorrhoidalis (Fabricius, 1787)	obligate mycetobiont	mycetophage	+++
Platydema triste Laporte de Castelnau et Brullé, 1831*	facultative mycetobiont	mycetophage	+
Zopheridae			
Nosodomodes diabolicus (Schaufuss, 1862)*	facultative mycetobiont	mycetophage	+
Synchita humeralis (Fabricius, 1792)	facultative mycetobiont	mycetophage	+

Notes: +++ — dominant species; ++ — common species; + — rare species; * — species that is known in Ukraine only in Crimea.

The species composition of Coleoptera within the complex of inhabitants of the tinder fungus fruiting bodies depends on the age of basidiome. While young carpophores are wet, the diversity of Coleoptera is low consisting of almost exclusively *Scaphisoma* Leach, 1815 (Staphylinidae), and several species of Mycetophagidae including their larvae. They feed on the young tissues, tunneling them mainly from the surface of the hymenophore. Six *Scaphisoma* species are registered: *S. agaricinum* (Linnaeus, 1758), *S. balcanicum* Tamanini, 1954, *S. boleti* (Panzer, 1793), *S. boreale* Lundblad, 1952, *S. inopinatum* Löbl, 1967, and *S. subalpinum* Reitter, 1880. The most common and abundant were *S. agaricinum* and *S. boleti*. All these species are quite mobile. 7 species from the Mycetophagidae family were found on the tinder fungus basidiomes: on most of Ukraine, the *Litargus connexus* (Geoffroy, 1785) and *Mycetophagus piceus* (Fabricius, 1777) were the most abundant on the fungus fruiting bodies, and *Mycetophagus ciscaucasicus* (Semenov, 1899) was found in the mountain forests of Crimea.

As the fruit bodies ripen, its relative moisture decreases and during sporulation the tubes of the hymenophore open, from which ripe spores begin to pour out. They are spread by air but a sufficient amount of them settles on the upper part of the basidioms and near them on the tree bark. The number of beetle species in the complex is increasing significantly, with mycetosporophages making up a significant part. These are Corylophidae: *Arthrolips obscura* (C. R. Sahlberg, 1833) and *Orthoperus corticalis* (Redtenbacher, 1849). Both of these species are also found on other tinder fruiting bodies and under the bark of dead trees (especially *O. corticalis*).

Spore-feeding Sphindidae, *Aspidiphorus orbiculatus* (Gyllenhal, 1808) and *A. lareyniei* Jacquelin du Val, 1859, are also common on *F. fomentarius* carpophores during sporulation. They are also the most spread in sporophores of some myxomycetes, *e. g. Fuligo, Stemonitis, Lycogala* and others.

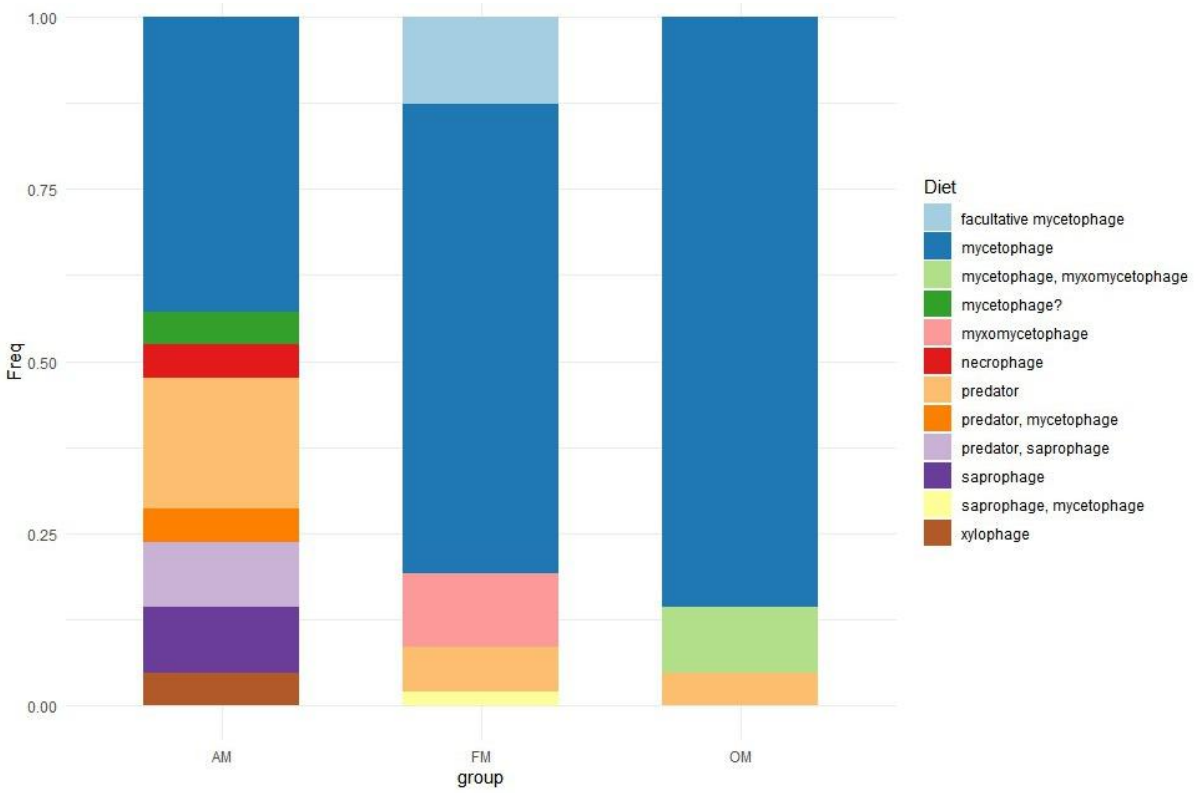

Fig. 2. Proportion of diets per group of mycetobionts: AM — accidental visitors, FM — facultative mycetobionts, OM — obligate mycetobionts.

Among mycetosporophagous Leiodidae registered on tinder fungus, *Agathidium varians* Beck, 1817, *A. rotundatum* (Gyllenhal, 1827), *Anisotoma axillaris* Gyllenhal, 1810 and *A. orbicularis* (Herbst, 1791) are quite rare and *Anisotoma humeralis* (Herbst, 1791) is abundant. Apart from tinder fungus, these leiodids are also associated mainly with slime molds.

Spore-feeders are also diverse among Latridiidae: *Corticaria lapponica* (Zetterstedt, 1838), *C. serrata* (Paykull, 1798), *Enicmus rugosus* (Herbst, 1793), *E. brevicornis* (Mannerheim, 1844), *E. varendorffi* Reitter, 1903, *Latridius brevicollis* (C.G. Thomson, 1868), *L consimilis* (Mannerheim, 1844), *L. hirtus* Gyllenhal, 1827, *L. minutus* (Linnaeus, 1767), and *L. porcatus* (Herbst, 1793). *E. varendorffi* is restricted to the mountain forests of Crimea. Latridiids are micromycetophages that feed on hyphae of many species, including microscopic fungi, and on spores of fungi and slime molds. They were found mainly under the bark of dead trees, and directly on host fungi or myxomycete sporophores, in leaf litter, and other decaying plant debris.

Some Staphylinidae are also sporophages, *e. g. Scaphisoma* species. Remarkably, *Gyrophaena affinis* Mannerheim, 1830, *G. joyi* Wendeler, 1924, *G. manca* Erichson, 1839, and *G. strictula* Erichson, 1839 are abundant in hymenophores. Adults of these rove beetles were found on fruiting bodies and the nearby bark coated with spores. Along with them, the larvae of *Arthrolips*, *Enicmus*, *Gyrophaena*, and *Scaphisoma* were spotted there.

In addition, on the hymenophore and near the basidioms, rather large and mobile larvae of dipterans of Keroplatidae family (Diptera) often developed, being also the sporophages and predators, and creating a web. Fungus gnats from Mycetophilidae family — *Sciophila rufa* Meigen, 1830, also developed on *F. fomentarius*. The appearance of predatory Staphylinidae family becomes frequent on the basidiomes of as a result of the abundant pray insects on the fruiting bodies, the, *e. g. Atheta gagatina* (Baudi di Selve, 1848) *A. liturata* (Stephens, 1832), *Bolitochara pulchra* (Gravenhorst, 1806), *Lordithon thoracicus* (Fabricius, 1777), and *Sepedophilus bipustulatus* (Gravenhorst, 1802).

After the end of sporulation, the spore-feeders gradually disappear from the fruiting bodies and migrate under bark towards other food sources. Simultaneously with the appearance of sporophages, the carpophores are gradually populated by species feeding and developing inside the fruiting bodies. These were the larvae of moths (Tineidae, Lepidopetra), flies (Heleomyzidae, Diptera), and beetles (Tenebrionidae, Ptinidae and Ciidae).

Throughout Ukraine the most typical inhabitants of the *F. fomentarius* carpophores are darkling beetles. *Bolitophagus reticulatus* (Linnaeus, 1767) and *Neomida haemorrhoidalis* (Fabricius, 1787) are most often. The fruit bodies are inhabited by at least one of these species, but sometimes both co-occur the same basidiome, although commonly one of them significantly predominates over another. The adults and larvae of these species can be abundant and continuously live in carpophore until it's completely decaying.

The perennial fruiting bodies of the fungus with dense tissues (*Phellinus*, *Fomitopsis*, *etc.*) or annual species that remain on trees for several years after dying (*Inonotus*, *etc.*, including tinder fungus), are the niche of development and residence of some deathwatch beetles (Ptinidae). We found *Dorcatoma dresdensis* Herbst, 1792, *D. minor* Zahradník, 1993, and *D. robusta* A. Strand, 1938 but other species are mentioned in the literature (Shchigel, 2002). The most common species are *D. dresdensis* and *D. robusta*, whose development lasts 2 years — their larvae inhabit the sterile part of the fruiting body (trama) in the upper part of the basidiome; they pupate near the bark, the exit hole is made on the upper side of the carpophore.

In the forest zone the adults of *Triplax russica* (Linnaeus, 1758) often feed on *F. fomentarius* basidioms. Sometimes their number can be quite significant, although the development occurs only in carpophores of *Inonotus*. Individuals of common *Dacne bipustulata* (Thunberg, 1781) are also noted on *F. fomentarius* fruiting bodies but they are most often and in large abundance found on the basidiomes of fungi with soft tissues, especially on Pleurotaceae.

Ciidae, the most species-reach group, live and develop in the middle of the fruiting bodies. Beetles and larvae inhabit mostly the trama. Ten species from genus *Cis* Latreille, 1796 are noted: *C. bidentatus* (Olivier, 1790), *C. castaneus* (Herbst, 1793), *C. comptus* Gyllenhal, 1827, *C. fagi* Waltl, 1839, *C. fusciclavis* Nyholm, 1953, *C. glabratus* Mellié, 1849, *C. jacquemartii* Mellié, 1849, *C. lineatocribratus* Mellié, 1849, *C. micans* (Fabricius, 1792), and *C. submicans* Abeille de Perrin, 1874. The most typical are *C. castaneus*, *C. jacquemartii*, and *C. lineatocribratus*. In the mainland of Ukraine *C. castaneus* and *C. jacquemartii* were found (sometimes together), and the latter dominated in *F. fomentarius*; in the western regions they co-occur with *C. lineatocribratus*. In Crimea, only *C. castaneus* is recorded.

The other Ciidae found on *F. fomentarius* are *Sulcacis fronticornis* (Panzer, 1805), *Ennearthron E. cornutum* (Gyllenhal, 1827), *E. palmi* Lohse, 1966, *Octotemnus glabriculus* (Gyllenhal, 1827), *O. rugosopunctatus* Drogvalenko, 2002, *Ropalodontus baudueri* (Abeille de Perrin, 1874), *R. perforatus* (Gyllenhal, 1813), *R. strandi* Lohse, 1969, and *Xylographus bostrichoides* (Dufour, 1843).

Most Ciidae species are oligophagous, feeding and developing on several close tinder species, but the species of genera *Ropalodontus* and *Xylographus* in Ukraine are monophagous and associated exclusively with the fruiting bodies of a tinder fungus and are typical inhabitants of such carpophores. *Ropalodontus perforatus* and *R. strandi* were distributed throughout Ukraine, except for the Crimea mountains; they are very close in biology and, according to our observations, they never occur together in the same biotope and the same carpophore. *Ropalodontus baudueri* replaced these two species in the Crimean Mountains, but all the three species together were common in the Carpathians. These species live and develop not only in the trama of fruiting bodies but also in the denser hymenophore. In the Crimean Mountains, *Octotemnus glabriculus*, common throughout Ukraine, was replaced by the close species *O. rugosopunctatus*. In general, these species were not quite typical on *F. fomentarius*, being more common on fungus having carpophores with soft tissues. The small gracile species of *Cis fagi* and *Ennearthron palmi* were not found directly in the carpophores but on the mycelial layer that formed under the bark of the tree next to the fruiting body.

The carpophores are destroyed mainly by the larvae of moths and darkling beetles. Woodpeckers, breaking the old and dry fruiting bodies while searching for insects, often contribute to the destruction. Although the inner tissure of the tinder fungus can be completely destroyed, due to the hard crust the carpophore most often keeps its shape unchanged. Such old basidiomes periodically fall to the soil, where they become available to epigeobiont saprotroph beetles from Geotrupidae and Hydrophilidae families. We noted the findings of *Geotrupes stercorarius* (Linnaeus, 1758) and *Cercyon lateralis* (Marsham, 1802), which, in general, are often found in rotten mushrooms, both cap and fallen tinder. The fallen carpophores are also inhabited by Ciidae, *e. g. Cis matchanus* Reitter, 1915. We registered this species only in western Ukraine, although it might be found in other regions as well. In addition, in such carpophores, if they do not become very wet, the Tenebrionidae adults and larvae continue to exist.

We noted, that size and number of fruiting bodies on the tree significantly impact the species richness and abundance of each taxon. Smaller basidiomes are prone to quicker destruction and produce fewer spores, resulting in a reduction in the number of specialist species.

Correlation is visible between species richness and abundance and the vertical location of carpophores on the tree, as well as the relative position of fruiting bodies to each other. This correlation may be explained by the

strong dependence of beetles on the humidity of dead carpophores, which, in turn, is influenced by the location of the fungus.

Facultative mycetobionts. Besides the obligate mycetobionts, other polyphagous fungivores, and facultative mycetobionts visiting *F. fomentarius* were found. They are living both under the bark of dead trees and associated with basidiomes of other fungi.

Biphyllidae. *Biphyllus lunatus* (Fabricius, 1787) and *Diplocoelus fagi* (Chevrolat, 1837) both are mycetophages. *B. lunatus* is associated with the stroma of Ascomycota, primarily *Daldinia concentrica*, where its larvae develop. *D. fagi* is a micromycetophagous, most often occurring under the bark of dead trees, where it feeds on the microscopic fungi.

Cerylonidae. Adults and larvae of *Cerylon histeroides* (Fabricius, 1792) feed on plasmodia of myxomycetes and are also mainly found under the bark of dead trees or on the rotten wood, but quite often penetrate from there into the old fruiting bodies.

Ciidae. *Orthocis alni* (Gyllenhal, 1813) is the obligate mycetophage, primarily associated with the fruiting bodies of *Exidia* and *Auricularia* on dead trees.

Monotomidae. *Rhizophagus bipustulatus* (Fabricius, 1792) is a micromycetophage that lives under the bark of dead trees, from where it often shifts to carpophores of fungi.

Cryptophagidae. *Atomaria elongatula* Erichson, 1846, *A. umbrina* (Gyllenhal, 1827), *Cryptophagus labilis* Erichson, 1846, *Micrambe bimaculatus* (Panzer, 1798), and *Pteryngium crenatum* (Fabricius, 1798). The vast majority of species of this family are micromycetophages and are not rare on the fruiting bodies, especially those covered with mold. Probably, other species from this family can be found on the basidiomes of *F. fomentarius*.

Laemophloeidae. *Cryptolestes pusillus* (Schoenherr, 1817) and *Placonotus testaceus* (Fabricius, 1787) both are subcortical micromycetophages living on moldy damage of living trees. *C. pusillus* is known as a pest of stored products, although the beetles appear in stocks when those are already infected with fungi.

Latridiidae. *Melanophthalma suturalis* (Mannerheim, 1844), *Corticarina minuta* (Fabricius, 1792), and *Stephostethus caucasicus* (Mannerheim, 1844) are micromycetophages living in litter, on dead tree branches, on dry grasses, in hay and straw. Like Cryptophagidae, they can be expected on the carpophores of *F. fomentarius*.

Lophocateridae. *Grynocharis oblonga* (Linnaeus, 1758) and *G. pubescens* Erichson, 1844 living under the bark, where those are associated with the microscopic fungi, occasionally visiting the fruiting bodies. *G. pubescens* in Ukraine was found only in Crimea.

Mycetaeidae. Micromycetophagous *Mycetaea subterranea* (Fabricius, 1801) is a common inhabitant of synanthropic habitats like cellars and basements, where it feeds on the mold. In natural habitats it lives on molded wood, occasionally under the bark, and in the nests of birds and rodents.

Mycetophagidae. *Litargus balteatus* LeConte, 1856, *Mycetophagus multipunctatus* Fabricius, 1792, *M. quadriguttatus* Ph.W. Müller, 1821, and *Triphyllus bicolor* (Fabricius, 1777) are the obligate mycetophages. Cosmopolitan *L. balteatus* lives in compost, hay, molded tinders, under the bark, on molded wood, and myxomycetes (Nikitsky, Bibin, 2010). It also occurs on the plant residues, noted as a minor pest of stocks (corn, dried fruits, *etc.*). The presence of Mycetophagidae in food stocks indicates poor storage conditions and molded products (Drogvalenko, 2019). *M. multipunctatus* and *T. bicolor* are most often found on the fruiting bodies of soft tinders, they are also common in the cap mushrooms. And *M. quadriguttatus* is rather associated with microscopic fungi, found on the molded tinders, in rodent nests, on plant remains, and even on the carrions.

Nitidulidae. *Epuraea biguttata* (Thunberg, 1784) and *E. terminalis* (Mannerheim, 1843) are micromycetophages associated with the molds and yeasts that develop in the sap that oozes from damaged bark of trees and old fruiting bodies of fungi with soft tissue. Although Nikitsky *et al.* (1996) noted that *E. biguttata* can develop on rotting spores of *F. fomentarius*, we did not observe that.

Salpingidae. *Salpingus planirostris* (Fabricius, 1787) is the obligate mycetophage and is developmentally associated with the various Ascomycota (*Diatrype*, *Hypoxylon*, *etc.*).

Silvanidae. *Ahasverus advena* (Waltl, 1834), *Silvanus unidentatus* (Olivier, 1790), and *Uleiota planatus* (Linnaeus, 1761). *A. advena* is mainly synanthropic and considered as a pest of stock. However, it develops in big abundance only on stocks already damaged by fungi. Two other species are micromycetophages, commonly living under the bark and occasionally shifting on the fruiting bodies.

Tenebrionidae. *Alphitophagus bifasciatus* (Say, 1824) is a cosmopolitan, in some cases injurious in food stocks. In natural habitats it is rare in tree hollows on the fungi. *Corticeus bicolor* (Olivier, 1790) is a common inhabitant of the space under the bark, sapromycetophagous, but we recorded a case when the beetles fed on soft tissues on the hymenophore of a young carpophore *F. fomentarius*. Two rare species are *Diaperis boleti* (Linnaeus, 1758), widely distributed and occurring fungi with low tissue density, and *Platydema triste* Laporte de Castelnau et Brullé, 1831, inhabiting carpophores of various fungi and rot wood in Crimean forests.

Zopheridae. *Nosodomodes diabolicus* (Schaufuss, 1862) is a representative of the Mediterranean fauna and is known in Ukraine only from mountainous Crimea, where it is quite common. It is found under the bark and on the trunks of the dead trees, especially at night, on the various tinders, in which the development of its larvae takes place. *Synchita humeralis* (Fabricius, 1792) is associated to the fungi from the class Ascomycota (*Daldinia*, *Diatrypella*, *Diatrype, Hypoxylon*, *etc.*) and is found on the dead trees damaged by these fungi.

The accidental visitors on fruiting bodies of *F. fomentarius* are also recorded.

Carabidae. The predatory species *Agonum viridicupreum* (Goeze, 1777) is the only ground beetle registered on the tinder fungus.

Histeridae. *Acritus minutus* (Herbst, 1791) and *Paromalus flavicornis* (Herbst, 1791) are predators and sapromycetophages living under the bark, especially if some layer of the bark is rotten.

Bothrideridae. The larvae of *Bothrideres bipunctatus* (Gmelin, 1790) parasitize on the larvae of various xylophagous Coleoptera and Hymenoptera, while the adults are possibly facultative mycetophages.

Coccinellidae. *Halyzia sedecimguttata* (Linnaeus, 1758), is a predatory or micromycetophagous ladybird consuming powdery mildews and frequently forming aggregations on tree trunks.

Leiodidae. Necrophagous *Catops fuliginosus* Erichson, 1837 was collected from a strongly decayed carpophore.

Ptinidae. *Ptinomorphus imperialis* (Linnaeus, 1767) is a xylophagous species developing in the dry wood of deciduous trees.

Staphylinidae. Yet another group of rove beetles occasionally visiting tinder fungus are three predatory species. *Dinaraea aequata* (Erichson, 1837) lives under the bark of dead trees, while *Anthobium atrocephalum* (Gyllenhal, 1827), and *Sepedophilus immaculatus* (Stephens, 1832) usually live in the leaf litter.

Conclusions. The species composition of the Coleoptera complexes in the *Fomes fomentarius* carpophores varies little depending on the geographical location of the study area. The core of species of the specialist complex remains constant and is represented by Tenebrionidae — Ciidae (*Cis* spp. from the *castaneus* species group) — Ciidae (*Ropalodontus* spp.) — Ptinidae (*Dorcatoma* spp.). The following coleopteran complexes may be delimited geographically.

Widespread complex. *Bolitophagus reticulatus* and/or *Neomida haemorrhoidalis* — *Cis jacquemartii* and/or *C. castaneus* — *Ropalodontus perforatus* or *R. strandi* — *Dorcatoma* spp.

Mountain Crimean complex. *Bolitophagus reticulatus* and/or *Neomida haemorrhoidalis* — *Cis castaneus* — *Ropalodontus baudueri* — *Dorcatoma* spp.

Carpathian complex. *Bolitophagus reticulatus* and/or *Neomida haemorrhoidalis* — *Cis jacquemartii* and/or *C. castaneus*, and/or *C. lineatocribratus* — *Ropalodontus perforatus* or *R. strandi* or *R. baudueri* — *Dorcatoma* spp.

These data generally coincide with the similar studies from other countries (Schigel, 2002; Jonsell *et al.*, 2016; Andrési, Tuba, 2018).

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