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Macromycete Fruit Bodies as a Habitat for Dipterans (Insecta, Diptera)

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Abstract—The complex of Diptera (except for Sciaroidea) breeding in the fruit bodies of fungi is analyzed. The larvae of some species, such as Cecidomyiidae, Platypezidae, Heleomyzidae (Suilliinae), Anthomyiidae (*Pegomya*), Sphaeroceridae, and possibly Phoridae and Syrphidae feed on fresh fungal tissues. The ecological groups of flies are distinguished with respect to the type of feeding and the way of using fungal fruit bodies as habitat. The larvae of most groups developing inside the fruit bodies are saprobionts, typically occurring in decaying organic substrates of various origins.

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The problems related to the colonization of fungal fruit bodies (also termed carpophores or basidiomes) by insects have attracted attention of many researchers. The interactions between insects and wood-destroying polypore fungi are mostly addressed in the literature devoted to forestry. Many publications have dealt with the composition of insects developing in pileate fungi. There are extensive data on the species composition of mycobiont beetles (Krasutskii, 2005, etc.) and dipterans (Buxton, 1960; Chandler, 1978; Krivosheina et al., 1986; Yakovlev, 1994; Ševčik, 2006, etc.). The review by P.J. Chandler (1978) contained the species list of such dipterans, belonging to 37 families. E.B. Yakovlev (1994) summarized the published and original data related to the members of 40 dipteran families. By the time of publication of his review, development in fungi had been reported for 700 Palaearctic species of dipterans. However, most of the relevant data were represented by mere lists of species reared from the fruit bodies of fungi. The condition of the fruit bodies at the time of colonization was almost never specified, with rare exceptions (Buxton, 1960; Chandler, 1978; Krivosheina et al., 1986; Zaitzev, 1994, 2003). At the same time, compact substrates of varying consistency and time of existence (carpophores of polypore and pileate macromycetes or decaying fruit bodies) provide very diverse conditions, determining the composition of mycobionts.

This communication deals with the complex of dipterans whose development, according to the recent data, is associated with the fruit bodies of fungi. The terminology used follows that of L. Papp (1976), who distinguished between the group of macromycophages, feeding directly on the fruit bodies, and that of micromycophages, feeding on the mycelium.

The entire complex of dipterans occurring in the fungal fruit bodies (mycobionts) can be subdivided into several groups:

(1) Obligatory macromycobionts, inhabiting fruit bodies of various fungi. These forms are endobionts; their type of feeding is macromycophagy.

(2) Obligatory sapromycobionts, inhabiting decomposing fruit bodies. They are endobionts, feeding by saprophagy.

(3) Facultative mycobionts, living on the surface of fruit bodies and mycelium. They are epibionts, and their type of feeding is micromycophagy and possibly saprosporophagy.

(4) Eurybiont forms, inhabiting fungal substrates in different states. Their type of feeding is mostly zoophagy, and also necrophagy.

(5) Species visiting the fruit bodies.

Obligatory Macromycobionts Inhabiting Fresh Fruit Bodies of Soft and Fleshy Consistency

The core of this ecological group is formed by fungus gnats of the families Bolitophilidae and Mycetophilidae. Their ecological associations are not considered here, most attention being focused on members of other dipteran families.

Little is known on the associations between the larvae of gall midges and pileate fungi[1]. The fruit bodies of macromycetes cannot be regarded as the typical habitat for these flies (Krivosheina, 2006). In particular, *Brachyneura fungicola* Mam. was reared from a russule in Karelia (Krivosheina et al., 1986). However, a large series of the same species was reared from a dead and softened fruit body of the sulphur shelf *Laetiporus sulphureus* (Mamaev and Krivosheina, 1965). *Camptodiplosis boleti* (Kieff.) was reared from the cup fungi *Peziza* sp., boletes, and agarics (Yakovlev, 1994); at the same time, this species was observed to develop in the semiliquid medium on the fruit bodies of *Polyporus confluens*. Development of one more species, *C. auriculariae* Barn., is associated with *Auricularia* (Buxton and Barnes, 1953; Ševčik, 2006), having large, ear-shaped, gelatinous fruit bodies.

Some species of Sciaridae have been reported as pests of fungi cultivated in hothouses (Pavlyuchenko, 1981, etc.). However, further research is needed to clarify if they really feed on the living tissues of the fruit bodies.

There are vast data in the literature on the relation of humpbacked flies of the genus *Megaselia* Rd. (Phoridae) with soft juicy fungal fruit bodies. These species were most often recorded in various agarics, less frequently in boletes. Some species, such as *M. halterata* (Wood) and others, were named as harmful pests of cultivated fungi (Binns, 1980; White, 1981; Disney, 1981, 1994, etc.).

Platypezidae is the only family of higher dipterans whose larvae are associated exclusively with fungal substrates (Buxton, 1960; Brindle, 1961; Krivosheina and Mamaev, 1967; Krivosheina, 1969; Shatalkin, 1985). Most of them are obligatory inhabitants of the carpophores.

The larvae of *Bolopus* (*Orthonevra*) *furcatus* (Fll.) were found in relatively soft carpophores of the dryad's saddle (*Polyporus squamosus*) (Buxton, 1960). We have observed the larvae of this species in a myxomycete plasmodium in Azerbaijan. The soft and juicy fruit bodies of agarics and boletes provide substrates for the larvae of *Platypeza* Mg. (Dušek, 1962). The species *P. consobrina* Ztt. was also recorded in the stinkhorn *Phallus impudicus*, and *P. fasciata* Mg., in the stump puffball (Buxton, 1960; Brindle, 1961). The studied species of *Lindneromyia* Kess. (= *Plesioclythia* Kess. et Magg.) and *Protoclythia modesta* (Ztt.) are also associated with soft and juicy fungal carpophores. Members of a new genus *Kesselimyia* Vaňhara were reared from *Lepiota* sp. (Vaňhara, 1981). The larvae developed quite rapidly in the juicy fruit bodies and diapaused as the substrate dried up. At the same time, *Paraplatypeza atra* (Mg.) was recorded both in agarics and polypores (*Trametes hirsuta*) (Khalidov, 1984; Yakovlev, 1994). In Moscow Province, this species was observed to develop in the fruit body of *Lactarius*; as the latter decayed, the larvae migrated into the surrounding substrates to pupate.

The larvae of some flower flies of the genus *Cheilosia* Mg. (Syrphidae) are known to occur in fungal substrates (Buxton, 1960; Dely-Draskovits, 1972; Hackman and Meinander, 1979; Khalidov, 1984; Yakovlev, 1994, etc). The most commonly recorded species is *C. scutellata* (Fll.), whose larvae live mostly in various boletes, sometimes also in agarics and russules. Associations with fruit bodies of boletes have also been observed for *C. longula* (Ztt.).

Species of the subfamily Suilliinae (Heleomyzidae) are typical inhabitants of the fruit bodies. For example, *Suillia affinis* (Mg.), *S. apicalis* (Lw.), *S. flavifrons* (Ztt.), *S. quadrilineata* Czerny, *S. oxyphora* (Mik), and others have been recorded in ascomycetes as well as in boletes, agarics, and russules (Dely-Draskovits, 1972a; Papp, 1994; Yakovlev, 1994). Such species as *Suillia atricornis* (Mg.), *S. bicolor* (Ztt.), *S. pallida* (Fll.), and *S. variegata* (Lw.) have been found in ascomycetes, including cup fungi and truffles, in xylotrophic pileate fungi (*Cantharellus cibarius*, *Pleurotus pulmonarius*, etc.), and also in boletes and many agarics. The condition of the substrate, unfortunately, was not reported. At the same time, the larvae of *S. variegata* (Lw.) were found in soil on the roots of aster (Andrews, 1945), and those of *S. ustulata* (Mg.), not only in truffles but also in dead stalks of elder (Chandler, 1978).

Some species of the genus *Suillia* R.-D. lay eggs in the subterranean fruit bodies of truffles: *Suillia gigantea* (Mg.), *S. hispanica* (Lw.), *S. humilis* (Mg.), *S. pallida* (Fll.), *S. tuberiperda* (Rd.), *S. ustulata* (Mg.), and *Tephrochlamys flavipes* (Ztt.). These dipterans have acquired specific ecological adaptations related to the subterranean development of truffles. For example, the females of *Suillia tuberiperda* fly close to the soil surface and lay eggs on the ground

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[1] The names of the fungi are given based on the manuals of M.A. Bondartseva (1998), L.V. Garibova and S.N. Lukomtseva (2005), and M. Knoop (2000).

above the concealed fungal fruit bodies. The newly hatched larvae are motile and can easily reach the fruit body (Janvier, 1963).

Development of the larvae of *Suillia* R.-D. proceeds rapidly (in 7–8 days) in the fresh fruit bodies of pileate fungi, usually in the absence of other mycophages. The larvae pupate in the surrounding substrates.

The larvae of Sphaeroceridae are typical inhabitants of the various fungal substrates. Some species of this family, for example, *Limosina parapusio* Dahl, are obligatory mycophages (Chandler, 1978; Hackman and Meinander, 1979). Some species, such as *Limosina heteroneura* Hal., were recorded only in the fungi cultivated in hothouses (Chandler, 1978); the conditions of their development were, unfortunately, not analyzed.

The larvae of root flies of the genus *Pegomya* R.-D. (Anthomyiidae) undoubtedly belong to the group of obligatory mycobionts. The ecological data for different species are summarized in the literature (Krivosheina et al., 1986; Yakovlev, 1994). These flies generally prefer boletes of the genera *Boletus* and *Leccinum*, a number of species having been recorded only in these fungi: *P. fulgens* (Mg.), *P. furva* Ringd., *P. tabida* (Mg.), *P. vittigera* (Ztt.), etc. However, some species, such as *P. calyptrata* (Ztt.), have been found only in agarics, while *P. geniculata* (Bouché) has been reared from soft fleshy fruit bodies of the wrinkled thimble-cap *Ptychoverpa bohemica* and some agaricoid fungi (Chandler, 1978; Yakovlev, 1994, etc.).

This group may also include some species of Phoridae and Drosophilidae when the future studies provide more precise ecological data.

With respect to the type of feeding, the larvae of these dipterans are obligatory macromycophages.

Obligatory Macromycobionts Inhabiting Fruit Bodies of Hard Consistency (Leathery, Suberose, or Woody)

Relatively young fruit bodies of the polypores *Trametes* and *Fomitopsis pinicola* provide substrate for development of the gall midges *Trichopteromyia* Will., *Monardia* Kieff., and some others (Mamaev and Krivosheina, 1965; Mamaev, 1968).

Some species of humpbacked flies, for example, *M. lapponica* Schmitz, *M. virilis* Schmitz, *M. frameata* Schmitz (=*buxtoni* Colyer), *M. flava* Fll., and others, were reared from fruit bodies of the polypores *Fomes* and *Fomitopsis* (Krivosheina et al., 1986). The condition of the fruit bodies was, however, not analyzed.

The larvae of flat-footed flies of the genus *Agathomyia* Verr. are well-known inhabitants of the carpophores of polypores. In particular, the larvae of *A. wankowiczii* (Schnabl) form elongated galls on the lower surface (hymenophore) of the growing fruit bodies of *Ganoderma applanatum* (Mamaev, 1972, etc). Fruit bodies of *Trametes* provide the most typical environment for the larvae of *Polyporivora* Kess. et Magg. (Kessel et al., 1973).

The carpophores of polypores are colonized on the initial phases of their development. The same trend is known in other groups of insects, for example, lepidopterans (Zagulyaev, 1969).

By the type of feeding, these larvae are obligatory macromycophages, and by their mode of life, they are endobionts.

Obligatory Sapromycobionts Living in Decomposing Fruit Bodies

The larvae of winter gnats of the genus *Trichocera* Mg. (Harris) were repeatedly recorded in the fungal substrates (Buxton, 1960; Dely-Draskovits, 1972a; Hackman and Meinander, 1979, etc.). Development of *T. hiemalis* and *T. saltator* can proceed both in the dense fruit bodies of *Piptoporus* or *Trametes* and in the soft carpophores of *Pleurotus* and *Sarcodon*. The larvae of *T. annulata* have been found in the fruit bodies of morels (*Ptychoverpa bohemica*). At the same time, the same species have been repeatedly observed to develop in decomposing leaves and other plant debris, manure, and corpses of vertebrates (Dahl, 1966; Broadhead, 1980; Krivosheina et al., 1986).

The larvae are sluggish, with terete bodies and massive, scraper-like mandibles. Such characters suggest a saprophagous, rather than predaceous, mode of feeding, possibly including sapromycophagy.

There are indications in the literature that members of some genera of crane flies (Limoniidae) may be associated with fungal fruit bodies (Lindner, 1958; Buxton, 1960; Dely-Draskovits, 1972a; Chandler, 1978; Krivosheina et al., 1986). They refer mostly to species of the genera *Metalimnobia* Mats., *Limonia* Mg., *Dicranomyia* Stephens, and others. However, many species of this family also develop in decomposing plant remains. For example, the larvae of *Neolimonia dumetorum* (Mg.), recorded in some agaric fungi (Dely-Draskovits, 1972a), also commonly occur in rotting wood of leaved trees. In Karelia, the larvae of *Discobola annulata* (L.) were reared from sac fungi, the tinder polypore *Fomes fomentarius*, and agarics (Yakovlev, 1994); however, these larvae typically occur in crumby wood, concentrating under detached bark in the areas penetrated by mycelium.

Adults of *Metalimnobia bifasciata* (Schr.) have been reared from fruit bodies of ascomycetes (morels and saddle fungi) as well as polypores, agarics, boletes, and russules (Buxton, 1960; Hackman and Meinander, 1979, etc.). At the same time, these larvae typically occur in the old, strongly decomposed carpophores of polypores and in the dust at their bases. Although the larvae of *M. quadrimaculata* (L.) are believed to develop in the fruit bodies of some polypores and the saddle fungus *Gyromitra* (Lindner, 1958; Chandler, 1978, etc.), they typically occur in sap concretions on trunks and stumps, in the brown dust under the bark of stumps, and in the decomposed wood of fallen tree trunks. The larvae were also found in the humid decomposed fruit bodies of *Laetiporus sulphureus* and in the loose old carpophores of *Fomes fomentarius*.

The larvae of the genus *Ula* Hal. are regarded as typical mycobionts (Brindle, 1967; Chandler, 1978, etc.). In particular, *U. sylvatica* (Mg.) have been reared from a broad range of fungi, from sacs and polypores to heterobasidial ones; this species was also reported to develop in the semi-liquid sap under the spruce bark (cited after Yakovlev, 1994). In the mountain forests of Tuva, the larvae typically occurred in sap concretions on birch trunks. The larvae of *Ula bolitophila* Lw. typically occur in strongly decomposed carpophores of various polypores as well as in some agarics. In the forests of Vologda Province the larvae developed in the dark brown dust of fallen spruce trunks and commonly occurred in strongly decomposed wood penetrated by mycelium. In the mountain forests of Tuva, they were recorded in the splits of sapping birch stumps, and in the Southern Primorye area, in the bark of dying and fallen trunks of the Amur linden.

Limonia nubeculosa Mg. and *U. mollissima* Hal. were reported to be associated with soft fruit bodies of various polypores, xylotrophic agarics, and boletes (Chandler, 1978). Besides the fungi, the larvae of these species typically occur in soil and forest litter. The larvae of *Rhipidia uniseriata* Schin. were recorded in fruit bodies of *Russula nigricans* and in decaying wood (Chandler, 1978). In Russia, these larvae were found in the core of fallen decomposing trunks of leaved trees: birch, linden, and aspen.

Among moth flies (Psychodidae), the larvae of *Chodopsycha lobata* (Tonn.) were reliably shown to develop in the fresh fruit bodies of *Russula* sp. This is the only representative of the family whose larvae are considered to be obligatory mycophages (Hackman and Meinander, 1979). This species was also reared from the carpophores of cup fungi, polypores, and a number of agarics (Chandler, 1978; Krivosheina et al., 1986) in varying conditions, and also from horse manure (Jezek, 1990). The larvae of *Psychodocha cinerea* (Banks.) and *P. phalaenoides* (L.) develop in decomposing agaric fungi and other decaying substrates (Chandler, 1978).

Among the Sciaridae, some species of *Scatopsciara* Edw., *Bradysia* Winn., and *Lycoriella* Frey have been reared from fruit bodies of polypores and agarics; however, they are common inhabitants of decomposing wood (Krivosheina et al., 1986). The larvae of *Epidapus schillei* (Börner) (=*titan* Frey), recorded in the fruit bodies of *Peziza* sp. (Yakovlev, 1994), are most common in the litter.

The biology of the larvae of Sciaridae known as pests of hothouse cultivars, including fungi, remains a subject of debate. In particular, the larvae of *Lycoriella ingenua* (Duf.) (=*solani* Winn.), *L. castanescens* (Lgd.) (=*fucorum* Frey), and *Bradysia brunnipes* Mg. are well-known pests of plant seedlings and fungi in greenhouses, while the most common species *L. ingenua* has been reared from fruit bodies of various disco- and basidiomycetes (Hackman and Meinander, 1979; Yakovlev, 1994, etc.). The larvae of *L. ingenua* also develop in the strobiles of conifers (Gerbachevskaya and Stadnitskii, 1969) and commonly occur in the decomposing wood of leaved trees. The larvae of *Bradysia brunnipes* Mg., *Lycoriella ingenua* (Duf.), and *L. modesta* Staeg. (=*Sciara frigida* Holm.) are also believed to damage wheat roots, cucumber seedlings, bulbs of Liliaceae, and various storage roots and fruit (Pavlyuchenko, 1981).

The above data mostly refer to plants and fungi cultivated in hothouses, where the fly larvae are common in organic-rich soil. Unfortunately, their detailed trophic relations remain unknown. It is not exactly clear whether the larvae feed on the dead parts or the living tissues of the roots. It is worth noting that some representatives of Sciaridae can develop in apples damaged by seedworms (Steffan, 1973), thus acting as satellites of phytophages. It still remains to be confirmed that some sciarid larvae can feed on fresh fruit bodies. In general, the species considered above can be characterized as sapro- and probably micromycophages. Some species appear to be mere satellites of the first-order consumers.

Among midges of the vast genus *Culicoides* Latr. (Ceratopogonidae), only 3–4 species are to a certain extent associated with fungal substrates. Although the larvae of *Culicoides chiopterus* (Mg.), *C. obsoletus* (Mg.), and *C. scoticus* Downes et Kettle have been reared from carpophores of pileate fungi and some polypores (*Poria*) (Glukhova, 1979; Chandler, 1978, etc.), their most typical environments are decomposing organic substrates surrounding the decaying fruit bodies, and also manure (Hackman and Meinander, 1979). The larvae of *C. scoticus* Downes et Kettle are more frequently recorded in various fungi (Buxton, 1960; Dely-Draskovits and Babos, 1993); however, this species occurs in humid soil as well.

Among the Scatopsidae, the widespread synanthropic species *Coboldia fuscipes* (Mg.) was found in decomposing soft fruit bodies (Buxton, 1960; Chandler, 1978; Krivosheina et al., 1986; Yakovlev, 1994). However, its larvae commonly occur in various plant remains, manure, litter, and rotting vegetables. In the Far East, this species developed in wet decaying bast fibers of fallen *Maackia* trunks. Although the fly *Scatopse notata* L. has been reared from boletes (Chandler, 1978, etc.), its larvae prefer various decomposing plant remains, including manure and rotting vegetables. There are also published data on fungal associations of species of the genus *Apiloscatopse* Cook: *A. flavicollis* (Mg.) with the Matsutake fungus *Tricholoma*, and *A. scutellata* (Lw.), with the aphyllophorous fungus *Bjerkandera adusta* (Buxton, 1960; Chandler, 1978).

Sylvicola fenestralis (Scop.) (Anisopodidae) has been reared from decomposing carpophores of agarics, russules, and *Piptoporus* (Chandler, 1978; Krivosheina and Mamaev, 1967). However, the larvae of this species are typical inhabitants of decomposing plant remains, including rotting roots, potato haulm, vegetables, and liquid manure. *Sylvicola ductus* (Fabr.) has been reared from the dryad's saddle (Ševčik, 2006), the honey mushroom, and a russule (Dely-Draskovits and Babos, 1993). However, the most common environments of the larvae are aggregations of trembling fungi on the surface of old fallen trunks of leaved trees, sap concretions on trunks and stumps, and loose wood soaked with sap.

In the Russian Far East, the fly *Sylvicola japonicus* (Mats.) was reared from decomposing fruit bodies of the sulphur shelf and *Pleurotus* sp. growing on elms, while the larvae of *S. matsumurai* (Okada) were collected, besides the sulphur shelf, also from a rotting fruit body of *Ganoderma* sp. and from sap concretions on an elm tree.

The biology and trophic relations of the larval Phoridae remain obscure. E.B. Yakovlev (1994) summarized the data on 36 species of *Megaselia* Rd. recorded in fungal fruit bodies. Unfortunately, almost no data are available as to the type of feeding of the species regarded as mycophagous. Some problems of their feeding will be considered in a special section.

The larvae of *Nemopoda nitidula* (Fll.) (Sepsidae) have been repeatedly recorded in fruit bodies of boletes and agarics, as well as in myxomycete plasmodia (Chandler, 1978; Yakovlev, 1994). At the same time, they typically occur in such substrates as manure and decomposing corpses of vertebrates (Ferrar, 1987; Ozerov, 1989a, 1989b, 2003).

Some species of Piophilidae, in particular, *Mycetaulus bipunctatus* (Fll.) and *Amphipogon flavum* (Ztt.) were recorded in fungal fruit bodies (Hennig, 1943; Zuska and Laštovka, 1965). The larvae of *M. bipunctatus* develop only in the decomposing fruit bodies (Chandler, 1978) but may also inhabit bird nests and decaying wood (Hennig, 1943).

There are scattered data concerning the associations of *Scathophaga furcata* (Say) and *S. lutaria* (F.) (Scathophagidae) with myxomycete plasmodia (Yakovlev, 1994). At the same time, the larvae of *S. furcata* develop in various kinds of manure (Skidmore, 1978), i.e., the typical substrate of species of the genus *Scathophaga* Mg.

Meoneura neottiophila Coll. (Carnidae) was reared from the birch bolete (*Leccinum scabrum*); its larvae were also reported to develop in bird nests (Hennig, 1937). The adults often visit fruit bodies of fungi, for example, *Pleurotus* (Chandler, 1998). The larvae were shown to be saprophagous (Hackman and Meinander, 1979). It should be noted that some species of the genus *Meoneura* Rond. develop in manure and dead bodies of vertebrates (Ozerov, 1989b).

Many species of Heleomyzidae are typical inhabitants of decomposing fungal substrates. *Neoleria ruficeps* (Ztt.) were shown to be associated with the polypores *Fomes fomentarius*, *Fomitopsis pinicola* (Yakovlev, 1994), agarics, and russules (Buxton, 1960; Chandler, 1978). *Heleomyza serrata* (L.) develops in the beefsteak fungus *Fistulina* (Chandler, 1978) with soft and juicy annual fruit bodies. This species was also recorded in excrements, bird nests, and decomposing plant remains (Skidmore, 1962, etc.). *Heteromyza oculata* Fll. develops in xylotrophic fungi and mammalian burrows (Chandler, 1978; Ferrar, 1987). The flies *Tephrochlamys flavipes* (Ztt.), *T. rufiventris* (Mg.), and *T. tarsalis* (Ztt.) have been reared from carpophores of various fungi, from caps to russules, and also from mammalian burrows, bird nests, manure, litter, and rotten meat (Buxton, 1960; Lobanov, 1970; Chandler, 1978; Hackman and Meinander, 1979; Ferrar, 1987; Yakovlev, 1994).

The larvae of Sphaeroceridae generally prefer rotting fruit bodies of fungi and various decaying substrates. For example, the larvae of *Copromyza fimetaria* (Mg.) develop in rotting fungi and corpses (Chandler, 1978). The larvae of *Ischiolepta pusilla* (Fll.) have been recorded in boletes and agarics, including cultivated ones, but often occur in other substrates, such as manure (Papp, 1979).

Species of the genus *Limosina* Macq., in particular *L. claviventris* Strobl, *L. fungicola* Hal., *L. clunipes* (Mg.), *L. flavipes* (Mg.), and others, have been repeatedly reared from fruit bodies of various agarics and boletes, and also from rotting plant substrates, nests of apoid hymenopterans and rodents, manure, etc. (Papp, 1972, 1979; Chandler, 1978). *Puncticorpus cribratum* (Villenv.) may develop, besides the carpophores of boletes, agarics, and russules (Papp, 1972), also in ant nests and mouse burrows (Richards, 1930; Hackman, 1967). The fly *Leptocera fontinalis* (Fll.) has been reared from the myxomycete *Fuligo septica* (Buxton, 1960).

Associations with fungal substrates are typical of some genera of Drosophilidae, namely *Drosophila* Fll., *Leucophenga* Mik, and *Stegana* Mg. Owing to the biological specificity of fruit fly larvae (living in liquid substrates), they mostly occur in decomposing fungi.

According to P.J. Chandler (1978), such substrates are characteristic of the larvae of *D. funebris* (Fll.), *D. busckii* Coq., and *D. subobscura* Coll. The former species develops, besides ascomycetes, aphyllophores, and agaricoid hymenomycetes, also in any decomposing plant material, kitchen garbage, and rotting fruit (Buxton, 1960; Burla and Bächli, 1968; Hackman and Meinander, 1979, etc.). The fly *D. busckii* Coq. has been reared from boletes, agarics, and russules, as well as *Ramaria* and *Cantharellus* (Burla and Bächli, 1968; Hackman and Meinander, 1979; Dely-Draskovits and Babos, 1993; Yakovlev, 1994, etc.). However, it also develops in compost, manure, and rotting fruit. *D. subobscura* Coll., besides agarics (including *Agrocybe dura*), may develop in sap concretions on trees, rotting fruit, and flowers (Shorrocks and Chalesworth, 1980).

The fly *D. cameraria* Hal. has been reared from a wide range of fungi, from polypores to agarics and russules, and also from the stinkhorn *Phallus impudicus* (Buxton, 1960; Chandler, 1978). However, some authors (Dely-Draskovits and Papp, 1973) did not regard this species as an obligatory mycobiont. The fly *D. repleta* Wollast. has been reared from fruit bodies of gilled fungi (paxil, russule), myxomycete plasmodia, and fermenting sap (Séguy, 1934; Buxton, 1960, etc.).

The species *Scaptomyza pallida* (Ztt.) has been reared from fungi (Dely-Draskovits and Papp, 1973), but also develops in decomposing plant substrates (Hackman, 1955).

The larvae of *Leucophenga maculata* (Duf.) commonly occur in old fruit bodies of various fungi, mostly polypores. The larvae of this species were recorded in the old carpophores of *Inonotus* sp. and *Polyporus squamosus* in such regions as Northern Caucasus, Kunashir and Sakhalin Islands, Southern Primorye Territory, and also in Kyrgyzstan and Turkmenia. The species *L. quinquemaculipennis* Okada develops in fruit bodies of agarics (*Oudemansiella mucida*, *Pholiota alnicola*) and in old softened carpophores of polypores, including the birch bracket *Piptoporus betulinus*. *L. quinquemaculata* Strobl was reared from the same polypore species (Yakovlev, 1994).

Sac fungi and sap concretions provide the environment for the larvae of *Amiota alboguttata* (Wahlb.) (Buxton, 1960; Ferrar, 1987). The larvae of *A. albilabris* (Roth) were discovered in Southern Primorye Territory under the bark of dying aspen trunks, where they concentrated in the areas damaged by flask fungi.

Based on the presently available data, some species of the genus *Drosophila* Fll. may be classified as obligatory and facultative mycobionts (Shorrocks and Charlesworth, 1980). Such species as *D. kuntzei* Duda, *D. testacea* Ros., *D. transversa* Fll., *D. phalerata* Mg., *D. confusa* Staeg., and some others have so far been recorded only in soft and juicy fungal fruit bodies (Dely-Draskovits and Papp, 1973; Krivosheina et al., 1986). However, they develop in decomposing semi-liquid fruit bodies.

In Moscow Province, a typical inhabitant of such substrates is *D. phalerata* Mg. Its larvae usually accompany the first-order consumers—larvae of sciaroid flies. The relations between fruit flies and other mycobiont groups have not yet been addressed in the literature.

Micromycophagy is considered to be the prevalent type of feeding in the larvae of Drosophilidae (Papp, 1976). It should be noted, however, that the larvae of fruit flies, like all the cyclorrhaphous dipterans, have external digestion.

Apart from the larvae of *Pegomya* R.-D., considered above, the representatives of Anthomyiidae do not reveal clear associations with fungal fruit bodies. For example, *Anthomyia pluvialis* (L.), reared from boletes, agarics, and the gasteromycete *Phallus impudicus* (Buxton, 1960; Chandler, 1978; Yakovlev, 1994), also develops in decomposing plant remains, bird nests, egg pods of acridoid grasshoppers, and corpses (Zimin, 1948). The larvae of *A. procellaris* Rd., commonly occurring in decaying plant remains, bird nests, rotting fruit, and carrion, were also found in the soft fruit bodies of such fungi as *Pleurotus*, *Tricholoma*, and *Agaricus* (Khalidov, 1984; Ferrar, 1987, etc.). Unfortunately, the condition of the fruit bodies was not specified.

A similar situation is observed in the genus *Delia* R.-D. The onion fly *Delia antiqua* (Mg.), a well-known pest of bulbous plants, was repeatedly reared from various agarics, such as *Armillariella mellea*, and russules (Elberg, 1981). The flies *D. florilega* (Ztt.) and *D. platura* (Mg.) are known as common seedling pests in greenhouses. However, the former species was reported to have been reared from boletes, and the latter, from fresh plasmodia of the myxomycete *Fuligo* (Buxton, 1954; Chandler, 1978; Krivosheina et al., 1986; Yakovlev, 1994).

The larvae of many anthomyiid species, developing in decomposing plant material, manure, wasp and bee nests, are usually regarded as sapro- or coprophages (Lobanov, 1962, etc.). The conflicting reports of the same species being observed to develop in fungal fruit bodies, living plants, and decomposing organic substrates may be explained by the fact that these species act as satellites of the phytophages utilizing the decaying phytomass.

Among the Fanniidae, 10 species of the genus *Fannia* R.-D. and 2 species of the genus *Piezura* Rd. were observed to develop in fungal fruit bodies (Lyneborg, 1970; Yakovlev, 1994; Rozkosny et al., 1997; Pont, 2000). However, all of these species except *P. graminicola* (Ztt) typically occur in sap concretions and hollows of tree trunks, in rotting wood and dust under the bark of dead and dying trees, decaying plant material, litter, compost, nests and burrows of rodents, nests of birds and hymenopterans, manure, and corpses.

The larvae of *F. canicularis* (L.), *F. difficilis* (Stein), *F. manicata* (Mg.), *F. melania* (Duf.), and *F. scalaris* (F.) are most common in carpophores of various pileate macromycetes. Development was observed only in the decomposing fungi (Chandler, 1978, etc.). At the same time, *F. canicularis* and *F. scalaris* may cause myiases in man and animals (Zimin, 1948; Stackelberg, 1956).

There are no direct observations of any species of Fanniidae developing in the fresh tissues of fungal fruit bodies. Their larvae use the fungi, as other organic substrates, during the period of intense decomposition.

Among the Muscidae, the larvae of the common synanthropic fly *Stomoxys calcitrans* (L.) were recorded in the king bolete and a russule (Chandler, 1978). However, these larvae typically occur in decomposing plant remains, horse and cow manure, garbage, straw and hay litter mixed with excrements (Porchinskii, 1910; Zimin, 1948; Derbeneva-Ukhova, 1952).

The common synanthropic species *Musca domestica* L. was reported to have been reared from *Peziza* sp. and *Russula delica* (Khalidov, 1984; Yakovlev, 1994). However, the larvae of this species usually develop in decaying substrates of both plant and animal origin. They were observed in manure, human feces, and kitchen garbage (Zimin, 1948; Derbeneva-Ukhova, 1952). We have repeatedly reared this fly from decomposing fruit bodies of various pileate fungi.

The data presented in this section show that the vast group of dipterans usually regarded as typical inhabitants of fungal fruit bodies actually consists of species developing in various decomposing substrates, including fungal ones. They should therefore be considered saprobionts in the broad sense. It would hardly be correct to regard the forms typically occurring in decomposing substrates of plant and fungal origin, as mycobionts, since most of them are evidently saprophages. However, it is quite possible that the larvae developing in the substrate surrounding the rotting fruit bodies may feed on the decomposing mycelium. Mycelium has been regarded as the main food source for the larvae of Sciaridae (Kennedy, 1974; Binns, 1975, etc.) and Sphaeroceridae (Papp, 1976). The fact that some species can develop in organic material of animal origin, including carrion, may indicate elements of necrophagy.

The larvae of *Gaurax* Lw., *Tricimba* Lioy, and some other members of the Chloropidae are common inhabitants of fungal fruit bodies. The fly *Tricimba fungicola* Dely-Drask. was reared from the fruit bodies of boletes, russules, and agarics, and *T. lineella* (Fll.), from puffballs, chanterelles, agarics, and russules as well as from living plant tissues. Although *T. cincta* (Mg.) was reared from the fruit bodies of hymenomycetes (mostly agarics), this species was also reported to occur in weakened plants, dying grass shoots, and damaged polypores (Dely-Draskovits, 1972a, 1983; Chandler, 1978; Nartshuk, 1987, etc.). The larvae of *Gaurax dubius* (Macq.) occur in old fruit bodies of polypores (Smith, 1964; Chandler, 1978; Økland and Hågvar, 1994), under the bark, and can be frequently found in the tunnels of bark beetles (Nartshuk, 1987). The fly *G. fascipes* Beck., reared from fungal substrates, was also observed under the bark of dying tree trunks and in bird nests (Smith, 1964, 1967). *Fiebrigella palposa* (Fll.) was reported to develop in fruit bodies of the brown cap bolete (Khalidov, 1984) and egg pods of acridoid grasshoppers (Séguy, 1934). The larvae of this species were also observed to feed as predators in aphid colonies.

Some species of Chloropidae act as satellites of first-order consumers, colonizing the plants only after they have been damaged by other insects. For example, the larvae of *Lasiosina cinctipes* (Mg.) are satellites of the phytophagous larvae of many species of the same family, such as *Chlorops pumilionis* (Bjerkander), which damages grasses (Nye, 1958; Wendt, 1968). Colonization of the stems damaged by primary phytophages is typical of the larvae of *Eribolus longulus* (Loew) and *E. nanus* (Zett.) (Valley and Foote, 1997). A similar mode of life was observed in the larvae of some representatives of Lauxaniidae, Syrphidae, and Lonchaeidae (Krivosheina, 1987).

The presence among Chloropidae of a number of species topically associated not only with fungal fruit bodies but also with decaying substrates of varying origin may be explained by their role as satellites of macromycophagous species. The satellites usually differ from the first-order consumers by being sapro- or coprophages. If the ecology of such species is insufficiently known, they may be erroneously regarded as macromycophages.

Facultative Mycobionts Living on the Surface of the Fungal Fruit Bodies and Mycelium (Epibionts)

There are published data on the association of the larvae of the biting midges *Forcipomyia* Mg. (Ceratopogonidae) with fruit bodies of asco- and hymenomycetes (Yakovlev, 1994, etc.). For example, *Forcipomyia ciliata* (Winn.) was reported to be associated with fruit bodies of *Gyromitra esculenta*, *Thelephora terrestris*, and also boletes, agarics, and russules (Saunders, 1924; Buxton, 1960). However, this species was also found in various decomposing plant remains and in rotting wood under the bark (Krivosheina and Mamaev, 1967).

The larvae of *Forcipomyia* Mg. usually occur on the surface of decomposing woody substrates, in the tunnels made by xylophilous insects, and in various cavities in the wood. The larvae concentrate in the areas containing mycelium or fruit bodies of lower ascomycetes. The epibiotic way of life of these larvae is largely correlated with their morphology: the presence of long, often branching outgrowths which may exceed half the body length. With such morphological features, it would be impossible for the larvae to live inside the carpophores.

With respect to the type of feeding, the larvae are saprosporophages, and possibly micromycophages.

There are occasional reports of flat footed flies of the genus *Callomyia* Mg. having been reared from agarics of the genus *Macrolepiota* (Khalidov, 1984). However, the larvae of this genus are obligatory epibionts, developing on the mycelium film. They have wide, strongly flattened bodies with specific branching lateral outgrowths (Krivosheina and Mamaev, 1967), excluding the possibility of endobiotic development.

With respect to the type of feeding, these larvae are micromycophages.

The associations between the larval gall midges (Cecidomyiidae) and the fruit bodies of fungi have been largely misinterpreted in the literature. For example, *Porricondyla media* Spungis was reared from the morel *Ptychoverpa bohemica* (Yakovlev, 1994), even though its larvae were also recorded in litter and soil cavities (Spungis, 1982). The larvae of porricondyline midges have slightly flattened bodies with long upright dorsal papillae, which prevent the larvae from living within the substrate. For the same reason, our previous report of adult Porricondylinae having been reared from fungal fruit bodies, in particular *Peziza* sp. (Krivosheina et al., 1986), appears to be erroneous.

Although *Bryomyia* Kieff. and *Peromyia* Kieff. (Lestremiinae) were reported to have been reared from *Piptoporus betulinus* (Yakovlev, 1994), the larvae of these genera possess well-developed, branching dorsal papillae, clearly indicating an epibiotic mode of life. The larvae of *Peromyia fungicola* (Kieff.) were found to develop on the surface of the fruit bodies of *Lactarius* sp., while the larvae of *P. monilis* Mam. were observed in a mold film on wood. Epibiotic biology is characteristic of the larvae of *Lestremia cinerea* Macq., which occur on the surface of various pileate fungi as well as on brown wood and moldy foliage (Mamaev and Krivosheina, 1965; Chandler, 1978). The species of Lestremiinae are typical epibionts, which accounts for their broad topical associations.

Eurybionts, Inhabiting Fungal Substrates in Different States

This group includes the dipteran species whose larvae are zoophagous.

Among Scenopinidae, Dolichopodidae, and Empididae, most of which have predaceous larvae, topical associations with fungal substrates are infrequent. In particular, the larvae of *Scenopinus sibirica* Kriv. occur in old dry fruit bodies of polypores (Krivosheina, 1982) as well as in dry wood dust in stumps and trunk hollows. Although there there is evidence of *S. fenestralis* (L.) developing in polypore fruit bodies, the larvae of this species normally occur in very diverse environments, feeding on insect larvae (Chandler, 1978).

The larvae of the dance fly *Tachypeza nubila* (Mg.) were recorded in the fruit bodies of various polypores (e.g., *Bjerkandera* sp.), agarics, paxils, the ascomycete *Daldinia*, and under tree bark (Chandler, 1978). The larvae of *Drapetis nigritellus* (Ztt.) were found in a myxomycete plasmodium but also occur in old cow manure (Laurence, 1953).

The larvae of *Medetera apicalis* Ztt. (Dolichopodidae) develop in the fruit bodies of the oyster mushroom *Pleurotus cornucopiae*, and those of *Medetera impigra* Coll., in the polypore *Abortiporus biennis* (Buxton, 1960). The latter species also commonly occurs in the tunnels of bark beetles and other xylobiont insects (Krivosheina, 1974). The larvae of *Dolichopus cruralis* Wahlb. were recorded in the xylotrophic polypores *Postia* sp., and also in the brown cap bolete (Yakovlev, 1994).

The larvae of house flies (Muscidae) developing in fungi are usually zoophagous (Karl, 1928; Hennig, 1964; Skidmore, 1985, etc.).

The predaceous larvae of *Hydrotaea dentipes* (F.), *H. armipes* (Fll.), and *Phaonia* R.-D. (Muscidae) can be found in the fresh fruit bodies of pileate fungi. The former two species also occur in manure, carrion, and other decaying organic remains (Porchinskii, 1910, 1911; Zimin, 1948; Stackelberg, 1956; Lobanov, 1984). The larvae of *Phaonia gobertii* (Mik) may be associated with *Inonotus hispidus* (Chandler, 1978) but usually occur under the bark of dying tree trunks, feeding on various xylophilous insects (Skidmore, 1985). The larvae of *P. subventa* (Harr.) [= *variegata* (Mg.)] were recorded in decomposing agarics, polypores (*Inonotus*, *Polyporus*), rotting wood, wasp nests, and even in corpses (Chandler, 1978). According to the published data (Buxton, 1960; Dely-Draskovits and Mihályi, 1972; Chandler, 1978), *P. rufiventris* (Scop.) (=*populi* Mg.) develops in chanterelles as well as in various agarics and russules. However, the larvae of this species typically develop in decomposing organic substrates, including carrion, and also in loose rotting wood of leaved trees, where they act as satellites of the larvae of Tipulidae, Rhagionidae, and other dipterans. The larvae of some species, for example, *P. trimaculata* (Bouché) are usual satellites of the phytophages developing on crucifers; they were observed to develop in cabbage, following its infestation by the phytophagous larvae of *Delia radicum* (L.) [=*brassicae* (Wied.)] and aphids (Uffen and Chandler, 1978).

The predaceous larvae of *Muscina levida* (Harr.) [=*assimilis* (Fll.)] and *M. stabulans* (Fll.), recorded in sac fungi, polypores, agarics, boletes, and russules (Buxton, 1960; Chandler, 1978, etc.), also live in decomposing materials of plant and animal origin (Porchinskii, 1910, 1913; Zimin, 1948).

Species of the genus *Mydaea* R.-D. are also associated with decomposing fruit bodies, mostly of pileate fungi, and with decaying plant remains (manure) (Buxton, 1960; Dely-Draskovits and Mihályi, 1972; Hackman and Meinander, 1979). The adults lay eggs directly on the surface of the fruit bodies, usually on the hymenophore. According to A.M. Lobanov (1977, 1984), some of the species recorded in fungi develop in cow manure. For example, *M. cornu* (Scop.) (=*scutellaris* R.-D.) was reared from russules, manure, and excrements. The species *M. humeralis* R.-D. [=*tincta* (Ztt.)] was reared from the fruit bodies of cup fungi and various agarics, but also from excrements and rotting wood. The larvae of *M. urbana* (Mg.) were recorded in the saddleback fungus, the stinkhorn, russules, and even in manure (Buxton, 1960; Lobanov, 1977; Yakovlev, 1994). According to the data of I.A. Porchinskii (1910), the larvae are predaceous.

Some specific biological features of the larvae of humpbacked flies (Phoridae) are considered below. A number of species, such as *M. giraudi* (Egg.), *M. pulicaria* Fll., *M. hirtiventris* (Wood) and others, can develop, besides fungal fruit bodies, also in bee nests, dead insects and mollusks, manure, etc. (Disney et al., 1981; Krivosheina et al., 1986), and also in inflorescences of the plantain (Disney, 1994; Disney and Evans, 1990). The larvae of *M. rufipes* (Mg.) were recorded in the fruit bodies of cap fungi (lorchel), boletes, russules, agarics, and even gasteromycetes, such as the stinkhorn (Buxton, 1960; Yakovlev, 1994, etc.). This species also develops in various decomposing substrates, including rotting fungi. In addition, it was reared from the xylobiont larvae of the beetles *Thanasimus formicarius* L. and *Blastophagus* (*Myelophilus*) *piniperda* L. (Morge, 1956). The fly *M. frameata* Schmitz was reared from the fruit bodies of xylotrophic fungi, varying in consistency from soft-leathery to spongy-suberose (Buxton, 1960; Disney, 1994, etc.). However, its larvae also inhabit the tunnels of bark beetles, often co-occurring with the larvae of Sciaridae and feeding on the dead larvae and pupae (Morge, 1956).

The larvae of some species of *Megaselia* Rd. feed as predators or necrophages, consuming aphids and eggs of slugs, coccids, and spiders (Schmitz, 1949; Yarkulov, 1972; Disney and Evans, 1979, etc.). The complex of species parasitizing the larvae and pupae of xylophilous insects, including such dipterans as Bibionidae, Sciaridae, and Tipulidae (Disney, 1980, 1997; Gemesi and Disney, 1991), is well known. We repeatedly observed development of these species in the larvae of Sciaridae. In fact, all the representatives of Phoridae reared by us from decomposing fungi and wood were parasites of dipteran larvae.

According to the published data, the larval trophic spectrum of humpbacked flies is considered to be very broad: from sapromycophagy to necro- and zoophagy. However, there is increasing evidence that these larvae prefer organic materials of animal origin (Disney, 1979). Feeding by necrophagy is not restricted to invertebrates, since some species can develop in corpses of warm-blooded vertebrates (Disney, 1974). Necro- and zoophagy may well represent the predominant types of feeding in this family.

A similar situation is observed in the larvae of *Lonchaea* Fll. (Lonchaeidae). The larvae of *L. chorea* (F.), *L. laticornis* Mg., and *Setisquamalonchaea fumosa* Egger were recorded in fungi (Chandler, 1978, etc.). In particular, *L. chorea* (F.) was reared from fresh plasmodia of the myxomycete *Fuligo septica* (Chandler, 1978). However, the larvae of this species normally occur in such organic-rich substrates as rotting vegetables or cow manure (Hennig, 1953; Lobanov, 1962, etc.). Although the larvae of *S. fumosa* were found to be associated with the fruit bodies of the fly agaric and the stinkhorn (at the "egg" stage), they more typically develop in decomposing plant remains.

The larvae of most species of *Lonchaea* Fall. are necro- and zoophagous. They reveal close topical associations with phyto- and xylophagous larvae of dipterans, beetles, and lepidopterans, after which they colonize the substrates. Therefore, these larvae may form topical, but not trophic, associations with fungal fruit bodies.

Zoophagy, often including elements of necrophagy, allows the species to develop in very diverse substrates. In the fungi, such species act as satellites of macromycophagous mycobionts, i.e., as second-order consumers, and may only provisionally be regarded as mycobionts. No species exclusively associated with fungal substrates have so far been found.

Species Visiting the Fungal Fruit Bodies

There is a relatively large group of dipterans whose adults visit the fruit bodies of fungi.

The adults of *Acartophthalmus nigrinus* (Ztt.) (Acartophthalmidae) were recorded as visitors of the polypore fruit bodies (Chandler, 1978). Fresh fruit bodies of *Pleurotus* are visited by *A. bicolor* Old. (Chandler, 1998), whose larvae develop in corpses of vertebrates (Ozerov, 1987). The polyporous fungi are visited by members of the family Odiniidae: *Odinia boletina* (Ztt.) and *O. maculata* (Mg.) (Chandler, 1978). The larvae of these species are predaceous and occur in the tunnels made by various xylophagous insects (Krivosheina, 1979).

The species *Anthomyza albimana* (Mg.) (Anthomyzidae) should be regarded merely as a visitor of fungi (Dely-Draskovits, 1972b; Chandler, 1978), rather than included in the list of species developing in the fungal fruit bodies (Yakovlev, 1994).

The specific carrion odor emitted by the stinkhorn *Phallus impudicus* efficiently attracts such dipterans as *Calliphora* R.-D., *Lucilia* R.-D. (Calliphoridae), *Dryomyza flaveola* (F.), *Neuroctena anilis* Fll. (Dryomyzidae), and others, whose larvae develop in decomposing animal substrates (Smith, 1956). E.B. Yakovlev (1994) erroneously suggested that these species developed in *Phallus*. Unfortunately, the insects visiting the fungal fruit bodies are often mistakenly described as typical mycobionts.

CONCLUSION

Fungi occupy a special position in the system of the living organisms, combining some characters of both animals and plants. With respect to chemical composition (Vasil'kov, 1966; Martin, 1979), the fungal fruit bodies contain a complete set of nutrients needed for the development of both phytophagous and zoophagous insects. This is why the same species of dipterans can develop in different decomposing organic substrates including fungal ones. The presence of toxins in the fruit bodies of some fungi, for example, *Amanita*, does not prevent insects from developing in them (Hackman and Meinander, 1979).

Based on the specific composition of mycobiont insects developing in fungal fruit bodies, some authors suggested that the association of a macromycete might be considered as a specific consortium (Beklemishev, 1951; Ostroverkhova, 1984). E.B. Yakovlev (1985) suggested that the mycelium with all its fruit bodies should be regarded as the core of the consortium. Without going into terminological discussion, it should be emphasized that the complex of organisms inhabiting living carpophores is specific enough to be studied separately.

Rapid preimaginal development is a necessary adaptation for the species inhabiting the fruit bodies of agaric fungi. This feature is observed both in the lower nematoceran families (Bolitophilidae, Mycetophilidae) and in representatives of the higher cyclorrhaphous dipterans. Development of many species of *Pegomya*, which are obligatory mycobionts, may take no more than 10 days (Hackman and Meinander, 1979).

One more ecological feature observed in some mycobionts inhabiting short-living agaricoid fruit bodies, is delayed development of eggs laid in the fresh substrate. This phenomenon is typical of the insects associated with the fruit bodies of *Phallus impudicus* (Smith, 1956). Of the few species inhabiting this fungus, the eggs of *Drosophila busckii* Curt. have been found on the growing fruit body. However, the larvae, preferring decomposing substrates (Basden, 1952), hatch only when the fruit body is decaying.

According to our observations of isolated fresh fruit bodies, development of the larvae of Psychodidae, Scatopsidae, and Drosophilidae started only after the decomposing substrate became liquid. Therefore, these dipterans laid eggs on the fruit bodies while they were fresh. It remains unknown whether the saprophages can develop in the absence of macromycophages, facilitating decomposition of the fruit bodies.

To summarize, the following points should be made. Among the dipterans ecologically and trophically associated with fungal fruit bodies, only several families include true macromycophages, whose larvae consume living tissues of the fruit bodies and thus belong to the first-order consumers.

Based on the scarce data, a specific group of macromycophage satellites can be distinguished. They have mostly saprophagous larvae living in the damaged fruit bodies. This group comprises some species of Sciaridae, Chloropidae, Sphaeroceridae, and possibly Anthomyiidae.

The largest group is that of the species topically associated with decomposing substrates. Most species from various families, regarded as mycobionts in the literature, are in fact saprobiont forms which may utilize fungal substrates in the same way as they use other decomposing organic materials of plant or animal origin.

It remains unknown if there are obligatory mycobiont dipteran species feeding as zoophages, i.e., acting as the second-order consumers. Most of the zoophagous forms recorded in fungal fruit bodies typically occur in many other substrates as well.

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REFERENCES

1. Andrews, H.W., "*Helomyza variegata* Lw. Breeding in Roots of Sea-Aster," Entomol. Rec. J. Var. **57**, 32 (1945).
2. Basden, E.B., "Some Drosophilidae (Diptera) of the British Isles," Entomol. Mon. Mag. **88**, 200–201 (1952).
3. Beklemishev, V.N., "On the Classification of Biocenotic (Symphysiological) Relations," Byul. Mosk. Obshch. Ispyt. Prirody Otd. Biol. **56** (5), 5–30 (1951).
4. Binns, E.S., "Mushrooms Mycelium and Compost Substrates in Relation to the Survival of the Larva of the Sciarid *Lycoriella auripila*," Ann. Appl. Biol. **80** (1), 1–15 (1975).
5. Binns, E.S., "Mating Behavior, Fecundity and Feeding in the Mushroom Phorid, *Megaselia halterata* (Wood) (Dipt.)," Entomol. Month. Mag. **116** (1388/1391), 45–57 (1980).
6. Bondartseva, M.A., *Keys to Fungi of Russia. Order Aphyllophorales. Part 2* (Nauka, St. Petersburg, 1998) [in Russian].
7. Brindle, A., "Taxonomic Notes on the Larvae of British Diptera. 75. The Clythiidae (Platypezidae)," Entomologist **94**, 275–278 (1961).
8. Brindle, A., "The Larvae and Pupae of the British Cylindrotominae and Limoniinae (Diptera, Tipulidae)," Trans. Soc. Brit. Entomol. **17** (7), 151–216 (1967).
9. Broadhead, E.C., "Larvae of Trichocerid Flies Found on Human Corpse," Entomol. Month. Mag. **116** (1388/1391), 23–24 (1980).
10. Burla, H. and Bächli, G., "Beitrag zur Kenntnis der schweizerischen Dipteren, insbesondere Drosophila-Arten, die sich in Fruchtkörpern von Hutpilzen entwickeln," Vierteljahresch. Naturforsch. Ges. Zurich. **113** (4), 311–336 (1968).
11. Buxton, P.A., "British Diptera Associated with Fungi. 2. Diptera Bred from Myxomycetes," Proc. Roy. Entomol. Soc. London **A29**, 163–171 (1954).
12. Buxton, P.A., "British Diptera Associated with Fungi. 3. Flies of All Families Reared from about 150 Species of Fungi," Entomol. Month. Mag. **96**, 61–91 (1960).
13. Buxton, P.A. and Barnes, H.E., "British Diptera Associated with Fungi. 1. Gall Midges (Cecidomyiidae) Reared from the Larger Fungi," Proc. Roy. Entomol. Soc. London **B22**, 195–200 (1953).
14. Chandler, P.J., "Associations with Plants. Fungi," Amateur Entomol. **15**, 199–228 (1978).
15. Chandler, P.J., "*Acartophthalmus bicolor* Oldenberg and *Meoneura neottiophila* Collin (Diptera, Acartophthalmidae and Carnidae) on *Pleurotus*," Dipterist's Digest **5**, 30–33 (1998).
16. Elberg, K.Yu., "24. Family Anthomyiidae, Rootmaggot Flies," in *Insect and Acarine Agricultural Pests. Vol. IV: Hymenoptera and Diptera* (Nauka, Leningrad, 1981), pp. 188–198 [in Russian].
17. Dahl, Ch., "Notes on the Taxonomy and Distribution of Swedish Trichoceridae (Dipt. Nemat.)," Opuscula Entomol. **31** (1/2), 93–118 (1966).
18. Dely-Draskovits, A., "Systematische und ökologische Untersuchungen an den in Ungarn als Schädlinge der Hutpilze auftretenden Fliegen. I. Limoniidae, Syrphidae, Platypezidae, Chloropidae (Diptera)," Acta Zool. Acad. Sci. Hung. **18** (1/2), 7–21 (1972a).
19. Dely-Draskovits, A., "Systematische und ökologische Untersuchungen an den in Ungarn als Schädlinge der Hutpilze auftretenden Fliegen. 4. Trichoceridae, Scatopsidae, Heleomyzidae, Anthomyzidae," Acta Zool. Acad. Sci. Hung. **18** (3/4), 283–290 (1972b).
20. Dely-Draskovits, A., "Revision der Typen der palaearktischen Arten der Gattung *Tricimba* Lioy, 1864 (Diptera, Chloropidae)," Acta Zool. Acad. Sci. Hung. **29** (4), 327–355 (1983).
21. Dely-Draskovits, A. and Babos, M., "Flies (Diptera) in Mar-Fungi Species in Hungary," Folia Entomol. Hung. **54**, 17–45 (1993).
22. Dely-Draskovits, A. and Mihályi, F., "Systematische und ökologische Untersuchungen an den in Ungarn als Schädlinge der Hutpilze auftretenden Fliegen. 3. Anthomyiidae, Muscidae (Diptera)," Annls Hist.-Nat. Mus. Natn. Hung. **64**, 323–329 (1972).
23. Dely-Draskovits, A. and Papp, L., "Systematical and Ecological Investigations of Fly Pests of Mushrooms in Hungary. 5. Drosophilidae (Diptera)," Folia Entomol. Hung. **26** (1), 21–29 (1973).
24. Derbeneva-Ukhova, V.P., *Flies and Their Epidemiological Significance* (Medgiz, Moscow, 1952) [in Russian].
25. Disney, R.H.L., "A Comment on the Identity of *Megaselia* Flies Reared from Dead Shrews," Naturalist, No. 931, 138 (1974).
26. Disney, R.H.L., "Natural History Notes on Some British Phoridae (Diptera) with Comments on a Changing Picture," Entomologist's Gazette **30**, 141–150 (1979).
27. Disney, R.H.L., "A Scuttle Fly (Dipt. Phoridae) that Parasitizes Larvae of *Trichosia* Winnertz (Dipt., Sciaridae)," Entomol. Mon. Mag. **116** (1388/1391), 5–6 (1980).
28. Disney, R.H.L., "*Megaselia sandhui* sp. n. (Diptera, Phoridae) a Pest of Cultivated Mushrooms in India," Bull. Entomol. Res. **71** (3), 509–512 (1981).
29. Disney, R.H.L., *Scuttle Flies: The Phoridae* (Chapman and Hall, L., 1994).

30. Disney, R.H.L., “A New Species of Phoridae (Diptera) that Parasitizes a Widespread Asian Ladybird Beetle (Coleoptera: Coccinellidae),” Entomologist **116**, 163–168 (1997).
31. Disney, R.H.L. and Evans, R.E., “Phoridae (Diptera) Whose Larvae Feed on Eggs of Spiders (Araneida),” Entomol. Month. Mag. **115** (1376/1379), 21–22 (1979).
32. Disney, R.H.L. and Evans, R.E., “Some New Records of Fungus-Breeding Phoridae (Diptera),” Dipterist’s Digest **7**, 20–23 (1990).
33. Disney, R.H.L., Coulson, J.C., and Butterfield, J., “A Survey of the Scuttle Flies (Diptera: Phoridae) of Upland Habitats in Northern England,” Naturalist **106**, 53–66 (1981).
34. Dušek, J., “Die Larve von *Clythia fasciata* Meigen (Diptera, Clythiidae),” Acta Soc. Entomol. Czechosl. **59** (3), 209–213 (1962).
35. Ferrar, P., *A Guide to the Breeding Habits and Immature Stages of Diptera Cyclorrhapha* (E.J. Brill and Scandinavian Science Press, Leiden and Copenhagen, 1987).
36. Garibova, L.V. and Lukomtseva, S.M., *Fundamentals of Mycology. Morphology and Taxonomy of Fungi and Fungus-Like Organisms* (KMK, Moscow, 2005) [in Russian].
37. Gemesi, O. and Disney, R.H.L., “A Further Case of Parasitization of Larval Bibionidae by a Scuttle Fly (Diptera: Phoridae),” Entomologist’s Gazette **42** (1), 67–69 (1991).
38. Gerbachevskaya, A.A. and Stadnitskii, G.V., “Dark-winged Fungus Gnats (Sciaridae, Diptera) Reared from Common Spruce Cones,” Entomol. Obozr. **48** (4), 812–815 (1969).
39. Glukhova, V.M., *Larvae of Biting Midges of the Subfamilies Palpomyiinae and Ceratopogoninae in the Fauna of the USSR (Diptera, Ceratopogonidae–Heleidae)* (Nauka, Leningrad, 1979) [in Russian].
40. Hackman, W., “On the Genera *Scaptomyza* Hardy and *Parascaptomyza* Duda (Dipt., Drosophilidae),” Notulae Entomol. **35**, 74–91 (1955).
41. Hackman, W., “On Diptera in Small Mammals’ Burrows in Northern Europe and Southern Spain,” Notulae Entomol. **67**, 1–14 (1967).
42. Hackman, W. and Meinander, M., “Diptera Feedings as Larvae on Macrofungi in Finland,” Ann. Zool. Fenn. **16** (1), 50–83 (1979).
43. Hennig, W., “Milichiidae et Carnidae,” in *Die Fliegen der palaearktischen Region. Vol. 6 (1)* (Stuttgart, 1937), pp. 1–91.
44. Hennig, W., “Piophilidae,” in *Die Fliegen der palaearktischen Region. Vol. 5* (Stuttgart, 1943), pp. 1–52.
45. Hennig, W., “Diptera. Zweiflügler,” in *Handbuch der Pflanzenkrankenheiten. Bd 5 (5). Lfr. I* (Berlin, 1953), pp. 108–110.
46. Hennig, W., “Muscidae,” in *Die Fliegen der palaearktischen Region. Vol. 7 (2)* (Stuttgart, 1964), pp. 1–1110.
47. Janvier, H., “La mouche de la truffe (*Helomyza tuberiperda* Rondani) (Dipt., Helomyzidae),” Bul. Soc. Entomol. France **68** (5/6), 140–147 (1963).
48. Jezek, J., “Redescription of Nine Common Palaearctic and Holarctic Species of Psychodini End. (Diptera: Psychodidae),” Acta Entomol. Mus. Nat. Pragae **43**, 33–83 (1990).
49. Karl, O., “Zweiflügler oder Diptera. 2. Muscidae,” in *Tierwelt Deutschlands. Bd 13* (1928), pp. 1–232.
50. Kennedy, M.K., “Survival and Development of *Bradysia impatiens* (Diptera: Sciaridae) on Fungal and Non-Fungal Food Sources,” Ann. Entomol. Soc. Amer. **67** (5), 745–749 (1974).
51. Kessel, E.L., Buegler, M.E., and Keyes, P.M., “A Survey of the Known Larvae and Puparia of Platypezidae, with a Key to Ten Genera Based on Immature Stages (Diptera),” Wasmann J. Biol. **31** (2), 233–259 (1973).
52. Khalidov, A.B., *Insects Destroying Fungi* (State Univ., Kazan, 1984) [in Russian].
53. Knoop, M., *Pilze: Bestimmen, Sammeln, Zubereiten* (Falken, 1997; BMM, Moscow, 2000) [in Russian].
54. Krasutskii, B.V., *Mycetophilic Beetles of the Urals and Transural Region. The Fungus-Insect System. Vol. 2* (Chelyabinsk, 2005) [in Russian].
55. Krivosheina, N.P., *Ontogenesis and Evolution of Diptera* (Nauka, Moscow, 1969) [in Russian].
56. Krivosheina, N.P., “Morphology of Larvae of Long-Legged Flies of the Genus *Medetera* Fisch. (Diptera, Dolichopodidae),” Entomol. Obozr. **53** (2), 309–323 (1974).
57. Krivosheina, N.P., “On the Taxonomy and Biology of the Palaearctic Species of Flies of the Family Odiniidae (Diptera) Feeding on Xylophilous Insects,” in *Wood-Destroying Insects and Their Entomophages* (Nauka, Moscow, 1979), pp. 130–157 [in Russian].
58. Krivosheina, N.P., “New Members of the Genus *Scenopinus* (Diptera, Scenopinidae) in the Fauna of the USSR,” Zool. Zh. **60** (1), 160–164 (1982).
59. Krivosheina, N.P., “Significance of Dipterans as Forest and Agricultural Pests,” in *Dipterans and Their Significance for Agriculture* (Zool. Inst., Leningrad, 1987), pp. 49–53 [in Russian].
60. Krivosheina, N.P., “Taxonomic Composition of Dendrobiontic Diptera and the Main Trends of Their Adaptive Radiation,” Zool. Zh. **85** (7), 842–852 (2006) [Entomol. Review **86** (5), 557–567 (2006)].
61. Krivosheina, N.P. and Mamaev, B.M., *Key to Xylophilous Larvae of Dipterans* (Nauka, Moscow, 1967) [in Russian].
62. Krivosheina, N.P., Zaitzev, A.I., and Yakovlev, E.B., *Mycetophilous Insects in Forests of the European Part of the USSR* (Nauka, Moscow, 1986) [in Russian].
63. Laurence, B.R., “Some Diptera Bred from Cow Dung,” Entomol. Month. Mag. **89**, 281–283 (1953).
64. Lindner, E., “Pilzbewohnende Limoniiden-Larven unter besonderer Berücksichtigung von *Limonia quadrinotata*

Mg. (Diptera)," Tijdschr. Entomol. **101**, 263–281 (1958).

65. Lobanov, A.M., "Wintering Places of the Preimaginal Stages of Synanthropic Flies," Nauchn. Doklady Vysshei Shkoly Biol. Nauki, No. 2, 36–40 (1962).
66. Lobanov, A.M., "Morphology of Old-Instar Larvae of Helomyzidae (Diptera)," Zool. Zh. **49** (11), 1671–1674 (1970).
67. Lobanov, A.M., "On the Position of the Genus *Graphomyia* in the System of Muscidae (Diptera)," in *Insects as Vectors of Transmissible Diseases* (Ivanovo, 1977), pp. 80–85 [in Russian].
68. Lobanov, A.M., "Prerequisites and Possible Ways of Transition to Synanthropic Life in Flies of the Family Muscidae," in *Morphology and Ecology of Flies as Possible Vectors of Transmissible Diseases* (State Med. Inst., Ivanovo, 1984), pp. 4–15 [in Russian].
69. Lyneborg, L., "Taxonomy of European *Fannia* Larvae (Diptera, Fanniidae)," Stuttgarter Beiträge zur Naturkunde, No. 215, 1–28 (1970).
70. Mamaev, B.M., *Evolution of Gall Midges* (Nauka, Leningrad, 1968) [in Russian].
71. Mamaev, B.M., "Dipterans Forming Galls on Polypore Fruit Bodies," Doklady Acad. Sci. USSR **202** (1), 243–244 (1972).
72. Mamaev, B.M. and Krivosheina, N.P., *Larvae of Gall Midges (Diptera, Cecidomyiidae). Comparative Morphology, Biology, and Keys* (Nauka, Moscow, 1965) [in Russian].
73. Martin, M.M., "Biochemical Implications of Insect Mycophagy," Biol. Review **54**, 1–21 (1979).
74. Morge, G., "Beobachtungen über parasitische Lebenswiese der Larven von *Megaselia rufipes* Meigen (Diptera, Phoridae)," Beitr. Entomol. **6** (1/2), 121–123 (1956).
75. Nartshuk, E.P., *Frit Flies, Their System, Evolution, and Relations with Plants* (Nauka, Leningrad, 1987) [in Russian].
76. Nye, I.W.B., "The External Morphology of Some of the Dipterous Larvae Living in the Gramineae of Britain," Trans. R. Entomol. Soc. Lond. **110**, 411–487 (1958).
77. Økland, B. and Hågvar, S., "The Insect Fauna Associated with Carpophores of the Fungus *Fomitopsis pinicola* (Fr.) Kartst. in Southern Norwegian Spruce Forest," Fauna Norv. Ser. B **41** (1), 29–42 (1994).
78. Ostroverkhova, G.P., "The Complex of Mycetophiloidea (Diptera) as a Natural Component of Forest Ecosystems," in *Dipterans in the Fauna of the USSR and Their Role in Ecosystems* (Zool. Inst., Leningrad, 1984), pp. 90–92 [in Russian].
79. Ozerov, A.L., "Preimaginal Morphology and Biology of *Acartophthalmus bicolor* Oldenberg (Diptera, Acartophthalmidae)," Nauchn. Doklady Vysshei Shkoly Biol. Nauki, No. 6, 32–35 (1987).
80. Ozerov, A.L., "Scavenger and Skipper Flies (Diptera: Sepsidae, Piophilidae) of the Zeya State Nature Reserve," Entomol. Obozr. **68** (4), 839–849 (1989a).
81. Ozerov, A.L., "On Necrobiotic Dipterans of the Far East," in *Insects in the Ecosystems of Siberia and the Far East* (Mos. State. Univ., Moscow, 1989b), pp. 114–142 [in Russian].
82. Ozerov, A.L., *Scavenger Flies (Diptera, Sepsidae) of the Russian Fauna* (Mos. State. Univ., Moscow, 2003) [in Russian].
83. Papp, L., "Systematical and Ecological Investigations on Fly Pest of Fungi in Hungary. II. Sphaeroceridae and Asteiidae (Diptera)," Annls Hist.-Nat. Mus. Natn. Hung. **64**, 315–317 (1972).
84. Papp, L., "Some Terricole Sphaerocerids and Drosophilids from Hungary (Diptera: Sphaeroceridae and Drosophilidae)," Folia Entomol. Hung. **29** (1), 75–85 (1976).
85. Papp, L., "Some Fungivorous Species of Sphaeroceridae and Drosophilidae (Diptera) from Karelia, USSR," Folia Entomol. Hung. **32** (2), 189–193 (1979).
86. Papp, L., "Morphology of Third Instar Larva and Puparium of Three Heleomyzid Species (Diptera: Heleomyzidae)," Acta Zool. Hung. **40** (3), 219–229 (1994).
87. Pavlyuchenko, A.A., "The Family Sciaridae (Lycoriidae)," in *Insect and Acarine Agricultural Pests. Vol. IV: Hymenoptera and Diptera* (Nauka, Leningrad, 1981), pp. 66–68 [in Russian].
88. Pont, A.C., "Family Fanniidae," in *Contributions to a Manual of Palaearctic Diptera* (Science Herald, Budapest, 2000), pp. 447–454.
89. Porchinskii, I.A., "The Stable Fly: Biology and Relations to Other Flies," Trudy Byuro Entomol. **8** (8), 1–90 (1910).
90. Porchinskii, I.A., "The Fly *Hydrotaea dentipes* F.," Trudy Byuro Entomol. **9** (5), 3–30 (1911).
91. Porchinskii, I.A., "The False Stable Fly (*Muscina stabulans* Fall.), Its Economic Significance and Relation to the House Fly," Trudy Byuro Entomol. **10** (1), 3–36 (1913).
92. Richards, O.W., "The British Species of Sphaeroceridae (Borboridae, Diptera)," Proc. Zool. Soc. London **18**, 261–345 (1930).
93. Rozkošný, R., Gregor, F., and Pont, A.C., "The European Fanniidae (Diptera)," Acta Sci. Nat. Brno **31** (2), 1–80 (1997).
94. Saunders, L.G., "On the Life History and the Anatomy of the Early Stages of *Forcipomyia* (Diptera, Nematocera, Ceratopogonidae)," Parasitology **16**, 164–213 (1924).
95. Schmitz, H., "Phoridae," in *Die Fliegen der palaearktischen Region. Lfg. 160* (Stuttgart, 1949), pp. 193–324.
96. Séguy, E., *Diptéres (Brachycéres). Faune de France. T. 28* (Paris, 1934).
97. Ševčik, J., "Diptera Associated with Fungi in the Czech and Slovak Republics," Cas. Slez. Mus. Opava (A) **55** (Suppl. 2), 1–84 (2006).

98. Shatalkin, A.I., "A Review of Flat-Footed Flies (Diptera, Platypezidae) in the Fauna of the USSR," in *Morphological and Geographic Aspects of Insect Evolution* (Mos. State. Univ., Moscow, 1985), pp. 69–136 [in Russian].
99. Shorrocks, B. and Charlesworth, P., "The Distribution and Abundance of the British Fungal-Breeding *Drosophila*," Ecol. Entomol. **5**, 61–78 (1980).
100. Skidmore, P., "Notes on the Helomyzidae of Lancashire and Cheshire, Including Records from Other Parts of North West England," Entomologist **95**, 193–198, 226–236 (1962).
101. Skidmore, P., "Some Micro-Habitats. Dung," Amateur Entomol. **15**, 73–79 (1978).
102. Skidmore, P., *The Biology of the Muscidae of the World. Series Entomol. 29* (Dr. W. Junk Publ., Dordrecht, 1985).
103. Smith, K.G.V., "On the Diptera Associated with the Stinkhorn (*Phallus impudicus* Pers.) with Notes on Other Insects and Invertebrates Found on This Fungus," Proc. Roy. Entomol. Soc. (A) **31**, 49–55 (1956).
104. Smith, K.G.V., "The Immature Stages of *Gaurax* (*=Botanobia*) *dubius* (Macquart) (Dipt., Chloropidae), with Notes on the Species Status of *G. fascipes* Becker," Entomol. Mon. Mag. **100**, 237–239 (1964).
105. Smith, K.G.V., "A Further Note on *Gaurax fascipes* Becker (Dipt., Chloropidae)," Entomol. Mon. Mag. **102**, 149 (1967).
106. Spungis, V.V., "Ecology of Soil-Dwelling Gall Midges in Latvia," in *Fauna, Protection, and Rational Use of Invertebrates in the Latvian SSR* (Riga, 1982), pp. 32–45 [in Russian].
107. Stackelberg, A.A., *Synanthropic Dipterans in the Fauna of the USSR* (Acad. Sci. USSR, Moscow, 1956) [in Russian].
108. Steffan, W.A., "Notes on Hawaiian Sciaridae (Diptera) and Descriptions of Two New Species," Pacif. Insects **15** (3/4), 353–361 (1973).
109. Uffen, R. and Chandler, P., "Associations with Plants. Higher Plants," Amateur Entomol. **15**, 213–228 (1978).
110. Valley, K.V. and Foote, B.A., "Biology and Immature Stages of *Eribolus longulus*, with Notes on *E. nanus* (Diptera: Chloropidae), Secondary Invaders of Herbaceous Wetland Plants," Mem. Entomol. Soc. Wash. **18**, 273–279 (1997).
111. Vaňhara, J., "*Kesselimyia chandleri* n. gen., n. sp. from Czechoslovakia (Diptera: Platypezidae)," Entomol. Scand. **12**, 183–186 (1981).
112. Vasil'kov, B.P., *The King Bolete. A One-Species Monograph* (Nauka, Moscow, 1966) [in Russian].
113. Wendt, H., "Faunistisch-ökologische Untersuchungen an Halmfliegen der Berliner Umgebung (Dipt., Chloropidae)," Deutsch. Entomol. Zeitschr. N. F. **15** (1–3), 49–105 (1968).
114. White, P.F., "Control of the Mushroom Phorid *Megaselia halterata* (Wood) with Dichlorvos Applied by an Automatic Atomiser," Plant Pathol. **30** (1), 37–40 (1981).
115. Yakovlev, E.B., "Consortive Relations between Insects and Macromycetes," in *Mycosymbiotropism and Other Consortive Relations in Northern Forests* (Karel. Branch Acad. Sci. USSR, Petrozavodsk, 1985), pp. 152–164 [in Russian].
116. Yakovlev, E.B., *Palaearctic Diptera Associated with Fungi and Myxomycetes* (Karel. Scientific Center, Petrozavodsk, 1994) [in Russian].
117. Yarkulov, F., "The Humpbacked Fly *Phora holosericea* (Diptera, Phoridae), a Predator of Root Aphids," Zool. Zh. **51** (9), 1415–1418 (1972).
118. Zagulyaev, A.K., "Trophic Specialization and Evolution of Feeding Modes in Tineid Moths (Lepidoptera, Tineidae)," in *N.A. Kholodkovsky Memorial Lectures, Issue 21* (Nauka, Leningrad, 1969), 3–26 [in Russian].
119. Zaitzev, A.I., *Fungus Gnats in the Fauna of Russia and Adjacent Countries. Part 1* (Nauka, Moscow, 1994) [in Russian].
120. Zaitzev, A.I., "Fungus Gnats (Diptera, Sciaroidea) of the Fauna of Russia and Adjacent Regions. Part II," Int. J. Dipterol. Res. **14** (2–4), 77–386 (2003).
121. Zimin, L.S., *Keys to Larvae of Synanthropic Flies of Tajikistan* (Acad. Sci. USSR, Moscow, 1948) [in Russian].
122. Zuska, J. and Laštovka, P., "A Review of the Czechoslovak Species of the Family Piophilidae with Special Reference to Their Importance to Food Industry (Diptera, Acalyptrata)," Acta Entomol. Bohemosl. **62** (2), 141–157 (1965).