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Large mites on wild mushrooms in Britain*

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Fungivorous mites and other acari associated with mushroom colonies are known since the beginning of acarology. Most of them are tiny and difficult or impossible to see with the naked eye. Most are myceliophagous mites (Behan & Hill, 1978; Renker *et al*., 2005; Werner *et al*., 2018). Large mites visible unaided on the stems, caps, or gills of the fleshy fruiting bodies of life wild mushrooms have been widely observed by naturalists but have rarely been documented in the acarological literature.

The mite fauna of living macrofungi may, in parts, be different from that of dead or decaying fungi (Hågvar & Steen, 2013; Gdula *et al*., 2021b; Gdula *et al*., 2022). We expect some overlap with oribatid mites from soil, especially stressed soil. A few studies explored the diversity of mites on particular groups of fungi (Gwiazdowicz & Lakomy, 2002; Makarova, 2004; Okabe, 2013; Faraji *et al*., 2021; Lunde *et al*., 2022). Some mite species have adapted to the fruiting bodies of bracket fungi (Basidiomyceta, Polyporales). For example, members of several mesostigmatid genera like *Hoploseius*, *Mycolaelaps*, *Fungiseius* and *Discoseius* (Ascidae/Blattisociidae) are found exclusively on or in the fungi.

Field surveys of various habitat classes (mixed broadleaf, coniferous mixed, hedgerow, mixed woodland, scrub, and pasture) in England and Wales yielded 218 mites, collected from the fruiting body of macrofungi belonging to the Ascomyceta (sac fungi) and Basidiomyceta (mushrooms and allies) (n = 67, comprising 15 orders, 20 families, and 32 species).

In these surveys, Oribatida are the dominant group (124 specimens), followed by Mesostigmata (28 specimens). Together, they represent more than 90 % of the identified species.

It could be expected that bigger mushrooms enable more diversity of mite species, and that longevity of the mushroom fruiting body determines the frequency with which mites are found. The acarological literature tells otherwise. There is surprisingly little correlation between mushroom size and mite diversity (Okabe, 2013). The most common mite species associated with mushrooms are more often found on ephemeral fruiting bodies that last only days to three weeks as in gilled mushrooms (Basidiomycota, Agraricales), Fig. 1 A–C. Voluminous, longer-lasting fruiting bodies such as in annual fruiting bodies, Fig. 1 D–F, and perennial fruiting bodies, Fig. 1 G, where subsequent layers are deposited on top of each other in shelf-like manner, pileate, or thin fruiting bodies covering large areas, resupinate, carry a higher diversity of mite species but are less likely to hold mite species common to mushroom cultures (Okabe, 2013). Shorter-lived fruiting bodies are soft while longer-lived are increasingly tougher. The extended time allows certain species to develop numbers in the hundreds on these fruiting bodies; for example, *Asca* and *Lasioseius* species (Ascidae), *Hoploseius* species (Blattisociidae), and *Ameroseius* species (Ameroseiidae) among the Mesostigmata, and *Boletoglyphus*, *Schwiebea*, and *Umakefeq* species (Acaridae) among the Astigmata. Fruiting bodies lasting for up to several years provide opportunities for more specialized associations (Lunde *et al*., 2022). Among the longer-lasting fruiting bodies, two contrasting scenarios are encountered that make it sometimes difficult to distinguish between mite species associated with dead or live tissues. For example, in the birch bracket

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fungus or razor strop, *Fomitopsis betulinus* (Basidiomycota, Fomitopsidaceae), Fig. 1 D, the sporophores die after discharging their spores, but persist in the living mushroom for two more years. The dead sporophores attract a divers mite fauna. In contrast, in the perennial bracket, hoof, tinder, or ice man fungus, *Fomes fomentarius* (Basidiomycota, Polyporaceae), the spore-producing tissue survives for several years. The hypothesis is that there should be some differences in the mite diversity between the two fungal life strategies. The mite fauna of three species of fungi with dead sporophores was compared with one species with live sporophores listed in Table 1.

TABLE 1. Differences in mite diversity between dead sporophores in living annual mushrooms and live sporophores in perennial mushrooms. Data for the birch bracket fungus, *Fomitopsis betulinus*, from Pielou and Verma (1968), data for the red belt conk, *F. pinicola*, in Poland, Mesostigmata and Oribatida only, from Gdula, Skubała, *et al.* (2021), data for the coal fungus, *Daldinia concentrica*, in England, United Kingdom, from (Hingley, 1971), and for *Fomes fomentarius*, from Pielou and Matthewman (1966) and Matthewman and Pielou (1971).

	Dead sporophores			**Live sporophores**
	Fomitopsis betulinus	*F. pinicola*	*Daldinia concentrica*	*Fomes fomentarius*
Astigmata				
Acarida	*Thyreophagus entomophagus*		*Thyreophagus* sp.	*Thyreophagus* nr *entomophagus*
Glycyphagidae			*Glycyphagus domesticus*.	
Hemisarcoptidae	*Nanacarus* sp.			*Nanacarus* sp.
Winterschmidtiidae	*Calvolia* spp.			*Calvolia* sp.
	Calvolia nr *elizabethae*			
Oribatida				
Achipteriidae		*Achipteria coleoptrata*		*Anachipteria* sp.
		A. nitens		
		Parachipteria punctata		
Autognetidae		*Autogneta dalecarlica*		
	Autogneta longilamellata	*A. longilamellata*	*Autogneta longilamellata*	
Caleremaeidae		*Caleremaeus monilipes*		
Camisiidae	*Camisia horrida*			
	C. segnis			
		Platynothrus peltifer		
Carabodidae	*Carabodes areolatus*	*Carabodes areolatus*		*Carabodes areolatus*
		C. coriaceus, C. femoralis		
		C. labyrinthicus	*Carabodes labyrinthicus*	
		C. ornatus, C. subarticus, C. tenuis		
Cepheiidae	*Cepheus* spp.	*Cepheus cepheiformis*		
	C. corae	*C.* sp		
		C. dentatus		
			Cepheus latus	
Ceratoppiidae	*Ceratoppia bipilis*	*Ceratoppia bipilis*		*Ceratoppia bipilis*
		C. quadridentata		

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TABLE 1. (Continued)

	Dead sporophores			Live sporophores
	Fomitopsis betulinus	*F. pinicola*	*Daldinia concentrica*	*Fomes fomentarius*
Ceratozetidae	*Diapterobates* sp.			
		Euzetes globulus		
		Fuscozetes setosus		
		Globozetes longipilus		
	Lepidozetes singularis			
		Melanozetes mollicomus		
Chamobatidae		*Chamobates borealis*	*Chamobates borealis*	
		C. cuspidatus, C. pusillus		
			C. schuetzi ?	
		C. spinosus, C. voigtsi		
Cymbaeremaeidae		*Cymbaeremaeus cymba*		
Damaeidae		*Belba corynopus*		
		Damaeus sp.		
		D. clavipes	*Damaeus clavipes*	
		D. onustus, D. riparius		
	Epidamaeus sp.	*Epidamaeus bituberculatus*		*Epidamaeus* sp.
		E. setiger		
		Kunstidamaeus tecticola		
		Metabelba sp.		
		Porobelba spinosa		
		Spatiodamaeus boreus		
Eniochthoniidae		*Eniochthonius minutissimus*		
Eremaeidae	*Eremaeus* nr *oblongus*	*Eueremaus oblongus*		*Eremaeus* nr *oblongus*
Euphthiracaridae		*Euphthiracarus cribrarius*		
Galumnidae		*Acrogalumna longipluma*		
		Pergalumna nervosa		
Haplozetidae		*Lagenobates lagenulus*		
	Peloribates sp.			*Peloribates* sp.
Hemileiidae		*Siculobata leontonycha*		
Hermanniellidae				*Hermanniella* sp.
Hypochthoniidae		*Hypochthonius rufulus*		
Liacaridae		*Adoristes ovatus*		
		Liacarus coracinus		
Licneremaeidae		*Licneremaeus licnophorus*		
Liebstadiidae	*Liebstadia humerata*			
	L. nr *lagenula*			
		Liebstadia longior, L. pannonica, L. similis		
Malaconothridae	*Malaconothrus* sp.	*Malaconothrus monodactylus*		*Malaconothrus* sp.

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TABLE 1. (Continued)

	Dead sporophores			Live sporophores
	Fomitopsis betulinus	*F. pinicola*	*Daldinia concentrica*	*Fomes fomentarius*
Nanhermanniidae		*Nanhermannia comitalis*		
		N. cf. *coronata,* *N. dorsalis, N. nana*		
Neoliodidae		*Neoliodes theleproctus*		
	Platyliodes sp.	*Platyliodes scaliger*		*Platyliodes* sp.
Nothridae		*Nothrus silvestris*		
Oppiidae		*Berniniella sigma*		
		Dissorhina ornata		
	Oppia sp.	*Oppia nitens*		*Oppia* sp.
		Oppiella sp.		
		O. falcata, O. keilbachi, *O. nova, O. subpectinata,* *O. translamellata,* *O. unicarinata*		
		Ramusella clavipectinata		
		R. furcata, R. insculpta		
		Subiasella quadrimaculata		
Oribatellidae	*Oribatella* sp.			*Oribatella* nr *berlesei*
		Oribatella calcarata		
	O. quadricornuta	*O. quadricornuta*		*O. quadricornuta*
				O. nr *reticulata*
		O. sexdentata, *O. similesuperbula,* *O. tibialis*		
Oribatulidae				*Eporibatula* sp.
	Lucoppia lucorum			*Lucoppia lucorum*
	Phauloppia spp.	*Phauloppia nemoralis*		*Phauloppia* sp.
	Oribatula exilis	*Oribatula exilis*		*Oribatula exilis*
	O. nr *propinqua*			*O.* nr *propinqua*
				O. pyrostigmata
Parakalummidae	*Neoribates* nr *aurantiacus*	*Neoribates aurantiacus*		*Neoribates* nr *aurantiacus*
				Neoribates sp.
Phthiracaridae		*Phthiracarus anonymus*		
		P. bryobius, P. compressus, *P. ferrugines, P. globosus,* *P. longulus*		
		Steganacarus carinatus		
Scheloribatidae	*Scheloribates* sp.	*Scheloribates latipes*		*Scheloribates* sp.
		S. pallidulus		*S.* nr *pallidulus*
Suctobelbidae		*Suctobelba atomaria*		
Tectocepheidae		*Tectocepheus* sp.		
		T. velatus		
Tenuialidae	*Hafenferrefia* sp.	*Hafenrefferia gilvipes*		

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TABLE 1. (Continued)

	Dead sporophores			Live sporophores
	Fomitopsis betulinus	*F. pinicola*	*Daldinia concentrica*	*Fomes fomentarius*
Xenillidae		*Xenillus tegeocranus*		
Mesostigmata Ameroseiidae	*Ameroseius longitrichus*			
Ascidae	*Gamasellodes* sp.	*Gamasellodes bicolor*		
		G. montanus		
		Lasioseius fimetorum		
		L. muricatus		
	Lasioseius ometes	*L. ometes*	*Lasioseius ometes*	
		L. zerconoides		
	Proctolaelaps hystricoides			*Proctolaelaps* sp.
		Proctolaelaps pygmaeus		
		Zerconopsis michaeli		
		Z. remiger	*Zerconopsis remiger*	
	Zerconopsis decemremiger	*Z. decemremiger*		
Blattisociidae		*Hoploseius oblongus*		
Celaenopsidae			*Pleuronectocelaeno austriaca*	
Dermanyssidae		*Dermanyssus gallinae*		
Digamasellidae		*Dendrolaelaps acornutus*		
		D. arvicolis, D. cornutulus, D. euarmatus, D. pini, D. procornutus, D. punctatulus, D. tenuipilus, D. trapezoides, D. zwoelferi		
	Digamasellus spp.			
Dinychidae		*Dinychus arcuatus*		
		D. perforatus		
Epicriidae			*Epicrius canestrinii*	
Laelapidae	*Androlaelaps casalis*			*Androlaelaps casalis*
	Haemolaelaps glasgowi			*Haemolaelaps* sp.
	H. nr *zulu*			
			Hypoaspis giffordi	
			H. oblonga	
		Pneumolaelaps lubrica		
Macrochelidae		*Geholaspis longispinosus*		
		G. mandibularis		
Microgyniidae		*Microgynium rectangulatum*		

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TABLE 1. (Continued)

	Dead sporophores			Live sporophores
	Fomitopsis betulinus	*F. pinicola*	*Daldinia concentrica*	*Fomes fomentarius*
Parasitidae		*Holoparasitus* sp.		
		Parasitus sp.		
		Pergamasus sp.	*Pergamassus crassipes*	
			P. longicornis	
		P. rühmi, P. runcatellus		
		Porrhostaspis lunulata		
Phytoseiidae		*Amblyseius* sp.		
			Typhlodromus bakeri	
Sejidae		*Sejus togatus*		
Trematuridae		*Trichouropoda ovalis*		
		T. sociata, T. structura		
Trachytidae		*Trachytes aegrota*		
Urodinychidae		*Uroobovella vinicolora*		
			Cilliba cassidea	
			Pseudouropoda sp.	
Veigaiidae		*Veigaia kochi*		
		V. nemorensis, V. transisalae		
Zerconidae		*Parazercon radiatus*		
		Zercon curiosus		
		Z. schweizer ?		
	Zercon nr *spatulatus*			
		Z. storkani		
Prostigmata Anystidae	*Anystis* sp.			*Anystis* sp.
Bdellidae	*Bdella longicornis*			*Bdella longicornis*
	Bdella sp.			*B. muscorum*
			Bdella semiscutata	
Cheyletidae			*Cheyletus eruditus*	
	Paracheyletia pyriformis			*Paracheyletia pyriformis*
Cunaxidae	*Cunaxoides biscutum*			
Ereynetidae				*Ereynetes* sp.
Erythraeidae	*Abrolophus* sp.			
	Balaustium sp.			
				Leptus sp.
Eupodidae	*Eupodes* sp.			
Tetranychidae	*Bryobia praetiosa*			
Tarsonemidae				*Tarsonemus fusarii**
Tydeidae				*Lorryia bedfordiensis*
				L. woolleyi
				Pertydeus nr. *schusteri*

* may have been a laboratory contaminant

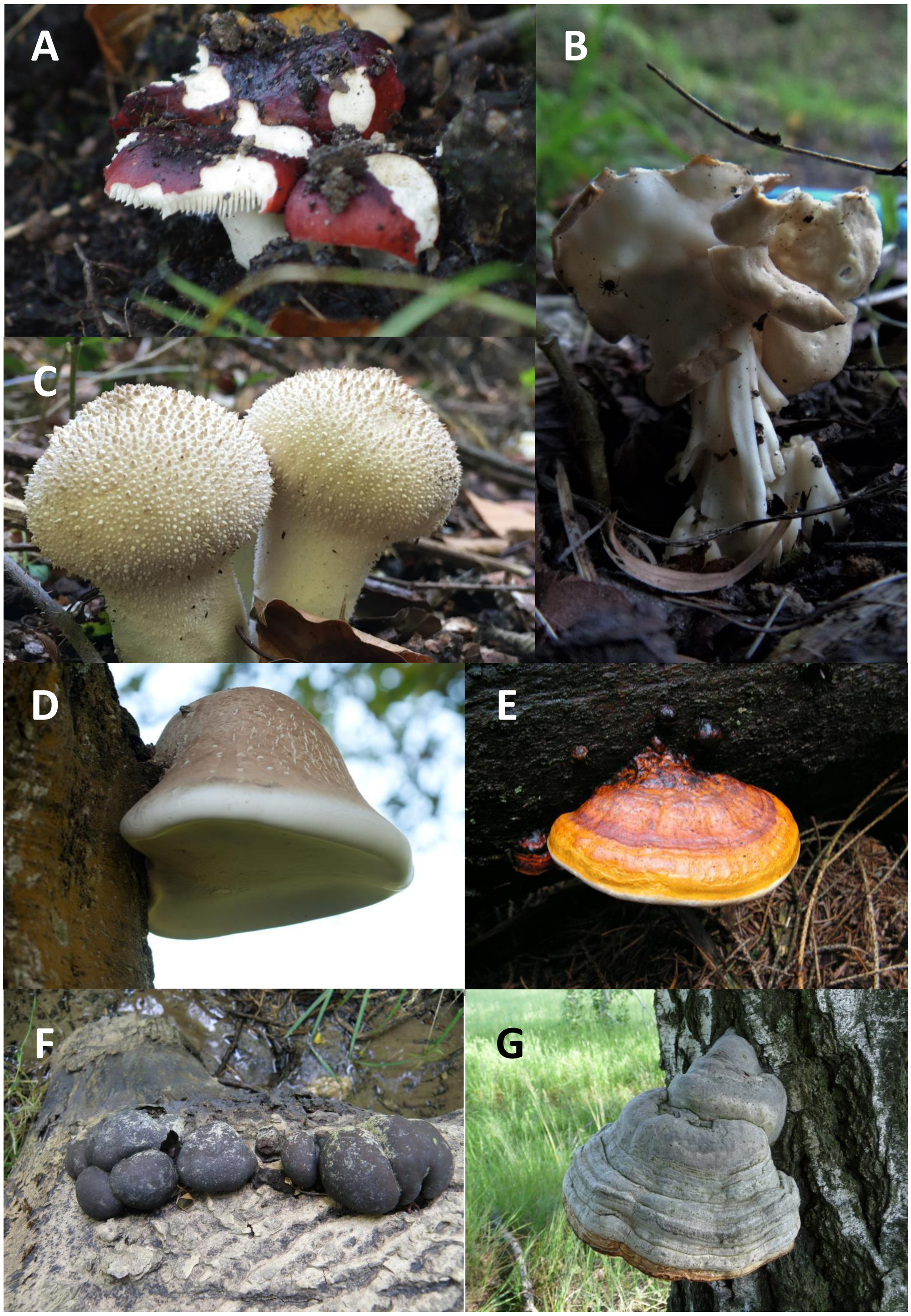

FIGURE 1. Examples of fungi used in our survey and in the comparison of Table 1. **A-C**: Fruiting bodies of fleshy fungi. Photos: Laura F. Garthwaite. **A**: Purple brittlegill, *Russula atropurpurea* (Basidiomycota, Russulaceae), England. **B**: Common puffball, *Lycoperdon perlatum* (Basidiomycota, Agaricaceae), England. **C**: White saddle, *Helvella crispa* (Ascomycota, Helvellaceae), England. *Damaeus* sp. (Oribatida, Damaeidae) is visible walking on the mushroom. **D-E**: Polypore fungi in which sporophore tissue dies after releasing spores. **D**: Razor strop, *Fomitopsis betulinus* (Polyporales, Fomitopsidaceae), on silver birch tree, *Piptoporus betulinus*. Photo: Captainpixel, in public domain. **E**: Young, red-belted conk, *Fomitopsis pinicola*, on dead pine log, Luxembourg. Photo: Jensbn~commonswiki, in public domain. **F**: Coal fungus, *Daldinia concentrica* (Ascomycota, Hypoxylaceae), on rotting log in marshland, England. Photo: J. Milburn, in public domain. **G**: Perennial polypore fungus, in which sporophore tissue survives after releasing spore. Tinder fungus, *Fomes fomentarius* (Basidiomycota, Polyporaceae), on dead birch, *Betula* sp. Approximately 10 years old mushroom. Ukraine. Photo: George Chernilevsky, in public domain.

The initial comparison between Pielou and Verma (1968) and Pielou and Matthewman (1966) showed differences that disappeared when more data were added. There is now a lot of overlap. For example, *Nanacarus* sp (Astigmata, Hemisarcoptidae) and *Phauloppia* sp. (Oribatida, Oribatulidae) are found in both, live and dead sporophores. Nevertheless, Matthewman and Pielou (1971) consider these two species as predominant characteristic for living sporophores.

Three families and three genera in three further families of mites in living sporophores are not listed for dead sporophores. As for the tree families, *Hermanniella* species in Hermanniellidae (Oribatida) are mites common in forest, hedgerow, meadow, and machair habitats rich in organic matter (Arroyo & Bolger, 2011; Ľuptáčik *et al*., 2012; Seniczak *et al*., 2022). Stable isotope analysis suggests that *Hermaniella dolosa* together with fellow oribatid species *Ceratozetes peritus* (Ceratozetidae), *Damaeus auritus, D. clavipes, D. maximus* (Damaeidae), *Eremaeus cordiformis* (Eremaeidae), *Minunthozetes semirufus* (Mycobatidae), *Nanhermannia variabilis*, *N. nana* (Nanhermanniidae), *Steganacarus anomalus* (Phthiracaridae), and *Xenillus tegeocranus* (Xenillidae) are secondary decomposers, feeding mostly on microorganisms and only every now and then on dead organic material (Corral-Hernandez *et al*., 2015). *Ereynetes* species in Ereynetidae (Prostigmata) in this case could be a free-living mite, a predator mite, or a mixophagous species feeding on fungi (Çobanoğlu *et al*., 2020). In Tydeidae (Prostigmata), *Lorryia bedfordiensis* has been described from humus, *L. woolleyi* has been associated with plants and fruits and mainly collected during quarantine procedures, and *Pertydeus schusteri* or *Tydeus schusteri* has been gathered from the rocky sea shore in the state of São Paulo, Brazil (Evans, 1952; Baker, 1968, 1970; Kazmierski, 2000).

The three genera so far distinctive for living sporophores are *Anachipteria* (Achipteriidae), *Eporibatula* (Oribatulidae) in the Oribatida and *Leptus* (Erythraeidae) in the Prostigmata. *Anachipteria* species are found in moss, arboreal lichen, under stones (Weigmann, 2006a; Subías, 2009). Maybe half of *Eporibatula* species are found on forest floors and half in the canopy (Behan-Pelletier & Winchester, 1998; Bayartogtokh & Aoki, 2000). Weigmann (2006b) considers *Eporibatula* a synonym of *Phauloppia*, which does not change the ecology much. There are some 260 mite species in the genus *Leptus*. Most are ectoparasites of insects and other invertebrates, however, species are also collected free-living of the ground, from leaves, moss, or in caves (Kapp & Brandstetter, 1998; Bassini-Silva *et al.*, 2020; Saboori *et al.*, 2020; Hakimitabar *et al.*, 2021). Here, the mite was likely associated with an insect visiting the fungus.

The comparison of mites from dead and live sporophores did not identify a single species likely to be characteristic for live sporophores, nor did it seemingly indicate any adaption of mite species to perennial fungal hosts. The limitations of these inquiries and comparisons lie in their physiological resolution. Tab. 1 lists for *Fomitopsis pinicola* with dead sporophores the mite species *Hoploseius oblongu*s (Mesostigmata, Blattisociidae), which is an obligate mycobiont of the fungus. It resides in the hymenopore and feeds on the living tissue, hymenium, that eventually provides for the development of spores (Mašán & Halliday, 2016; Gdula *et al.*, 2021a; Andrianov *et al*., 2022). Considering just the fate of sporophores is too limiting. Although only a single species of fungus is used in this small comparison, the suggestion that mite diversity is reduced for live sporophores is appealing. The comparison also shows how difficult it is to come up with sweeping statements of mite genera characteristic for particular groups of fungi (O'Connell & Bolger, 1997b, 1997a).

Most non-cultivated mushrooms are poisonous. For example, rye ergot, *Claviceps purpurea* (Ascomycota, Clavicipitaceae), hosts several mite species feeding on it; for example, *Tyroglyphus dimidiatus* now *Tyrophagus longior*, *Tyroglyphus siro* now *Acarus siro*, and *Histiogaster entomophagus* now *Thyreophagus entomophagus* (despite its name) (Astigmata, Acaridae) (Monier, 1893 (1894); Michael, 1903). Early on the question was raised of how the species cope with the alkaloids in the fungi. The question remains still open today. On the other hand, mites might sequester alkaloids from saprophytic fungi or plants, or synthesize alkaloids themselves (Raspotnig *et al.* 2011). Currently, alkaloid-bearing mites are known from a few brachypyline families in the Oribatida and from Uropodidae in the Mesostigmata (Coleman & Cannatella, 2022). Interestingly, most mite species carry alkaloids only as adults.

Wild mushrooms in Britain carried, in addition to many of the species listed in Table 1, oribatid species of the families Cepheidae, Cymbaraemaeida, Euzetidae, Mycobatidae, and Plateremaeoidea.

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