Chapter 14
Mycophagy

Facultative mycophagy is likely the one of the most pervasive and least documented forms of omnivory within entomophagous species. The simple fact is that when scientists actually search for fungal material during gut analyses of natural enemies, they typically find it to some degree. The evolutionary development of mycophagy in entomophagous species is best described for beetles, notably the Coccinellidae and the Staphylinidae. But each group of natural enemies under study has at least a few scattered reports of mycophagy in species normally regarded as predators or parasitoids. Although fungus contains a rich assortment of nutrients critical to the nutrition of entomophagous species, the importance of mycophagy to the natural history of most natural enemies is poorly understood relative to other non-prey foods.

14.1 Fungi as Food for Natural Enemies

The diversity of fungi is staggering, and for several reasons it is to be expected that we know very little of the nutritional quality of most fungi. First, the nutritional value of different tissues within the same fungus can vary widely; hyphae/mycelium, conidia, fruiting bodies, and spores of a single species all have different nutritional profiles (Garraway and Evans, 1984), and support very different arthropod communities (Lawrence, 1989). Moreover, fungi are very sensitive to environmental fluctuations, and

> within the bounds set by the metabolic capacities of the species, the composition [of a fungus] varies widely with the environment. The quantities of fat, carbohydrate, ash, wall material, and total nitrogen are all more or less responsive to the culture medium. (Cochrane, 1958)

Also, as mushrooms age, they change substantially with respect to nutrition. The current state of knowledge with respect to the nutritional value of fungi stems largely from commercially produced species (mushrooms) of interest to humans. Although many of the nutrient analyses presented below are derived from commercial mushrooms, and are questionably applicable to most fungus-entomophage interac-

tions, the nutrient analyses presented at least give us a ballpark range of the nutrition of this non-prey food.

14.1.1   Water Content

One fairly consistent nutritional component of fungi is that they have a fairly high water content. Typically, more than 85% of the fresh weight of vegetative tissues of fungi is comprised of water (Chang and Miles, 2004; Cochrane, 1958; Kalberer, 1990; Kurtzmann, 1997; Leschen and Beutel, 2001). Nonetheless, environmental conditions affect the water content of fungi, and spores are lower in water than other fungal tissues. For instance, Todd and Bretherick (1942) found uredospores of unknown origin to be composed of only 15% water.

14.1.2   Carbohydrates

The major nutritional component of fungi is carbohydrates, primarily in the form of polysaccharides (Griffin, 1994). Proximate analysis usually shows that carbohydrates comprise around half the dry weight of fungi, but range from 3–85% (Chang and Miles, 2004; Cochrane, 1958; Griffin, 1994; Kurtzmann, 1997; Mueller et al., 2001). Very little of this carbohydrate is in the form of mono- or oligosaccharides. Chitin, cellulose, and glucan are the major structural polysaccharides found in the cell walls of fungi, and glycogen is the major storage polysaccharide (Garraway and Evans, 1984; Griffin, 1994; Kurtzmann, 1997; Phaff et al., 1966). Cochrane (1958) discusses that 5.5–10.6% of fungal dry weight is composed of chitin. Cellulose and lignin are other structural polysaccharides found in fungi, but many insects are unable to digest these polysaccharides (Garraway and Evans, 1984). The glycogen found in fungi is very similar to that found in animal tissues (Cochrane, 1958), and so is likely readily digestible by entomophagous arthropods. It is interesting to note that while most fungi have few simple sugars, the mutualistic fungi symbiotic with attine ants tend to have high levels of trehalose, in addition to protein-bound amino acids, that make the nutrients more accessible to ants (see below for more discussion of this relationship) (Swift et al., 1979). Finally, spores are nutritionally disparate from most other fungal tissues, and carbohydrate content is no exception to this pattern. Todd and Bretherick (1942) found that uredospores contain approximately 26% of their dry weight as carbohydrates, the majority of which were reducing sugars and only 0.78% being starch.

14.1.3   Proteins

Proteins, including their amino acid precursors, are the next most abundant nutrient found in fungi. Relative to some non-prey foods, fungi are an excellent source of protein. Typically, from 20–40% (actual range from 4.6–61%) of fungal dry weight

is protein-based nitrogen (Chang and Miles, 2004; Cochrane, 1958; Griffin, 1994; Kurtzmann, 1997; Mueller et al., 2001; Todd and Bretherick, 1942). In their survey, Mueller et al. (2001) determine that mean (±SD) protein content of 49 species of Basidiomycetes is 21.37% ± 10.26% of dry weight. Fungi are also an appreciable source of amino acids essential to insect growth and development (Chang and Miles, 2004; Kurtzmann, 1997). The least concentrated amino acid is tryptophan in many fungi; the most abundant is often lysine (Chang and Miles, 2004).

14.1.4   Lipids

A variety of lipids are present in fungi, including sterols that are a dietary requirement for insects. Lipids typically comprise less than 10% of fungal dry weight (Chang and Miles, 2004; Cochrane, 1958; Mueller et al., 2001), but can reach as high as 87% of tissues in some species (Griffin, 1994). Fatty acids in fungi are typically unsaturated, and all fungi have palmitic and stearic acids (Chang and Miles, 2004; Harwood and Russell, 1984). Myristic, palmitoleic, stearic, oleic, arachidonic, and linoleic acids are also found in many fungi (Chang and Miles, 2004; Cochrane, 1958; Harwood and Russell, 1984). Longer-chained fatty acids may be common in certain species, but generally are minor components of fungi (Harwood and Russell, 1984). Sterols are invariably present as ergosterol, but other C27, C28, and C29 sterols are also present in fungi (Chang and Miles, 2004; Griffin, 1994; Harwood and Russell, 1984; Kurtzmann, 1997). An exception to this is the Uridinales, which replace ergosterol with C29 sterols (Harwood and Russell, 1984). Sterols represent 4.0–5.4% of total lipids in fungi (Cochrane, 1958), but some yeasts can contain 10% of their dry weight as sterols (Harwood and Russell, 1984). Ultraviolet light converts ergosterol into vitamin D (Chang and Miles, 2004; Kurtzmann, 1997), and it isn't clear how this vitamin functions in entomophagous insects. Inositol and choline, two important dietary requirements of insects, are also important to the physiology of fungi and are thus ubiquitously present in this non-prey food (Cochrane, 1958; Garraway and Evans, 1984; Griffin, 1994; Harwood and Russell, 1984).

14.1.5   Vitamins and Minerals

Up to 12% of the dry weight of most fungi is ash (Chang and Miles, 2004; Cochrane, 1958; Griffin, 1994), and fungi are a good source of many minerals and vitamins necessary for insect fitness. Potassium is invariably the most abundant mineral found in fungi, followed by the elements Na, Ca, P, Mg (Chang and Miles, 2004; Cochrane, 1958; Garraway and Evans, 1984; Griffin, 1994; Kurtzmann, 1997; Todd and Bretherick, 1942). Cu, Zn, Fe, Mn, Mo, Cd, S, Ca, Co, and Al are also found in many fungi, but at much lower concentrations (Chang and Miles, 2004; Cochrane, 1958; Garraway and Evans, 1984; Kurtzmann, 1997). In addition to minerals, fungi are a good source of B-vitamins, including thiamine, biotin,

pyridoxine, riboflavin, and vitamin B12 (Cochrane, 1958; Garraway and Evans, 1984; Kurtzmann, 1997). Finally, β-carotene is the predominant carotenoid found in fungi, and while γ-carotene is not infrequent in fungi, α-carotene has yet to be detected (Harwood and Russell, 1984).

14.1.6   Defensive Properties of Fungi

Finally, just as with the preceding non-prey foods, fungi possess a whole range of non-nutritive secondary chemicals that presumably defend the fungus from mycophages. Although the toxicity of mycotoxins has made a strong impression on the human race for hundreds of years, the importance of secondary chemicals in anti-predator defense is surprisingly understudied (Rohlfs et al., 2007). In addition to deterring predators, the secondary chemicals found in fungi may have important implications for the suitability, apparency, and acceptability of a given fungus to a mycophagous insect (Kukor and Martin, 1987). Although there are a few examples where natural enemies use fungal secondary metabolites as kairomones for finding mycophagous hosts or prey (Dicke, 1988a; Kukor and Martin, 1987), the direct role of these chemicals in the nutrition of facultative mycophages is unknown. In addition to these protective secondary chemicals, fungi (especially spores) also possess a range of structural defenses that are presumed to deter unwanted mycophagy. Spores often have rigid and protective walls that must be overcome by mycophagous entomophages in order to access the nutrients (Lawrence and Newton, 1980; Savile, 1976). In fungus-like myxomycetes, these spore walls have calcium carbonate that further lend to their rigidity (Lawrence and Newton, 1980). The spore walls of some rust fungi have warts or spines that have a dual function of defense and dispersal (Savile, 1976). Moreover, the spore-bearing sori of certain rust fungi, (examples occur in *Puccinia*, *Uridinopsis* and *Uromyces*, as well as many others) are protected against mycophagy by spikes or spines of various origins (Savile, 1976). Exploration of the interactions between the defenses of fungi and natural enemies seems a fruitful branch of research heretofore untouched.

As detailed above, fungi are composed of a series of substances that are simply not encountered in entomophagy and phytophagy. Consequently, mycophagous arthropods require a series of digestive adaptations that enable them to exploit the maximum nutrition from this food source. Most notably, many mycophagous insects possess digestive enzymes that allow them to digest β-1, 3-glucans, α-1, 4-glucans, and β-1, 6-glucans, and chitin, which are major structural polysaccharides fairly distinct from plants and insects (except for chitin in insects, of course) (Hanski, 1989; Kukor and Martin, 1987; Martin et al., 1981). The gut pH may also be indicative of diet in that it may support the enzymatic and metabolic reactions unique to mycophagy; the guts of herbivores tend to be alkaline, whereas mycophagous species tend to have a neutral gut pH (Martin et al., 1981). Fungi have a high caloric content for those species that can unlock fungal nutrients. One estimate for mushrooms is that energy content ranges from 2,760–3,920 calories g^{-1} of dry weight (Chang and Miles, 2004).

14.2   When Mycophagy Benefits the Fungus

Not all cases of mycophagy by arthropods are at the expense of the fungus, and several instances of fungi capitalizing on facultative mycophagy as a means of spore dispersal are documented. A range of fungi, especially within the rust fungi (Uridinales) produce sugary secretions to attract mycophagous entomophages (Stoffolano, 1995). Spores that attach to the bodies of insects attracted to the sugary secretions are then transferred to other fungi, thereby encouraging the outbreeding of the fungus (Webber and Gibbs, 1989). Gilbert and Jervis (1998) mention that at least members of the Syrphidae, Phoridae and Tachinidae are attracted to the sugary secretion of rust fungi and ergot (*Claviceps purpurea*). But the 'honeydew' of these fungi may be spiked with numerous secondary chemicals with unknown effects on visiting insects (Todd, 1967). Paracelsus recognized the delusional side effects of consuming the honeydew of ergot, and it may be that Coleridge was referring to this as he describes the delusional visions of paradise held by Kubla Khan (Todd, 1967).

> *And all who heard shall see him there,*
> *And all should cry, Beware! Beware!*
> *His flashing eyes, his floating hair!*
> *Weave a circle round him thrice,*
> *And close your eyes with holy dread,*
> *For he on honey-dew hath fed,*
> *And drunk the milk of Paradise*
> (Kubla Khan, S. T. Coleridge, 1798)

Also worth mentioning is that being consumed by an entomophagous arthropod is not always a death sentence for a spore, which may use beneficial insects as vectors to reach new hosts. *Hippodamia convergens* is an effective vector of *Discula destructiva*, a pathogen of *Cornus florida*. In addition to carrying spores of this pathogen on their bodies (Colby et al., 1995), *H. convergens* consumes the fungus, and transmits spores in its frass to new plants. A substantial number of spores (10^8 per beetle) of *D. destructiva* can survive in the digestive tract of *H. convergens* for up to 96 hours in the laboratory (Hed et al., 1999), and fewer can survive for up to 16 days (Colby et al., 1996). Also, the plant-pathogenic yeast, *Nematospora coryli*, is vectored to new *Brassica* plants through the mouthparts of the nabid, *Nabis alternatus* (Burgess et al., 1983; Lattin, 1989).

14.3   Mycophagous Taxa

14.3.1   *Arachnida: Araneae*

In addition to trapping pollen grains (discussed in Chapter 6), spider webs often trap substantial quantities of fungal material, and these spores likely provide nutrition to web-building spiders when they consume their webs. Bera et al. (2002) found that up to 13% of organic material recovered from spider webs is fungal, including spores of *Alternaria*, *Curvularia*, and Microthyriaceae. Still, pollen tends to be intercepted by spider webs more frequently than fungal material (Bera et al., 2002; Linskins et al., 1993).

14.3.2   Arachnida: Acari

Mites got their start evolutionarily as predators, but the diets of many taxa designated as predaceous also include fungus to varying degrees (Krantz and Lindquist, 1979; OConnor, 1984). Indeed, some tydaeid mites initially regarded as predators of herbivorous mites in orchards are determined to be exclusively mycophagous under closer examination in the laboratory (McCoy et al., 1969). The most mycophagous of mites attract interest as potential biocontrol agents of powdery mildews in some crops, especially grapes (English-Loeb et al., 1999; Norton et al., 2000). Another mite, in this case presumed to be mostly mycophagous, is the cheese mite, *Tyrophagus putrescentiae*. This mite is able to detect volatile extracts, namely cis- and trans-octa-1, 5-dien-3-ol, produced by numerous species of fungi (Vanhaelen et al., 1979, 1980). Vanhaelen et al. speculate that these volatiles, which give fungus its 'mushroomy' scent, may be broadly important in mitigating mite-fungus interactions. Interestingly, this same soil-dwelling mite is a key predator of *Diabrotica undecimpunctata howardi* eggs. *Tyrophagous putrescentiae* is able to detect rootworm eggs from up to 5 cm away (quite a distance for a mite!), and inflict a heavy toll on *D. u. howardi* eggs in the field (Brust and House, 1988a). The bottom line is that the feeding behavior of mites with respect to mycophagy is seldom as clear as it seems upon superficial examination.

Within the Phytoseiidae, a number of species can complete development and even reproduce on food of fungal origin, although these seldom are ideal foods for predaceous mites (Huffaker et al., 1970; McMurtry et al., 1970). Mites in the genus *Typhlodromus* receive the most attention for their mycophagous habits, but unsurprisingly, not all fungal species are equally suitable for these mites (Chant, 1959; Putnam, 1962; Zaher and Shehata, 1971; Zemek and Prenerova, 1997). In one set of experiments, powdery mildew (*Plasmopara viticola*) densities are correlated with increased abundance of two phytoseiids, *Amblyseius andersoni* and *Typhlodromus pyri* in vineyards (Duso et al., 2003; Duso et al., 2005). When powdery mildew populations are controlled, these predaceous mites suffer. Gut analysis revealed that 39 of 40 individuals of *A. andersoni* had consumed the fungus. Ultimately, the prevalence of fungus on the phylloplane may facilitate the persistence of predaceous mites in cropland in the absence of prey, as first postulated by Chant (1959).

14.3.3   Coleoptera: Carabidae

Mycophagy in Carabidae is fairly widespread, although its importance to their life history is entirely unexplored. To date, all records of mycophagy in carabids stem from gut dissections of field-collected specimens, and nearly all records can be ascribed to one of two researchers, Stephen Forbes and Michael Davies. In addition to the fungal species listed in Table 14.1, Hammond and Lawrence (1989) mention that carabids will consume Sphaeriales (Ascomycotina), Aphyllophorales, Agaricales, Russulales (Basidiomycotina).

Fungal material is known from the guts of 41 species, but taxonomically, mycophagy involves a slightly different subset of carabids than of those that are granivorous

Table 14.1 Species of Carabidae recorded as mycophagous under field conditions

Species	Reference	Notes
Abax parallelepipedus	(Davies, 1953)	
Abacidus permundus	(Forbes, 1883)	
Agonum gratiosum	(Davies, 1953)	
Amara aenea	(Davies, 1953)	
Amara aulica	(Davies, 1953)	
Amara carinata	(Forbes, 1883)	About ¼ of the food ingested was fungal in origin (*Peronospora*)
Amara familiaris	(Davies, 1953)	
Amara impuncticollis	(Forbes, 1883)	Had traces of fungi in their diet
Amara montivaga	(Davies, 1959)	
Amara plebeja	(Davies, 1953)	
Amara sp. (listed as *A. vulgaris*)	(Davies, 1953)	
Anchomenus dorsalis	(Davies, 1953)	
Anisodactylus rusticus	(Forbes, 1883)	Ate *Cladosporium* and *Peronospora* fungi
Bembidion guttula	(Davies, 1953)	
Bembidion lampros	(Davies, 1953; Sunderland, 1975)	
Bembidion lunulatum	(Davies, 1953)	
Bembidion obtusum	(Davies, 1953)	
Bembidion tetracolum tetracolum	(Davies, 1953)	
Calathus fuscipes	(Davies, 1953)	
Calathus melanocephalus	(Blunck, 1925; Larochelle, 1990)	
Chlaenius	(Forbes, 1881, 1883)	In one field, around 10% of their diet consisted of fungi, *Coprinus* and *Dematei*. Around 5% of food at another site was fungal. Spores and fungal material were found in the stomachs of *C. platyderus*
Cratacanthus dubius	(Forbes, 1881)	A few fungal spores were found in their otherwise empty gut
Cyclotrachelus faber	(Freitag, 1969)	Spores of fungi were found in the gut contents
Cyclotrachelus sodalis colossus	(Forbes, 1883)	A few fungal spores were found in their stomachs (2 of 5 specimens)

Table 14.1 (continued)

Species	Reference	Notes
Eurycoleus	(Erwin and Erwin, 1976)	Adults are ectoparasitoids of fungus beetles, and consume fungal spores during the adult stage, as well as host-feeding of sorts. They like smooth, polyspore fungi, and by passing spores in their feces, they probably help to disseminate the host fungus to new trees
Harpalus	(Forbes, 1883)	
Harpalus affinis	(Davies, 1953)	
Harpalus attenuatus	(Davies, 1953)	
Harpalus caliginosus	(Forbes, 1881, 1883)	Ate a little *Helminthosporium* at one site
Harpalus herbivagus	(Forbes, 1881, 1883)	About a third of their diet was fungal. In 1881, a fleshy, cartilaginous fungus was found in their stomachs.
Harpalus pensylvanicus	(Forbes, 1881, 1883; Kirk, 1973)	At one site, 8% of food was fungal, *Peronospora* (mostly) and *Helminthosporium*. A few spores were found in some of the guts.
Harpalus rufipes	(Larochelle, 1990)	
Lebia atriventris	(Forbes, 1881, 1883)	Spores of *Phoma* and *Helminthosporium* were found in guts (five of seven specimens; the others hadn't eaten anything).
Notiophilus rufipes	(Davies, 1953)	
Notiophilus substriatus	(Davies, 1953)	
Paradromius linearis	(Davies, 1953)	
Poecilus cupreus	(Davies, 1953)	
Pterostichus	(Forbes, 1883)	Around 10% of the food taken by half the beetles contained fungal spores. *Helminthosporium* was the only fungus noted.
Pterostichus madidus	(Davies, 1953)	
Pterostichus oblongopunctatus	(Davies, 1953)	
Stenolophus	(Forbes, 1883)	Only 2% of their diet was fungal, split equally between *Helminthosporium* and *Peronospora*. *Ramularia* and *Coleosporium* were also found in *Stenolophus* stomachs.

(discussed in Chapter 9). For instance, species of *Cyclotrachelus*, *Notiophilus*, and *Bembidion* consume fungal material, but seldom seeds. Meanwhile, the granivorous members of Harpalini and *Amara* are broadly represented in the list of mycophagous taxa. Another set of observations gives some additional information on the potential importance of mycophagy for carabids. As mentioned in Section III, *Harpalus pensylvanicus* and *H. eraticus* larvae create burrows in which they reside, overwinter, and cache seeds (Kirk, 1972). The larvae of *H. pensylvanicus* also make shallow trenches outside the entrance to their burrows, where Kirk (1973) hypothesizes that they consume soil microorganisms as food. Also striking is that Kirk noted no evidence of actual seed consumption within the burrows of the larvae, even though the larvae are confined with the seeds all winter. It would be fascinating if these seed caches serve as a substrate for microorganisms that are then consumed by the *Harpalus* larvae, essentially constituting a similar nutritional system to that seen in leaf-cutting ants.

14.3.4   *Coleoptera: Coccinellidae*

Mycophagy pervades many clades of this family. On one extreme, the Halaziini (formerly the Psylloborini) are a tribe of exclusively mycophagous coccinellids (Hodek and Honěk, 1996). Like mycophagous mites, coccinellids in the genera *Psyllobora* and *Ileis* receive attention as a potential source of biological control of powdery mildews (Davidson, 1921; Takeuchi et al., 2000). The most mycophagous species possess morphological adaptations to the mouthparts that facilitate the collection and consumption of fungal spores, similar to those rakes and combs used in pollinivory. Specifically, the mandibles of members of the Halaziini have two tips and a series of spines or teeth on their inner, ventral margin that help to scrape spores from fungal material (Kovar, 1996; Samways et al., 1997) (Fig. 14.1). *Tytthaspsis sedecimpunctata* is a great example of this adaptation (Ricci, 1982; Samways et al., 1997). Polyphagous species typically lack these morphological adaptations to fungal feeding, but this is not to say that fungi are not important to their life histories.

   In several published gut analyses, even the best appreciated of aphidophagous coccinellids consumed fungal spores as an important component of their diet. In his examination of the gut contents of agricultural coccinellids, Forbes found fungal material in the guts of all eight species examined (31 of 39 individuals), and this class of food comprised 45% of the food that these beetles had consumed (Forbes, 1881, 1883). In fact, 90% of food found in the guts of *Coccinella novemnotata* was *Ustilago helminthosporium* spores. Subsequent gut dissections concur with the early findings of Forbes that predaceous ladybeetles in agriculture are frequently mycophagous (Anderson, 1982; Hagen et al., 1976; Lundgren et al., 2004; Ricci et al., 2005). Putman (1964) found that nearly all of the four most abundant predaceous cocci-nellids found in peach trees consisted of 'detritus', in other words plant material, fungal spores and pollen (507 guts dissected in total). Indeed, 50% of these
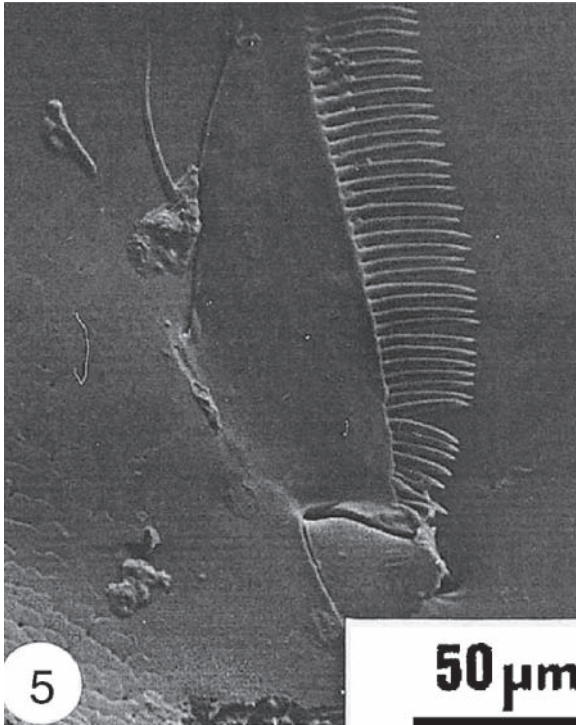
Fig. 14.1 Ventral view of the right mandible of *Tytthaspis sedecimpunctata*, showing the distinct comb-like prostheca (Reproduced from Samways, 1997. With permission from Taylor and Francis)

beetles had no other solid food in their guts besides this detritus. Nearly all adults of *Hippodamia notata*, in addition to consuming aphids, also consumed *Cladosporium* in one observation series (Ricci and Ponti, 2005); larvae were also very mycophagous. Quite a range of fungal groups have been found in the guts of coccinellids, including tissues or spores of *Helminthosporium*, *Ustilago*, *Cladosporium*, *Discula*, *Septoria*, *Uredo*, *Coleosporium*, *Menispora*, *Stemphylium*, *Sphaeronemei*, *Myxogastres*, *Macrosporium*, *Oidium, Peronospora*, *Alternaria*, *Monilinia fructicola*, and *Puccinia* (Anderson, 1982; Forbes, 1883; Hed et al., 1999; Putnam, 1964; Ricci, 1986a; Ricci et al., 1983; Ricci and Ponti, 2005; Ricci et al., 2005; Triltsch, 1997, 1999).

In addition to supporting prolonged survival in the absence of prey, mycophagy frequently coincides with two critical life processes in ladybeetles, diapause and reproduction. In part, the importance of mycophagy to overwintering success in coccinellids may be related to the fact that other foods become scarce late in the growing season, whereas fungi sometimes persist into this time of year. Regardless of why, it is a fact that numerous ladybeetles rely on fungi the most late in the growing season, building up nutrient reserves for dormancy (Anderson, 1982; Ricci et al., 1983) In *Coccinella septempunctata*, adults increase their consumption of *Alternaria* and *Puccinia* spores during pre-dormancy, even when aphids are abundant.

This suggests that self-selection of nutrients present in fungi may be necessary for overwintering (Triltsch, 1997, 1999). Spring is another critical time for mycophagy in ladybeetles, when ladybeetles require nutrition for dispersal and reproduction (Anderson, 1982; Triltsch, 1997) (see Chapter 1). Mycophagy in coccinellid larvae is not well explored and solid conclusions on the importance of fungi in larval diets really can't be drawn at this point. However, what little information is available suggests less reliance on fungal material by larvae compared with adults (Hukusima and Itoh, 1976; Ricci, 1986a; Triltsch, 1999).

14.3.5   *Coleoptera: Staphylinidae*

Given that the Staphylinidae is such a large and diverse family for which we have comparatively little biological understanding, it is surprising that staphylinids are probably the best understood group of natural enemies with regard to their adaptations to facultative mycophagy. The three subfamilies where many economically important natural enemies reside (Aleocharinae, Staphylininae, and Tachyporinae), all have members that are facultatively mycophagous to varying degrees (Hammond and Lawrence, 1989; Leschen, 1993). Only a few staphylinid lineages are obligate mycophages (the subtribe Gyrophaenina within Aleocharinae, and the genus *Oxyoporus*) (Ashe, 1984). Evolutionarily, the Aleocharinae as a whole arises from primitively predaceous ancestors (Ashe, 1984, 1993). However, those tribes within the Aleocharinae with a more mycophagous lifestyle originate from ancestors with distinct brushes on their mandibles, the function of which is adapted to collecting fungal spores (Ashe, 1984).

The structure of the mouthparts is well correlated with diet in many staphylinids, making this a useful group in understanding the adaptations diagnostic for mycophagy in natural enemies. A first key point in relating mouthpart morphology with the consumption of fungus is that different fungal tissues present unique challenges for consumption. For example, feeding on the context of a sporophore is much different than grazing the surface of the hymenium or eating free spores or conidia. Lawrence (1989) classifies these two processes as macrophagy and microphagy, respectively, and notes that feeding on fungal context is a difficult process likened to feeding on wood. Consequently, there are few instances of facultative context feeders, and many of the predaceous species of interest to this book are best classified as microphagous mycophages. Another caveat worth discussing with regard to structure and function in staphylinid feeding behavior is that feeding adaptations are often more evolved in the larval stage, since this is the primary feeding stage and populations are potentially more limited by the larvae's ability to feed efficiently (Lawrence, 1989). Moreover, mouthpart structure is highly conserved in staphylinid adults (Lawrence, 1989; Leschen, 1993), further blurring the relationship between structure and diet.

In summarizing the evolution of mouthpart structure in relation to mycophagy in staphylinids, Ashe (1993) figures that most adaptations to this lifestyle occur on the

maxillae, mandibles, and epipharynx of the insects. Various components of the maxillae have combs or rakes that are useful in harvesting spores, or grazing the hymenium of fungi (Ashe, 1984, 1993; Lawrence, 1989). Once the spores are collected by the maxillae, the mandibles are used to grind the material into digestible matter. The molar lobe of the Staphylinidae is largely lost in the predaceous ancestors of the group, but in mycophagous species a pseudomola has resurfaced secondarily to accomplish the work tackled by the molar lobe in other beetles (Newton, 1984). Specifically, the pseudomola grinds the fungal spores, and often this structure has denticles or teeth that allow the trituration of fungal material (Ashe, 1984, 1993; Lawrence, 1989; Leschen, 1993; Leschen and Beutel, 2001) (Fig. 14.2). The larvae of staphylinids (at least the Aleocharinae) have simplified, sickle-shaped mandible with a small subapical tooth. This tooth is one aspect of the larval mouthparts that varies little in response to diet (Ashe, 1993). Infrequently, the larval mandible of mycophagous species have a bifid tip or set of spines that assist in filtering spores from a substrate (Ashe, 1993; Leschen and Beutel, 2001) as in Fig. 14.3. Within larvae of *Sepedophilus*, Leschen and Beutel (2001) speculate that different mandibular tips have evolved in response to feeding on different fungal structures. Those species whose larvae feed on persistent and tough fruiting bodies of mushrooms have a chisel-ended or serrate mandible. Those species that specialize on softer fungi are associated with a more robust mandible containing fine asparites (filters). Finally, the epipharynx is adapted to mycophagy in several respects. In microphagous staphylinids, the epipharynx has denticles that further triturate spores (Ashe, 1993), whereas a few genera that feed by juicing the context of a fruiting body tend to have a number of epipharyngeal tubes that facilitate the drinking of fluids squeezed from
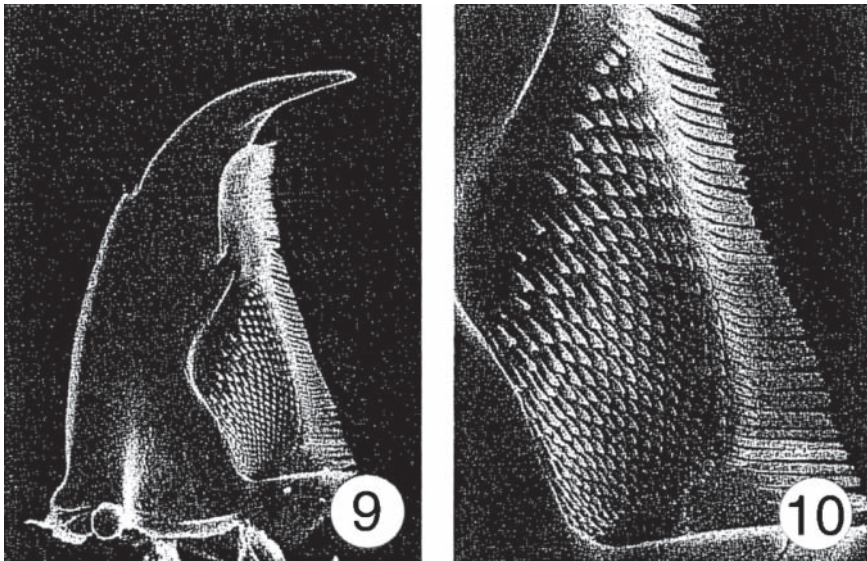

Fig. 14.2 Details of the denticles on molar surface of the adult mandibles of *Bolitochara lunulata* (Reproduced from Ashe, 1993. With permission from the Entomological Society of America)
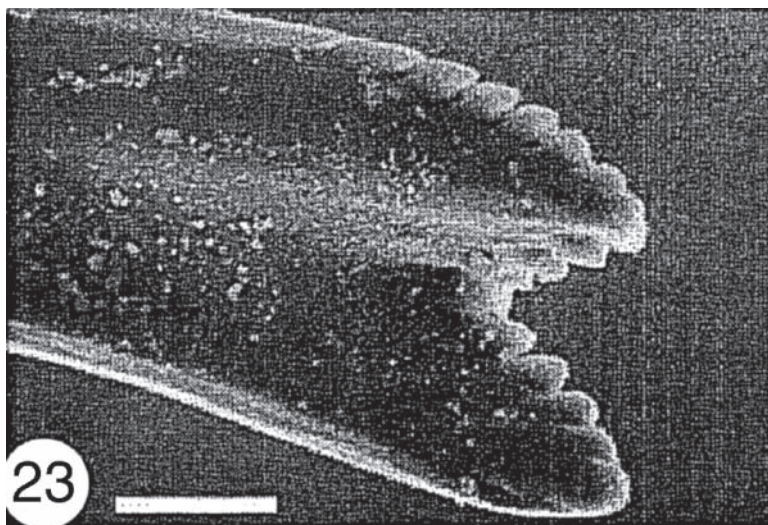
Fig. 14.3 Lateral view of bifid mandible of *Sepedophilus* type C (Reproduced from Letschen and Beutel, 2001. With permission from Blackwell)

the fungal cells (Leschen and Beutel, 2001). Finally, although partially diagnostic, mouthpart structure is fairly conserved within certain taxonomic groups, and it is advisable to back any presumptions on diet based upon morphology with gut analysis.

Several agriculturally important staphylinids consume fungal material in cropland, and mycophagy in these staphylinids is an important consideration when designing biological control programs. In cereal fields, *Tachyporus hypnorum* and *T. chrysomelinus* adults, and *Tachyporus* larvae consume substantial quantities of powdery mildew (*Erysiphe*) spores (more than 85% of meals) in addition to consuming cereal aphids (Sunderland, 1975). Under no-choice conditions in the laboratory, each beetle can consume 300–450 spores per day (Dennis et al., 1991). Another key staphylinid predator in this system, *Philonthus cognatus*, does not eat the fungus even under no-choice conditions. The mass production of staphylinids for augmentation biological control depends on understanding the mycophagous nature of some species, and incorporating fungi into the rearing regimens of these agents (Birken and Cloyd, 2007).

14.3.6 Neuroptera: Chrysopidae

The predaceous and non-predaceous adults of Chrysopidae consume fungal material, especially yeasts (Canard, 2001). In a comprehensive survey on the nutrition of Hungarian chrysopids, Bozsik (1992) found that yeasts (and some spores) are commonly found in the stomachs of *Chrysoperla carnea*, *Dichochrysa prasina*, *Chrysopa formosa*, *C. pallens*, *C. perla*, and *C. viridana*. Although present in all species examined, the predaceous species are less likely to have yeast in their stomachs. The potential role of symbiotic yeasts in the nutrition of lacewings is

discussed more extensively in the Chapter 15. A final piece of evidence that suggests the importance of fungi, especially yeasts, to the nutrition of chrysopids is that these species are commonly reared on Wheast (a commercial formulation of *Saccharomyces fragilis* with a milk whey substrate) and yeast hydrolysates in the laboratory (Hagen and Tassan, 1966, 1970; Sheldon and MacLeod, 1971), and are attracted to cropland sprayed with this artificial food (Hagen et al., 1976).

14.3.7   Heteroptera

Reports of mycophagy in predaceous bugs are rare, but some anthocorids are adapted to consuming fungi as part of their diet. Chu (1969) presents that two predaceous anthocorids, *Lyctocoris beneficus* and *Xylocoris galactinus*, are capable of completing development on a diet of only moldy corn seed. Although not as suitable as prey for normal predator fitness, these bugs sustain themselves for long periods of time on fungus, but cannot lay eggs on this diet by itself. Also, the anthocorid *Anthocoris nemorum* can detect the presence of the entomopathogenic fungus, *Beauveria bassiana*, on nettle leaves (Meyling and Pell, 2006). Although they are deterred by this entomopathogenic fungus, the same sensory mechanisms used to recognize *Beauveria* may be useful in identifying other fungi as food. Clearly, the topic of mycophagy in predaceous bugs is ripe for exploration.

14.3.8   Diptera

Generally speaking, fungus is a minor component of the diets of predatory or parasitoid species of flies. It is interesting that some species of entomophagous Diptera share their familial designation with mycophagous species. These include Stratiomyidae, Scenopinidae, Syrphidae, Phoridae, and Empididae (Hackman and Meinander, 1979; Hammond and Lawrence, 1989; Maier, 1978). The nutritional ecology of syrphids that are mycophagous as larvae is not entirely understood. In addition to consuming fungi, it is conceivable that closer examination will reveal that some of these species are predaceous on other insects they encounter (as suggested by Hackman and Meinander, 1979). Indeed, ancestral syrphids are mycophagous, and entomophagy is a derived state for the family (Rotheray and Gilbert, 1999), so it should not be surprising to see overlap in the dietary ranges of mycophagous and entomophagous guilds to some degree. Closer examination of the cyclorrhaphous flies may reveal a greater degree of mycophagy than is currently realized. Many of the adaptations by flies to pollinivory that are noted in earlier chapters are transferable to the consumption of fungal material. Broadhead (1984) mentions that the prongs or scoops of the labellum are used in snipping fungal material, in addition to the width of the pseudotracheal canals (and reduced number), are diagnostic of mycophagy in non-predaceous lauxaniid flies. Some of these same adaptations are described to aid pollinivory in entomophagous species of Diptera.

14.3.9   Parasitoid Hymenoptera

Although numerous parasitoids are associated with mycophagous hosts (Hammond and Lawrence, 1989; Rotheray, 1990), I am unable to report even a single instance of direct mycophagy in parasitoid Hymenoptera. In laboratory feeding trials, yeast does not prolong the lives of *Trichogramma* wasps (Ashley and Gonzalez, 1974; Leatemia et al., 1995). Given the importance of nectar and pollen to the fitness of many parasitoid wasps, it would not be surprising to find fungal material in the guts of some parasitoid wasps, especially in the larger ichneumonoid species.

14.3.10   Formicidae

The best documented case of mycophagy in ants is inarguably the case of Attini (subfamily Myrmicinae) ants and their symbiotic fungus (Beattie and Hughes, 2002; Cherrett et al., 1989). All ants within this group, the main diversity of which occurs in *Atta* and *Acromyrmex*, are obligate mycophages on *Leucocoprinus* or *Leucoagaricus* species. The intricacies of the mutualism between these two groups of organisms are amazing, and the relationship results in leaf-cutter ants dominating many Neotropical habitats. In leaf-cutter genera, the ants harvest only the plants that promote fungal growth (Carroll and Janzen, 1973; Hubbell et al., 1983; Ridley et al., 1996; Swift et al., 1979), and remove microbial competitors from their nests (Swift et al., 1979). The fungus is capable of accessing nutrients from vegetation that are otherwise unavailable to these insects, and it packages the nutrients into a mycelial food body that is nutritionally complete for developing ant larvae (Beattie and Hughes, 2002; Hartzell, 1967; Stradling, 1987). The relationship likely evolved from ant and fungal forerunners associated with the same nest cavity (i.e., wood inhabiting ants). Another option is that the fungus initially relied on the ants as dispersal agents, as seen with myrmecochory and seeds (Mueller et al., 2001; Sanchez-Pena, 2005) (Chapter 12). These fungus-growing associations likely evolved 45–60 million years ago (Mueller et al., 2001).

Even though Attini-fungus interactions involve strict mycophagy in the ant, there are a few aspects of this relationship that may improve our understanding of how entomophagous insects use fungi as food. Facultative mycophagy in ants is rare at best (Mueller et al., 2001), although it would not be unexpected to find instances of this phenomenon in some ant species. Some evidence for more widespread facultative mycophagy in ants come from Torres (1984), who reports that 15 of 21 ants species carry "fungi or feces" (a somewhat contrived food category) back to their nests. The infrabuccal cavity of ants is frequently loaded with fungus, but it appears that most ants discard fungal material to the midden rather than provide it to the fourth instar for digestion (Mueller et al., 2001). Also, the physiological adaptations to mycophagy found in leaf-cutter ants may shed light on this feeding behavior in other ant groups (many of these adaptations are listed in Cherrett et al., 1989). In conclusion, this is an excellent group of insects with which to transition

to the next chapter, which deals extensively with the nutritional symbioses between entomophagous species, non-prey foods, and microbes.

14.4   Conclusions

Numerous entomophagous species consume fungus routinely, and under-represented taxa in this chapter are likely to yield more reports under closer scrutiny. Fungus presents a diverse suite of tissues and organs that can be exploited by entomophagous arthropods, but each presents structural and chemical obstacles that need to be overcome before the rich nutrition found in fungus can meet the energetic needs of the arthropods (Leschen, 1993). The importance of this food to natural enemies is evident in the morphological and physiological adaptations that are expressed in those entomophagous species that have come to rely the most on this fungus. It is interesting to note that the anatomical features that employed to facilitate spore-feeding in insects (a series of brush-like abrasive features on the mouthparts for collecting and crushing the spores) are similar to those seen in pollinivorous species. A closer look at these relationships may reveal how isolated morphological adaptations can have wide implications for the dietary breadth of an omnivorous species. Finally, although numerous instances of mycophagy are noted for natural enemies, very little is known about the function of fungus in the nutritional ecology of these arthropods.