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Staphylinidae and fungi[1]

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Summary

Associations with fungi have played an important role within the evolution of the Staphylinidae. Interactions with fungi occur in each of the four subfamily groups in the form of mycophagy or predation on other fungus-dwelling organisms. Mycophagous/fungivorous species are found in the following subfamilies: Micropeplinae, Neophoninae, Habrocerinae, Aleocharinae (e.g. *Gyrophaena* Mannerheim, *Phanerota* Casey, *Eumicrota* Casey, *Placusa* Erichson, *Homalota* Mannerheim, *Stictalia* Casey, *Pseudatheta* Cameron, *Pagla* Blackwelder, *Polylobus* Solier), Tachyporinae (e.g. *Sepedophilus* Gistel), Scaphidiinae (e.g. *Scaphisoma* Leach, *Cyparium* Erichson), Oxyporinae (*Oxyporus* Fabricius). The following subfamilies include species with at least facultative mycophagy: Glypholomatinae, Omaliinae, Proteininae, Dasycerinae, Trichophyinae, Osoriinae. This review summarizes the diversity of relationships between beetles and fungi for several subfamilies and elucidates possible adaptations of their mouthparts to mycophagy (especially sporophagy). Based on a microphagous groundplan, the mouthparts of several lineages of sporophagous staphylinids have convergently experienced particular modifications that can be explained as specific adaptations to this feeding type. These modifications involve advanced rake- and brush-like maxillae and special differentiation of the mandibular mola. Several staphylinids of the tachyporine and oxyteline groups with primarily reduced mandibular molae have evolved secondary grindig surfaces (pseudomolae), which, in some aleocharines, are paralleled by a re-construction of the labium-hypopharynx.

Additional aspects of this review reveal the types and strengths of the relationships between staphylinids and fungi and consider the characteristics of larval development, parental care and behaviour of fungus-dwelling staphylinids. Young sporocarps of Basidiomycetes in the stage of sporulation are preferred by the mycophagous staphylinids *Gyrophaena*, *Eumicrota*, *Sepedophilus*, *Oxyporus*, and the predators *Bolitobius* Mannerheim and *Aleochara* Gravenhorst. Older sporocarps in the stage of decay are prefered by predators such as *Tachinus* Gravenhorst, *Philonthus* Curtis, *Ontholestes* Ganglbauer, and *Atheta* Thomson. As an adaptation to fleshy ephemeral Agaricales the larval development of staphylinids is short. The larval instar period (LI - LIII) at 22-24°C takes three days in *Phanerota fasciata* (Say) and *Gyrophaena joyioides* Wüsthoff, and five days in *Oxyporus stygicus* Say. In tough persistent Polyporales the larval development lasts longer (e.g., 10 days in *Scaphisoma castaneum* Motschulsky). Ovoviviparity in *Gyrophaena gentilis* Erichson seems to be an adaptation to the rapid decay of fungi as hosts. Parental care is known from the genera *Eumicrota* and *Oxyporus*.

[1] Professor Dr. Berndt Heydemann to his 75th anniversary

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Introduction

The fruiting bodies of macrofungi probably serve as hotspots of insect diversity, being of great importance for biodiversity maintenance in fungicolous insect communities (KOMONEN 2003). Among the rove beetles (Staphylinidae), associations with fungi have been of special importance during their evolution. Interactions with fungi occur in all of the four subfamily-groups of LAWRENCE & NEWTON (1982), either in the form of direct mycophagy or with respect to preying on other fungal feeders such as dipteran larvae. Moreover, staphylinids may use fungi as breeding and mating sites or might be affected by parasitic fungi. Thus, such interactions have significantly contributed to the enormous diversification of this group of beetles (NEWTON 1984).

The goal of this work is to review the major literature concerning associations between Staphylinidae and fungi and to explain the adaptations to the mouthparts of tissue- and spore-feeding forms. In general, the life history, habits and host relationships of Staphylinidae are poorly known. Our intent is to develop initial hypotheses that will provide a framework within which more specific questions regarding associations between Staphylinidae and fungi can be formulated.

Only a small part of this paper refers to our own observations in the field and the laboratory. We mostly draw on the results of research performed by other authors.

This article is dedicated to Prof. Dr. Berndt Heydemann on the occasion of his 75th birthday.

General characteristics of Staphylinidae

Staphylinidae are distinguished from other Polyphaga by the presence of articulated larval urogomphi and a high-grade wing folding mechanism in which an intrinsic spring is absent and the wings are folded with the aid of abdominal movements. The flexible elongated body resulting from the shortening of the elytra, typical of adult Staphylinidae, may allow for greater mobility in small holes and crevices and has probably been of selective advantage in the evolution of this group. Adults are generally long-lived in comparison to larvae, which typically complete development within a few days or weeks. Both stages usually occur in the same habitat and exploit the same resources (LAWRENCE & NEWTON 1982). Immature forms undergo three larval instars. Larvae burrow into the surrounding soil and form pupal chambers.

Staphylinids are mostly ground-living and inhabit the upper humus and litter layer of the soil, preferring moist conditions. This probably represents the ancestral habitat of the entire superfamily Staphylinoidea (LAWRENCE & NEWTON 1982, HANSEN 1997 b). Many species occur in various kinds of rotting plant debris, rotten wood, fungi, dung, carrion, etc. Most staphylinids are univoltine. In some cases, two to several generations occur per year, e.g. in the genera *Bledius* Leach (LARSEN 1936) and *Gyrophaena* Mannerheim (ASHE 1984 b, HENNEBERG 2004). Staphylinids, which live in temperate climates, generally hibernate in the adult stage. Staphylinidae may have originated from "lower" microphagous staphylinoids as predatory inhabitants of interstitial spaces of the forest litter (LAWRENCE & NEWTON 1982). Detailed biological information is only available for a small fraction of the more than 46,000 species of Staphylinidae (NEWTON et al. 2000). Furthermore, the vast majority of this species group is only known from the adult stage (HANSEN 1997a).

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Observational methods for establishing mycophagy in staphylinids

Observations in the field and the laboratory comprise (i) direct observations of the feeding behaviour, (ii) analyses of the gut content or (iii) experiments on the food preference. The results of gut-content analyses can be misleading, since the gut might contain fungal material despite the feeder being a predator with no preference for fungi. In this case, the fungal material might have been associated with the prey rather than with the predator.

Studying the behaviour of small staphylinids such as *Gyrophaena* in the wild is not easy. Adults and larvae often live between the gills on the underside of the cap of a mushroom and adults tend to abandon a mushroom once it has been disturbed. Thus, use of a mirror beneath the hymenium of the mushroom might be helpful for observing the beetles in their natural habitat (BENICK 1952, ANDREESSEN 1984, HENNEBERG 2004). Both gyrophaenine larvae and adults can often be collected together on the host fungus, especially on middle-aged, fleshy gilled mushrooms. In this way, larvae can be identified by their association with the adults on the same host. The identification of late instar larvae found on older fleshy mushrooms without rearing the larvae is, however, often difficult, because adults have commonly abandoned these older mushrooms (ASHE 1984b).

Specimens of the 1-mm-long *Eumicrota* Casey are more reluctant to leave a fruiting body. Therefore, *Eumicrota* can be easily transported to the laboratory for detailed observations under the microscope (ASHE 1987).

Association between beetles and fungi

DONISTHORPE (1935) was the first author to list the proper names of the fungi with which beetles associate. SCHEERPELTZ & HÖFLER (1948), BENICK (1952), REHFOUS (1955), GRAVES (1960), HÖFLER (1960), KLIMASZEWSKI & PECK (1987), HENNEBERG (2004) and others who have investigated the communities of insects inhabiting the fruiting bodies of the larger mushrooms have recognized three categories of fungus-associated insects, (i) obligatorily dependent species ("mycetobionts"), (ii) regular but not obligate users of the fungal resource, including predators of mycophagous dipteran larvae ("mycetophiles") and (iii) occasional or casual users ("mycetoxenes").

However, this concept of closeness of association with a fungal host and the notion of successional host stages cannot be applied to all fungal resources fed on by insects, since many of them are small or microscopic and thus are not easily distinguishable from other food material such as bacteria or detritus. Moreover, there are saprophagous, predaceous or parasitic species that are fungus-dwelling but that do not feed on living fungal tissue or spores.

As trophic and spatial resources for insects and other invertebrates, fungi have been very unevenly studied. "Hymenomycetes" (i.e. Basidiomycetes with hymenial fruiting bodies) have been the focus of most attention. The fruiting bodies of hymenomycete fungi, although of unpredictable occurrence, mostly represent large resources, which are readily exploitable. In comparison with the Basidiomycetes as "macrofungi", the number of insect taxa recorded for the Ascomycetes (CROWSON 1984, DENNIS et al. 1991), Zygomycetes and Myxomycetes (LAWRENCE & NEWTON 1980, STEPHENSON et al. 1994) is very small.

Little is known of insect associations with the fungi in the soil, in leaf litter and other decaying plant material, or with the small saprobic fungi found in association with

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dead wood, dung and carrion. The majority of these fungi belongs to the Ascomycetes, the Zygomycetes and the Fungi imperfecti (STRASBURGER 1983). The minute fungi found on the surfaces of living plants, the so-called phylloplane species, have been reported as being the food of only a few insects (e.g., THAYER 1987).

The two most important mycophagous insect orders are the Diptera (HACKMANN & MEINANDER 1979) and the Coleoptera (HAMMOND & LAWRENCE 1989). Among the Diptera, the larval stages are usually exploiters of the fruiting bodies of the larger fungi. However, in the Lauxaniidae, feeding on fungal hyphae and spores has also been reported for the adults (BROADHEAD 1984). Among the Coleoptera, both the adults and the larvae can be fungivorous/mycophagous. In the superfamily Staphylinoidea, the following families include mycophagous species: Ptiliidae, Leiodidae, Staphylinidae and perhaps Agyrtidae. Probably many thousands of beetle species are exclusively mycophagous (HAMMOND & LAWRENCE 1989). Much remains to be discovered, especially in the tropical species, including the precise food source of at least facultative fungus-feeders and dead-wood-associated beetles (HAMMOND & LAWRENCE 1989).

Instead of placing an insect into one of three feeding categories as fungivores, detritivores or predators, the determination of a trophic continuum might provide a more accurate description, since many species might occupy more than one trophic level (BRUNS 1984).

Mycophagous Staphylinidae (e.g. *Oxyporus* Fabricius, *Gyrophaena* Mannerheim, *Sepedophilus* Gistel) and some predaceous Staphylinidae (e.g. *Aleochara* Gravenhorst and *Bolitobius* Leach) prefer young fresh mushrooms containing spores. In contrast, mushrooms in the stage of decay mainly attract predaceous Staphylinidae, e.g. *Tachinus* Gravenhorst, *Philonthus* Stephens, *Ontholestes* Ganglbauer and *Atheta* Thomson (SCHEERPELTZ & HÖFLER 1948, LIPKOW in prep.).

Mycophagy is presumably a major means of spore dispersal, especially for hypogeous fungi. Most of these fungi do not forcibly discharge spores; their sporocarps have sterile tissue that completely encloses the sporogeneous tissue. If their dispersal is via mycophagy and if spores do not attach to the body surface of the insect, spores of these fungi have to be capable of germination following defaecation (FOGEL & PECK 1975).

Associations with fungi have also been studied by LESCHEN (1994a), comparing ecological and behavioral correlates among mycophagous Coleoptera in tough persistent fungi *versus* soft ephemeral ones. Moreover, HENNEBERG (2004) studied the interactions of four aleocharines (*Gyrophaena joyioides* Wüsthoff, *G. gentilis* Erichson, *G. affinis* Sahlberg, and *Oxypoda alternans* Gravenhorst) with the Agaricales *Megacollybia platyphylla* (Pers. Fr.) Kofl. & Pouz and *Marasmius alliaceus* (Jacqu. Fr.) Fr.

Kinds of mycophagy

Mycophagy (fungus-feeding) has independently evolved many times in the Staphylinoidea (NEWTON 1984). Facultative mycophagy seems to occur to various degrees in many groups, although such forms are probably considered to be more saprophagous. Indeed, a clear distinction between saprophagy and mycophagy is difficult to make, since both feeding substrates might be closely interwoven.

LAWRENCE (1989) distinguished between two types of mycophagy, viz macrophagy and microphagy. Macrophagy is the habit of feeding on "tissue" in the cap and/or the stem of a mushroom, whereas microphagy is defined as the habit of feeding on

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very small particles or loosely organized food masses consisting of spores, hyphae or highly decomposed animal or plant tissue. Usually, many of such "microphages" would be considered saprophagous, although some of them may be able to subsist on fungal material only. The exact nature of the food may be determined by examining the gut contents (LESCHEN 1993).

Staphylinid taxa associated with fungi

Out of 31 subfamilies of Staphylinidae in total, the species of 21 subfamilies are found on or in fungi (THAYER 2005). However, mycophagy occurs probably only in 16 subfamilies, since several species found on fungi are predators. Mycophagy is probably a secondary feeding mode, because Staphylinidae in general seem to be a primarily predatory group (cf. THAYER 2005). Shifts in feeding preference are found not only between tribes and genera, but even within the same genus (e.g. *Sepedophilus*: NEWTON 1984, LESCHEN 1993).

Omaliine group

Glypholomatinae: The guts of some *Glypholoma* Jeannel spp. have been shown to contain fungal spores (THAYER 1997). Spores of *Bondarzewia guaitecasensis* (Basidiomycetes: Hericiales) were found in the gut of *G. germaini* Thayer, which lives in Argentina (THAYER 2005).

Omaliinae: *Hypopycna rufula* (Erichson) is assumed to be at least facultatively mycophagous. WHITEHEAD (1999) has found spores of *Cladosporium* sp. (Hyphomycetes) in the gut of these omaliine species. CROWSON (1982) has reported *Phyllodrepoidea crenata* (Gravenhorst) as having hyphae, yeast and decaying cambium in their guts.

Proteininae: Proteininae are often associated with rotten fungi. They are probably sapro-/mycophagous liquid feeders on decomposing products (NEWTON 1984). Some Proteininae are considered mycophagous (NEWTON & THAYER 1995).

Micropeplinae: Micropeplinae, which are often referred to as being saprophagous, probably feed primarily on Ascomycotina (HAMMOND & LAWRENCE 1989), sampling the spores with their spore brush (LAWRENCE 1989). According to NEWTON (1984), these beetles feed on moulds and decaying organic matter.

Neophoninae: *Neophonus bruchi* Fauvel sweeps fungi into its mouth that grow on or adhere to the surface of leaves (THAYER 1987, LAWRENCE & MILNER 1996).

Dasycerinae: WHEELER (1984) has found Dasycerinae on various moulds or polypores. It remains unclear whether they are obligately mycophagous.

Tachyporine group

Tachyporinae: The Tachyporinae are probably a basal predatory group but mycophagy may have evolved at least twice in this subfamily, e.g. in some *Sepedophilus* and probably some *Tachinus* species. *T. signatus* Gravenhorst (*rufipes*) is a predator. However, in the laboratory, some larvae of *T. signatus* can be exclusively fed on yeast (Protascomycedidae). In this case, the time of development is much longer in comparison with predaceous feeding (LIPKOW 1966).

NEWTON (1984) describes *Sepedophilus* as an ecologically diverse genus, which, at least in the larval stage, consists of clearly predatory and apparently obligatorily mycophagous forms. Some *Sepedophilus* species may practice preoral digestion as reported for the mycophagous beetles of *Oxyporus* (HANLEY & GOODRICH 1995), *Mega-*

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lopinus Eichelbaum (LESCHEN & NEWTON 2003) and the predators *Tachyporus* Gravenhorst and *Tachinus* (LIPKOW 1966).

Adults of *Bolitobius* species are found in Boletales and other macrofungi. They feed on larvae of fungivorous Diptera (LIPKOW in prep.).

Trichophyinae: The Trichophyinae are related to the Tachyporinae and feed on both fungi and, perhaps predominantly, small arthropods (ASHE & NEWTON 1993).

Habrocerinae: At least some Habrocerinae feed on spores and hyphae (THAYER 2005).

Aleocharinae: *Gyrophaena*, *Phanerota* Casey and *Eumicrota* feed, both as larvae and adults, on spores of the hymenium of Agaricales and Polyporales (ANDREESSEN 1984, ASHE 1984b, 1986a, 1993, RUSCH 1990) (Fig. 1). *Placusa* Erichson larvae and adults (ASHE 1991) and some *Homalota* Mannerheim adults (ASHE 1993) feed on subcortical spores and hyphae. *Meronera* Sharp beetles feed on surface hyphae.

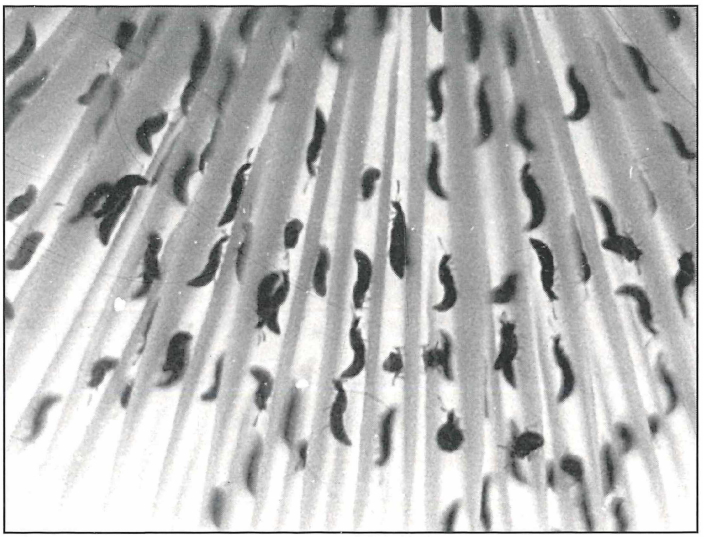

Fig. 1: Adults of *Gyrophaena joyioides* in the interlamellar space of a fruiting body of *Megacollybia platyphylla* (Agaricales) (modified according to ANDREESSEN 1984).

Beetles of the termitophilous *Termitogerrus* Bernhauer (GRASSE & POISSON 1940) and *Termitodiscus* Wasmann (SEEVERS 1978) feed on conidea, blastopores and fungus filaments in the fungal gardens of their termite host *Macrotermes natalensis* (Hav.). ASHE (1993) has examined the mouthparts of *Termitodiscus heimi* Wasmann but found no mouthpart modifications that could be clearly correlated with fungivory (ASHE 1991). *Pleurotobia tristigmata* (Erichson) is a predator. Adults feed on the larvae of fungivorous flies, whereas the larvae eat fungivorous nematodes (ASHE 1990).

Members of *Bolitochara* Mannerheim are often believed to be mycophagous, although TOPP (1973) has observed them feeding on mycetophilid fly larvae in fungi. ASHE (1990) has confirmed that adults of the closely related *Pleurotobia* Casey are primarily predaceous on fungivorous fly larvae and that the larvae feed on fungivorous nematodes. However, facultative feeding on fungal tissue by adults has also been observed.

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Gut contents in larvae and adults of the closely related species *Stictalia californica* (Casey), *S. rufipennis* Casey and *S. minor* Casey and in adults of *Pseudatheta elegans* Cameron are composed primarily or exclusively of fungal spores and some hyphae, suggesting that mycophagy may be obligatory among members of these taxa (ASHE 1993).

Adults of *Aleochara,* observed in *Boletus* (*Leccinum*) *scabrum* (Bull ex Fr.) S.F. Gray (Boletales), feed on the fungivorous larvae of flies (e.g., Anthomyidae) (LIPKOW in prep.). Larvae of *Aleochara* are solitary parasitoids of the pupae of cyclorrhapheous Diptera (e.g., MAUS et al. 1998). Several species of *Atheta* are consistently found on mushrooms (NEWTON 1984). *Atheta* beetles are known or believed to be predators. Those found on fungi are probably attracted there to feed by the abundance of fly larvae and other arthropods present on older fruiting bodies. Consistent with this interpretation is the report of SCHEERPELTZ & HÖFLER (1948) showing that members of *Atheta* are most abundant and diverse on older or decaying mushrooms in contrast to the colonization of younger fruiting bodies by the exclusively mycophagous Gyrophaenina.

Within the Paglini, *Pagla* Blackwelder and Oxypodini, *Polylobus* Solier beetles are considered obligate spore-feeders (BETZ et al. 2003). The adults of *Oxypoda* Mannerheim (*Mycetodrepa* Thoms. spp.) are found in many species of Polyporales and Agaricales. HENNEBERG (2004) assumes that *Oxypoda alternans* (Gravenhorst) feeds on spores of agaricoid Basidiomycetes. The exact nature of their relationship with fungi remains to be investigated (ZERCHE 1999).

Oxyteline group

Scaphidiinae: The Scaphidiinae are apparently an exlusively mycophagous group, feeding mainly on fungal hyphae.

Some species of *Scaphisoma* Leach beetles feed on a wide variety of fungi, including Clavariaceae, Agaricales, Thelophoraceae, Heterobasidiomycetes, Polyporales, Myxomycetes, and Moniliaceae (HANLEY 1996). *Cyparium* Erichson spp. are internal context feeders on Agaricales (NEWTON 1984, LAWRENCE 1989), whereas representatives of *Scaphium* Kirby feed on fleshy Agaricales, *Baeocera* Erichson and *Scaphobaeocera* Csiki, and some *Scaphisoma* beetles are spore feeders on a variety of Myxomycetes (LAWRENCE & NEWTON 1980, NEWTON 1984, NEWTON & STEPHENSON 1990, STEPHENSON et al. 1994).

Osoriinae: Little is known about the diet of the Osoriinae. Although basically a saprophagous group, *Renardia* Motschulsky, *Thoracophorus* Motschulsky and possibly *Holotrochus* Erichson, beetles appear to feed on the "ambrosia" fungi. These subcortical fungi are also grazed by some bark beetles (Scolytidae, Platypodidae) (NEWTON 1984).

Piestinae: The Piestinae seem to be saprophagous. Some species may feed on Ascomycotina (THAYER 2005).

Staphylinine group

Oxyporinae: The Oxyporinae are obligatorily mycophagous. *Oxyporus* larvae and adults feed on the context of Agaricales and occasionally on other macrofungi (BRUNS 1984, NEWTON 1984, LESCHEN & ALLEN 1988, HANLEY & GOODRICH 1995, LIPKOW 1997). *Oxyporus* beetles show pre-oral digestion of the fungal material (HANLEY & GOODRICH 1995).

Pseudopsinae: NEWTON (1982, 1984) has summarized the reports of collections of

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Polyporaceae but concludes that both larvae and adults are probably predaceous.

Megalopsidiinae: The Megalopsidiinae, which also show a close association with fungi, perhaps primarily bracket fungi (Polyporales), have been reported to be predaceous (LESCHEN & NEWTON 2003).

Host relationships of mycophagous Staphylinidae

Fungal tissue must be considered a valuable resource with high nutritional value for those organisms that have the metabolic capabilities to digest it. However, fungi may produce substances that serve as chemical defenses against consumers (MARTIN 1979). These secondary metabolites may play an important role in host relationships of mycophagous staphylinids. However, fungal host specifity has not as yet been clearly worked out at the species level and might be largely dictated by the age of the fruiting body (SCHEERPLETZ & HÖFLER 1948, HÖFLER 1960). Moreover, host specifity might be generally weakened, because most mycophagous staphylinids are microphagous (LAWRENCE 1989) feeding on fine material such as spores, which might contain fewer secondary metabolites than fungal flesh. Some details on species-specific host preferences are available for the genera *Gyrophaena* and *Oxyporus*.

Tachyporine group

Gyrophaena: Most of the North American Gyrophaenina prefer a group of hosts and not only one species. When the preferred mushrooms within the host spectrum of a gyrophaenine are not available, less preferred mushrooms outside the spectrum are used (ASHE 1984 a, b).

ANDREESSEN (1984) has found significant differences in host specifity in Central European *Gyrophaena* species. *Gyrophaena joyioides*, *G. gentilis*, *G. affinis*, *G. fasciata* Marsham and *G. nana* Paykull have a broad host spectrum, whereas that of *Gyrophaena minima* Erichson and *G. bihamata* Thomson is narrow. According to HENNEBERG (2004) beetles of various species of *Gyrophaena* might co-occcur on the same host mushroom. He concludes that interspecific competition between different *Gyrophaena* species is probably more important for the larvae than for the adults.

In the laboratory, ANDREESSEN (1984) added eggs of *Gyrophaena joyioides* to the fresh fruiting bodies (gills) of the host fungus of *G. affinis*. The hatched first instar larvae of *G. joyioides* did not use the spores of the new fungus and died within one day. In the laboratory, *G. joyioides* fed on fungal "tissue" if spores of the preferred fungus were not available. Adults of *G. gentilis* and *G. affinis* can be fed with pieces of larvae of the meal worm *Tenebrio molitor*.

One mushroom can contain individuals of several species of *Gyrophaena*. In a dry summer with a low density of mushrooms, hundreds to thousands of adults of *Gyrophaena* might live in one single fruiting body. Despite the high density, their interindividual distances might be more or less uniform. At high population densities, gyrophaenine beetles show aggressive behaviour, i.e. each beetle defends its small territory. In this way, maximum densities of about 25 individuals per cm^2 can be maintained (Fig. 1). Most gyrophaenine beetles leave a mushroom before the decaying process starts. The preferred time for flight is the late afternoon but dusk appears to be a trigger for increased flight activity in the context of finding new fungal hosts. The normal height of flight is about 60 cm above the ground. There seems to be a balanced sex ratio on the mushrooms. The number of generations per year is unknown in *Gyro-*

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phaena spp. but, for Central Europe, 2-3 generations seem to occur (HENNEBERG 2004).

There is no obvious correlation between the population densities of mushrooms and the densities of *Gyrophaena* beetles (ANDREESSEN 1984). In Germany, the highest density of *Gyrophaena* beetles occurs in the summer, whereas the highest densities of mushrooms occur in late summer and autumn, following a dry summer.

Staphylinine group

Oxyporus: Some species of New World Oxyporinae exhibit a distinct preference towards certain hosts within a wide selection of "acceptable" hosts. Other species either exhibit no distinct preference at all or are species-specific in their host selection (HANLEY & GOODRICH 1995).

Few collection records for species of *Oxyporus* include the fungal hosts of the larvae. The available host data indicate that larvae are specialized to one or two species of related fungi within a small portion of the preferences exhibited by the adults.

Whether competition plays a significant role in the utilization of fungal hosts by members of the Oxyporinae is unknown. Partitioning of the larval environment probably occurs between different species of *Oxyporus*. For example, whereas large numbers of adults of the two species *O. stygicus* Say and *O. rufipennis* LeConte were collected from the fungus *Omphalotus illudens* (Schw.), there was only one species (*O. stygicus*) represented as larvae (HANLEY & GOODRICH 1995).

Feeding mode and structure of the mouthparts

LESCHEN (1993) suggests that four different patterns describe the general relationship between food material and the structure of the mouthparts in Staphylinidae: (i) mouthparts and feeding habits are similar among taxa, (ii) mouthparts are similar among taxa and feeding habits are diverse, (iii) mouthparts are variable among taxa and feeding habits are similar and (iv) mouthparts and feeding habits are both variable but similar in some terminal taxa. The structure of the mouthparts does not necessarily present a barrier in regard to changes in the diet and any shifts between saprophagy, predation and mycophagy are constrained by physiological or behavioural mechanisms. Changes from a soft to a more compact type of food, however, seem to be consistently associated with structural modifications of the mouthparts.

The general conclusions of LESCHEN (1993) have been confirmed in a comparative study on the mouthpart morphology in spore-feeding Staphylinoidea by BETZ et al. (2003). These authors have established that shifts from general microphagy to sporophagy are not necessarily constrained by nor strongly reflected in mouthpart morphology. Most lineages investigated in this study show a complex of mouthpart features, which can be considered to constitute the groundplan of microphagous polyphagan beetles in general (cf. LAWRENCE 1989, 1991, BEUTEL et al. 2001) (Fig. 2): (i) cibarial roof with series of parallel rows lined with microtrichia (Fig. 2a), (ii) maxillae with brush-, rake- or comb-like structures for sweeping in diffuse food material (Fig. 2b, f), (iii) mandibles with subapical hyaline and/or setose lobe (prostheca) for transporting food posteriorly and preventing its escape from the processing area (Fig. 2c, f), (iv) mandibles with well-developed basal mandibular mola often provided with mesal crushing or grinding structures and basal hyaline and/or setose lobe ("molar velum") for transporting the food proximally (Fig. 2d), (v) epipharynx, prementum and hypopharynx with medial longitudinal groove ("bristle-trough") bordered by hairs or spines, involved in concentrating and directing the food stream in the median line

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(Fig. 2e) and (vi) epipharynx and hypopharynx with a tuft of posteriorly directed hairs ("cram-brushes") for directing food towards the pharynx (ht in Fig. 2f).

Nevertheless, in several spore feeders, the organs of food intake and grinding have experienced particular derived fine-structural modifications, which have convergently evolved, probably in response to specialized mycophagy such as spore-feeding (BETZ et al. 2003, BETZ 2004). In the following, we summarize established mouthpart features in various lineages of staphylinids as correlated with mycophagy (mostly sporophagy). If not explicitly otherwise mentioned, the followings descriptions refer to the adult stages.

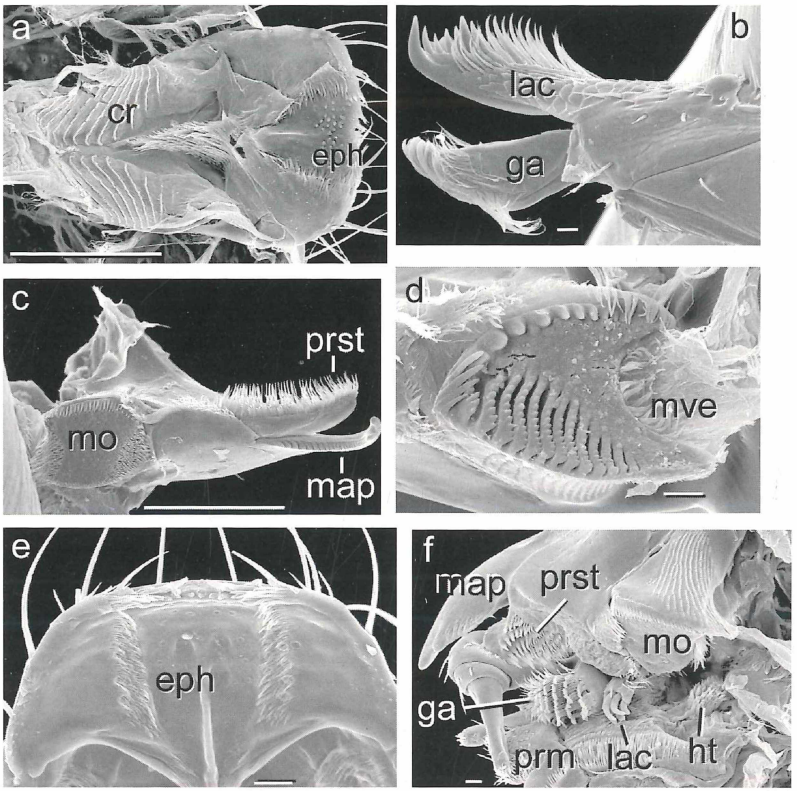

Fig. 2: Scanning-electron microscopical (SEM) views of mouthpart features illustrating the microphagous groundplan of spore feeding staphylinids. (a) *Dropephylla cacti* (Schwarz). Epipharynx and cibarial roof. Bar = 100 µm. (b) *D. cacti.* Ventral aspect of right maxilla. Bar = 10 µm. (c) *Sepedophilus basalis* (Erichson). Medial aspect of right mandible. Bar = 100 µm. (d) *Hapalaraea megarthroides* (Fauvel). Medial aspect of mola of left mandible. Bar = 10 µm. (e) *Dasycerus angusticollis* Horn. Epipharynx. Bar = 10 µm. (f) *Micropeplus neotomae* Campbell. Medial aspect of mouthparts of the right body side. Bar = 10 µm. Abbreviations: cr, cibarial roof; eph, epipharynx; ga, galea; ht, tuft of hair-like trichomes; lac, lacinia; map, mandibular apex; mo, mola; mve, molar velum; prm, prementum; prst, prostheca.

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Omaliine group

Proteininae: *Megarthrus* Steph. larvae have evolved mouthparts that are markedly distinct from other staphylinids. Their styliform malae (Fig. 3a) are provided with a ventral longitudinal groove. Although KEMNER (1925) considered these larvae spore-feeders, the special structure of their mouthparts suggests some kind of fluid feeding on fungi. This is supported by the observations of NEWTON (1984) who found virtually no solid matter in the guts of these larvae collected from slime-mould fruiting bodies.

Micropeplinae: Apart from their groundplan features, facultative spore feeders of the genus *Micropeplus* Latreille have a dorsal molar layer similar to that described for *Proteinus* Latreille (BETZ et al. 2003). Additional derived features are (i) the shovel-like mandibular apex, (ii) a mace-like prostheca (Fig. 3b), which might act as a grinding tool in addition to the mola and (iii) the complex rake-like galeae (BETZ et al. 2003).

Neophoninae: Special features of the mouthparts of *Neophonus bruchi* Fauvel are its brushy laciniae (Fig. 3c), which must be assumed to play a special role in their singular mode of food intake mentioned above (THAYER 1987, BETZ et al. 2003).

Dasycerinae: In the facultative spore-feeder *Dasycerus angusticollis* Horn, the galeae have developed into complex excavator-like devices, whereas the laciniae are advanced brush-like structures (Fig. 3d) (BETZ et al. 2003). Both features have to be considered as highly evolved types of microphagous mouthparts. In particular, the laciniae might well function in removing and sweeping surface hyphae and spores into the pharynx. Analogous structures are known from *Dasycerus* Brongniart larvae, in which the apical surface of the mandible has become modified to brush spores or hyphae from surfaces (cf. Fig.34.170 in NEWTON 1991).

Tachyporine group

Tachyporinae: The mouthparts of the spore-feeding genera among the tribe Tachyporini show the complete set of attributes of adult mouthparts plesiotypic for microphagous polyphagans (as outlined above). Hence, at least in the facultative spore-feeders of this tribe, no substantial modifications of the microphagous ground pattern have taken place in response to sporophagy (BETZ et al. 2003). However, several of the groundplan features associated with microphagy in Polyphaga have obviously experienced structural modification in Tachyporinae. These might represent functional upgrades of an ancestrally simpler structure or might be a response to specific pressures arising from specific feeding modes and/or substrates (BETZ et al. 2003): (1) The prostheca is not hyaline but reinforced, forming an obliquely ventrad-oriented fringed lobe. This type of prostheca is also present in most aleocharines (cf. ASHE 1993) and might represent an improved device for sweeping particulate food material off the maxillae. (2) Whereas the galea is apically truncated in *Tachinus*, forming a brush of simple hairs, it appears much more differentiated and advanced in *Coproporus* Kraatz and *Sepedophilus*. In the latter genus, it forms a ventrally oriented ellipsoid lobe, bearing a dense array of complex spoon-like hairs (Fig 3e). Direct feeding observations have confirmed that these lobes are not only the major organs of food intake, but also function in sweeping food particles off the mandibles and *vice versa* (BETZ et al. 2003). In their general structure and ventral orientation, they show astonishing convergence to the laciniae of the staphylinid *Dasycerus* (Fig. 3d), which probably function in a similar way.

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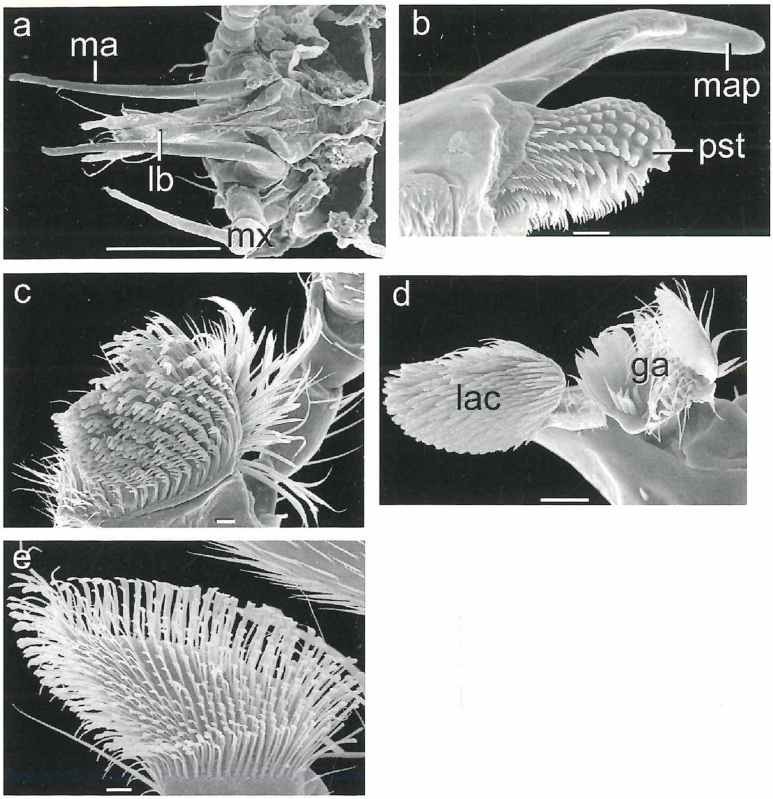

Fig. 3: SEM views of sporophagous mouthparts of selected members of the omaliine and tachyporine group. (a) *Magarthrus* cf. *angusticollis* Mäklin larva. Dorsal aspect of styliform maxillary malae. Bar = 100 µm. (b) *Micropeplus neotomae*. Medio-dorsal aspect of apex plus prostheca of left mandible. Bar = 10 µm. (c) *Neophonus bruchi* Fauvel. Ventro-medial aspect of left maxilla. Bar = 10 µm. (d) *Dasycerus angusticollis*. Fronto-medial aspect of galea and lacinia. Bar = 10 µm. (e) *Sepedophilus* sp. [Australia]. Ventro-medial aspect of galea. Bar = 10 µm. Abbreviations: ga, galea; lac, lacinia; lb, labium; ma, mala; map, mandibular apex; mx, maxilla; pst, prostheca.

The mouthparts of the larvae of the genus *Sepedophilus* are variable. Some *Sepedophilus* species are predators like their ancestors, whereas others are mycophagous on spores of fleshy or persistent mushrooms, and the rest have mixed feeding strategies (NEWTON 1984, LESCHEN & BEUTEL 2001, BETZ et al. 2003). In *Sepedophilus basalis* (Erichson) larvae, the dorsal surface of the mala bears a dense array of prominent tubercles (LESCHEN & BEUTEL 2001). This structure probably serves as a secondary triturating surface for fungal material such as spores and hyphae, since primary grinding structures such as true molae seem to be absent in the groundplan of staphylinid larvae. Such structures are characteristic for "type C" *Sepedophilus* larvae (according to the classification of morphological types in NEWTON 1984) and have probably evolved in connection with obligate specialized mycophagy (LESCHEN 1993; LESCHEN & BEUTEL 2001). No grinding structures have been found in other spore-feeding larvae of

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Tachinus and *Sepedophilus* (BETZ et al. 2003). In these taxa, spores probably pass into the gut undamaged, so that mechanisms other than mechanical trituration (e.g. pseudo-germination or enzymatic penetration) might be involved in opening up the spores. Direct feeding observations of *Sepedophilus* larvae have revealed that the labium plays a major role not only in gathering food, but also in transporting it proximad (BETZ et al. 2003). Moreover, these observations show that the prementum is predominantly involved in food gathering, supporting the mandibular apices and the malae by its excavator-like action.

Aleocharinae: Three feeding modes have been mentioned with respect to mycophagous Aleocharinae, i.e. (i) hymenium scraping/sporophagy, (ii) context feeding and (iii) microphagous feeding on surface moulds, spores and hyphae (ASHE 1993). Types that are at least facultative spore-feeders and/or microphagous fungivores are known from the (sub-)tribes Homalotini-Gyrophaenina (*Gyrophaena, Phanerota, Eumicrota*), Homalotini-Bolitocharina (*Stictalia* Casey), Homalotina (*Homalota*), Placusini (*Placusa*), Termitodiscini (*Termitodiscus*), Oxypodini (*Polylobus*) and Paglini (*Pagla*) (cf. BETZ et al. 2003). Future studies will perhaps reveal additional mycophagous aleocharines. In the following, we review the feeding modes and correlated mouthpart structures in selected taxa of this list. A more detailed description of the mouthpart morphology of these taxa can be found in ASHE (1984a,b, 1993) and BETZ et al. (2003).

Hymenium scraping/sporophagy: Within the subtribe Gyrophaenina (tribe Homalotini), hymenium scraping/sporophagy is well known from the obligately mycophagous genera *Gyrophaena*, *Phanerota* and *Eumicrota* (ASHE 1993; BETZ et al. 2003). Both larvae and adults live closely associated with the hymenium of Polyporaceae or Agaricales. They scrape their maxillary apices across the hymenium, thereby removing maturing spores, basidia and other hymenial structures. While doing so, the maxillae describe an especially large working angle (BETZ et al. 2003). This kind of feeding is correlated with the development of highly derived lacinial spore brushes in the adults (Fig. 4a), analogous to those found in *Neophonus* Fauvel, *Dasycerus* and the galeae in the tachyporines *Coproporus* and *Sepedophilus* (cf. Fig. 3e). Interestingly, there is striking variation in the number, density and size of teeth or denticles on this maxillary spore brush of gyrophaenines (ANDREESSEN 1984, ASHE 1993) (Fig. 5), which in both larvae and adults appears to be correlated with the host type. Both larval and adult gyrophaenines, like *Brachycara* Thomson spp., which lives on woody polypore mushrooms, have maxillary spore brushes, whose teeth are much more numerous and more densely arranged than those of species that live on fleshy gilled mushrooms (e.g. *Gyrophaena nana* Paykull). In the woody polypores, the pores are too small to allow direct contact with the hymenium surface. Hence, these beetles may graze maturing spores, hyphae that protrude from the pore mouths and hyphae from the mushroom surface (ASHE 1993). The gut contents of larval *Agaricomorpha apacheana* (Seevers) beetles, which inhabit the ventral surface of woody polypores, contain a mixture of mature fungal spores, broken cells and large masses of hyphae. In contrast, the gut contents of larval Gyrophaenina that live on gilled mushrooms consist mostly of maturing spores and basidia (ASHE 1993).

The galeae of the adults are also substantially modified. Among gyrophaenines, there is a tendency towards reducing the number of rake-like rows on the galeae and modifying filiform galeal setae into sub-spatulate or plate-like forms (ASHE 1984a). These developments probably reflect post-adaptational functional improvements in the context of hymenium grazing and spore-feeding. Examples of probably still more functionally advanced galeal structures are those that have developed in the obli-

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gatorily spore-feeding oxypodine *Polylobus*, in which the apex forms a scoop-like device (Fig. 4b) that might both scrape and prevent loss of material even more efficaciously (BETZ et al. 2003).

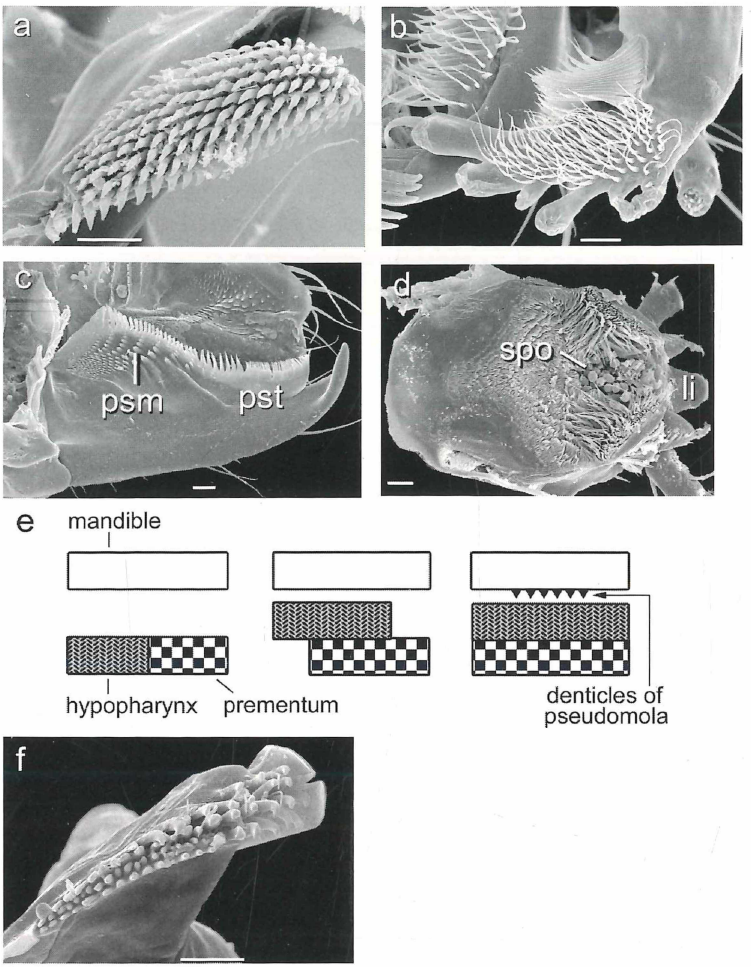

Fig.4: SEM views of sporophagous mouthparts of various Aleocharinae. (a) *Eumicrota spinosa* (Seevers). Medial aspect of left lacinia. Bar = 10 µm. (b) *Polylobus* sp. [Chile]. Ventro-medial aspect of galea. Bar = 10 µm. (c) *Homalota* sp. [Mexico]. Ventral aspect of left mandible. Bar = 10 µm. (d) *Gyrophaena tenebrosa* Casey. Dorsal aspect of labium-hypopharynx. Note accumulation of spores within hypopharyngeal depression. Bar = 10 µm. (e) Scheme illustrating the stepwise re-construction of the labium-hypopharynx in derived spore-feeding aleocharines (right) starting from the plesiotypic condition (left). For further explanations see text. (f) *Eumicrota spinosa* larva. Medial aspect of mala. Bar = 10 µm. Abbreviations: li, ligula; pst, prostheca; psm, pseudomola; spo, spores

In most aleocharines, a well-developed molar lobe with a mesal grinding surface

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has been completely reduced (ASHE 1993) in connection with their primarily predaceous feeding habit. However, after the shift of feeding preference towards mycophagy in several groups, secondary trituration surfaces ("pseudomolae") as substitutes for true molae have evolved *de novo* at various places on the mandible (cf. ASHE 1993). Most often, secondary grinding structures are established on the ventral inner side of the mandibles in the form of an array of prominent pointed grinding teeth (Fig. 4c). In all sporophagous taxa investigated by BETZ et al. (2003), these structures are correlated with an extensive reconfiguration of the hypopharynx, which is elevated and displaced anteriorly, forming a "second layer" on top of the prementum. The hypopharynx has thus been moved adjacent to the ventral mandibular surface, where it can function as an abutment for the ventral trituration surface of the mandibles (Fig. 4e). The bowl-like depression of the hypopharyngeal surface surrounded by hairs functions like a mortar, concentrating the spores (Fig. 4d) when they are triturated between hypopharynx and mandibles. Feeding observations (BETZ et al. 2003) have confirmed the hypothesis of ASHE (1993) that the mandibles in many (if not all) mycophagous aleocharines function mainly in triturating the food and are not involved in food gathering. The conditions described so far represent a relatively advanced state, which almost certainly has evolved in the context of obligate mycophagy such as sporophagy.

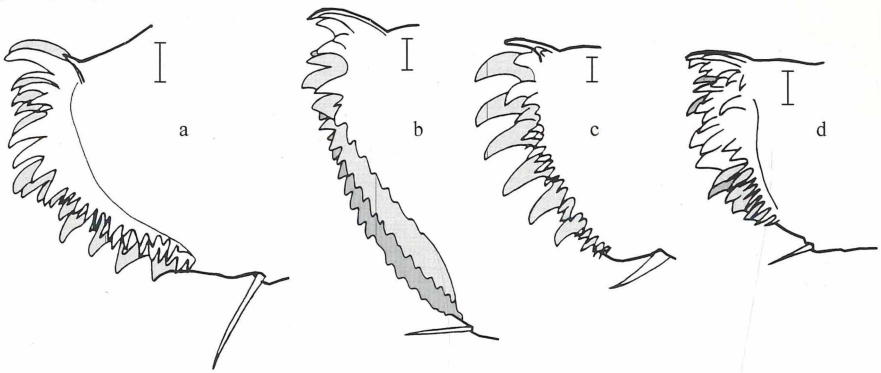

Fig.5: Ventral aspects of cuticular teeth at the distal margin of the maxillary mala of third instar *Gyrophaena* larvae. (a) *Gyrophaena gentilis*. Bar = 8 µm (= spore size of preferred host fungus *Megacollybia platyphylla*). (b) *Gyrophaena joyioides*. Bar = 8 µm (= spore size of preferred host fungus *Megacollybia platyphylla*). (c) *Gyrophaena affinis*. Bar = 6 µm (= spore size of preferred host fungus *Collybia dryophila*). (d) *Gyrophaena minima*. Bar = 7 µm (= spore size of preferred host fungus *Hypholoma fasciculare*) (modified according to ANDREESSEN 1984).

The gross structural and functional features of the maxillae of gyrophaenine larvae are remarkably similar to those of the adults and differ from the malae of other aleocharine larvae. In *Gyrophaena* and *Eumicrota*, the mesal surface of the maxillary mala bears a dense array of heavily sclerotized thorns and teeth (Fig. 4f, 5). These structures might be involved not only in scraping maturing spores and basidia from the hymenium of fresh mushrooms (ASHE 1986a), but also in crushing spore material. Comparative studies of the mala among gyrophaenines have revealed variations in the size and density of these malar structures; these variations appear to be correlated with their phylogenetic position and host type (ASHE 1986a). An additional peculiarity of

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many gyrophaenine malae is the cup-like plate at their distal margin, which most probably prevents loss of food from the mesal molar area (ASHE 1986a, 1993).

Context feeding: No Aleocharinae are known to feed internally on the context of fungal tissues. Members of the subtribe Bolitocharina feed at least facultatively on the context tissue of fleshy to persistent polypore mushrooms (ASHE 1993). This feeding mode is correlated with the proliferation and increased density of the denticles in the ventral molar region of adult mandibles (ASHE 1993). *Pleurotobia* beetles are primarily predaceous. However, facultative feeding on the context of fungal tissue by adults has also been observed (ASHE 1990).

Unlike the adults, larvae of Bolitocharina lack any obvious modifications associated with fungivory in either their mandibles or maxillae. Mouthparts of all known larval Bolitocharina are similar with respect to most general features to those of the Aleocharinae that are known to be predaceous.

Microphagous feeding: Microphagous feeding on surface moulds, spores and hyphae has evolved independently in *Meronera* (tribe Athetini) and *Placusa* (tribe Placusini). Observations have been made in laboratory cultures (ASHE 1991). Gut content analyses of larvae and adults of the subcortical species *Placusa despecta* Erichson indicate that these beetles feed almost exclusively on surface fungal hyphae and spores that grow beneath bark (ASHE 1991). The degree of microphagous fungivory among *Placusa* and other subcortical aleocharines is unknown but they might be assigned as facultative spore feeders. As in the obligate spore-feeders *Pagla* and *Polylobus*, *Placusa* beetles have independently evolved rows of sharp denticles on the dorsal molar surface of the adult mandibles (ASHE 1993; BETZ et al. 2003). These structures appear to be modifications of the pattern of asperites usually found on the dorsal molar surface not only in aleocharines, but in staphylinoids in general. Their modification into sharp denticles might make it possible to grind fungal material such as spores between the dorsal molar surface and the cibarial roof. Another feature found in *Placusa* are the rake-like galeae, which are similar to those described above in the Gyrophaenina (BETZ et al. 2003). As suggested above, these structures probably represent particularly advanced types of microphagous mouthparts that might be especially suited for scraping together particulate (fungal) food material.

Oxyteline group

Scaphidiinae: Mycophagy in scaphidiines has probably evolved from saprophagy (NEWTON 1984, LESCHEN 1993, HANSEN 1997b). Accordingly, the general plesiotypic pattern of mouthpart features connected with this ancestral feeding type (as outlined above) is represented in adult scaphidiines. Direct observations of *Scaphisoma* and *Baeocera* adults feeding on slime-mould sporangia has revealed that, in addition to the maxillae, the terminal parts of the mandibles are involved in spore intake (BETZ et al. 2003). Intermittent resting phases of the maxillae, although mandibular movements continue, are indicative of regular grinding phases in the feeding process. Some peculiarities in the scaphidiines might be regarded as special features correlated with mycophagy or, in the case of the obligate spore-feeders, specialized sporophagy (BETZ et al. 2003): (i) The mola is sclerotized and firmly united with the rest of the mandible. (ii) The mesal molar surface is well-developed and provided with an extensive array of grinding tubercles (Fig. 6a). (iii) In the obligate spore-feeding members of the genus *Scaphisoma*, the galea is differentiated into a prominent rasp-like "spore brush" (Fig. 6b) that should be considered the major organ of food intake. Adult *Baeocera* and

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Scaphobaeocera beetles are provided with ventral cavities between the pro- and mesothorax, which may be involved in transporting spores (NEWTON 1984).

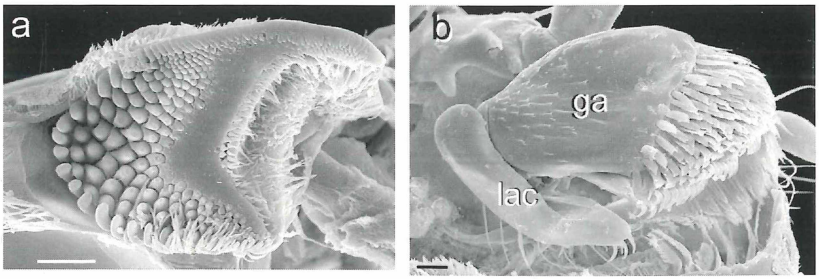

Fig.6: SEM views of of sporophagous mouthparts of selected members of the Scaphidiinae. (a) *Scaphobaeocera* n. sp. [Australia]. Medial aspect of mola of right mandible. Bar = 10 µm. (b) *Scaphisoma teres* Löbl. Dorsal aspect of left maxilla. Bar = 10 µm. Abbreviations: ga, galea; lac, lacinia.

On the mesal side of the larval *Baeocera* mandible, there is a sub-apical prominent pseudomola consisting of a dense array of sharp teeth (cf. LAWRENCE 1989, NEWTON 1991, LESCHEN 1993). Similar (though less prominent) pseudomolae have developed in many other scaphidiine genera (except *Scaphidium* Olivier) (LESCHEN 1993). The feeding behaviour of *Baeocera* larvae is similar to that previously described for *Sepedophilus* larvae (BETZ et al. 2003).

Staphylinine group

Oxyporinae: The large head of the representatives of the genus *Oxyporus* with its long and crossing mandibles has led entomologists to assume that *Oxyporus* is predaceous (SCHEERPELTZ & HÖFLER 1948). However, LESCHEN & ALLEN (1988) have observered *Oxyporus* larvae and adults feeding exclusively on higher fleshy Basidiomycetes. In food choice experiments in the laboratory, hungry adults of *Oxyporus rufus* Linné have been observed to avoid larvae of fungivorous Diptera. They only feed on the fungal tissue of the Agaricales (LIPKOW 1997, HANLEY & SETSUDA 1999, HANLEY 2001).

Fungal material chewed by the mouthparts of members of this group is saturated with digestive fluid. Both larvae and adults digest their food preorally (NAVARRETE-HEREDA & NOVELO-GUTIERREZ 1990), as do the members of the staphylinid subfamilies Staphylininae and Paederinae and *Tachyporus* and *Tachinus* in the Tachyporinae (LIPKOW 1966). LESCHEN & ALLEN (1988) interpret the derived character states of the mouthparts as adaptations to preoral digestion in *Oxyporus* adults. The adults have sickle-shaped mandibles used for slicing off pieces of mushroom tissue. The horizontally opposed cutting edges of the mandibles form a shearing plane. The closed mandibles form a container that may aid in manipulating the preoral juices. When the mandibles are open, the clypeus forms a container. A pseudomolar region is found posterior to the slicing edge of the mandible. Its anterior region is denticulate, whereas the posterior region is brush-like. Observations by HANLEY & GOODRICH (1995) indicate that the labrum forms a container by which preoral juices are directed when the mandibles are open. When the mandibles are closed, their denticulate areas may aid in the maceration of the fungus, increasing the surface area exposed to digestive en-

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zymes. The posterior brushes of the mandibles probably assist in the movement of the food towards the buccal cavity.

Larvae of *Oxyporus* are equipped with anterodorsally compressed, bifurcate mandibles with knife-like serrations at their margins. The larvae have been observed to make an initial cut into the host fungus by using the bifid tips and the antero-ventral edges of the mandibles, which possess serrate margins. The posterior and anterior asperate surfaces of the mandible probably function in finely grinding the fungal tissue. Pre-oral juices are then flooded over the food particles, which are subsequently sucked into the buccal cavity.

Life history: oviposition, larval development and pupation

One of the major parameters that determine the life history of organisms is the duration, stability and predictability of their feeding and breeding sites, although other parameters such as microclimate, refugia and exposure to predators may also be important (e.g. STEARNS 1976). The fruiting bodies of higher macrofungi often represent a short-lived and unpredictable resource for many fungicolous beetles as these bodies only last from a few days to several weeks and are widely scattered in space and time. These conditions might especially affect stationary larval stages, which cannot easily move to another habitat in case of the unforeseen detioration of their initial breeding place. Hence, in fungus-breeding beetles, we might expect special adaptations in specific life-history traits, such as short developmental times. Life history traits in fungicolous staphylinids have not been systematically examined, although valuable data has been collected in a few cases.

Tachyporine group

Aleocharinae: *Phanerota*: Under laboratory conditions (22-24°C), *Phanerota fasciata* (Say), a spore-feeding aleocharine staphylinid of about 2 mm body length, completes its larval development within just three days (ASHE 1986b). Eggs are laid on the gills of young fruiting bodies. The larvae hatch within 24 hours. The first instar larva lasts for 14 hours on average, instar II for 15 hours, and instar III for 2 days. The fully mature larva leaves the mushroom for pupation, which occurs within a silken pupal cell constructed in the interstices of soil or leaf litter and lasts 4 to 14 days (ASHE 1981).

Agaricomorpha Ashe, *Brachycara, Agaricochara* Kraatz: In contrast, members of the *Agaricomorpha*, *Brachycara* and *Agaricochara*, which are found on more persistent, woody polypore mushrooms, appear to have a longer time of development. This would support the hypothesis that non-mycophagous staphylinids need much longer to develop from oviposition to adult emergence than mycophagous staphylinids. However, quantitative features of the life history of these gyrophaenines are lacking (ASHE 1993).

Gyrophaena: *Gyrophaena* species prefer young fruiting bodies of Agaricales for oviposition. Mating in *G. joyioides* Wüsthoff takes place at the base of the cap of the mushroom and lasts about 20 minutes (ANDREESSEN 1984, HENNEBERG 2004). *Gyrophaena* species prefer young fruiting bodies of Agaricales for oviposition and deposit their eggs in the hymenium when sporulation begins (ANDREESSEN 1984, HENNEBERG 2004). The place for depositing the egg differs between *Gyrophaena* species (ANDREESSEN 1984, HENNEBERG 2004): comparing different Central European species, ANDREESSEN (1984) found that the distal part of the gill is preferred by *G. affinis* Sahlberg, the general surface of the gill by *G. minima* Erichson and the proximal basis of the gill by *G. joyioides*. *G. joyioides* produces clusters of three eggs (ANDREESSEN 1984) (Fig. 7a)

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or deposits the eggs individually (HENNEBERG 2004), whereas in *G. minima* and *G. affinis*, the eggs are oviposited individually (Fig. 7b). The eggs are covered with material of the periphery of the gills. Measuring 0.45 x 0.29 mm on average, the eggs of *G. joyioides* are relatively large in comparison with the length of the adults (ca. 2 mm). There are interspecific differences in the number of mature eggs in the ovaries of *Gyrophaena* species. Per ovary, up to 6 eggs have been found in *G. joyioides* (Fig. 7c) and about 3 eggs in *G. affinis* (ANDREESSEN 1984). WHITE (1977) has observed *Gyrophaena gentilis* Erichson depositing its eggs seperately between the gills of the agaricoid Basidiomycete *Tricholomopsis rutilans* (Schff. ex Fr.) Sing. *G. gentilis* is ovoviviparous, i.e. the first instar larva completely develops within the egg within the females' body (Fig. 7d). Ovoviviparity is very rare in Staphylinidae and has been documented only for *Gyrophaena gentilis* (ANDREESSEN 1984, HENNEBERG 2004) and the termitophilous aleocharine *Corotoca* Schiødte (SEEVERS 1957). Viviparity in *Gyrophaena gentilis* seems to be an adaptation to the rapid decay of fungi as hosts (ANDREESSEN 1984, HENNEBERG 2004).

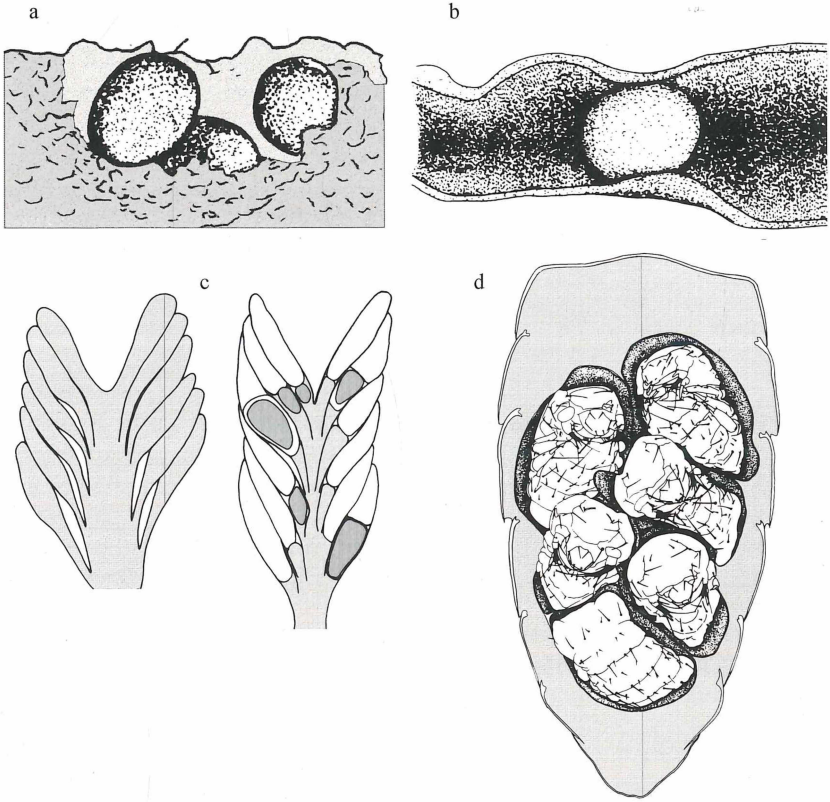

Fig.7: (a-b) Oviposited eggs of (a) *Gyrophaena joyioides* (cluster of 3 eggs) and (b) *G. affinis* (individually oviposited egg). (c) *G. joyoides*. Ovarioles of freshly hatched imago without visible oocytes (left) and of fully developed imago with visble oocytes (right); (d) Ovoviviparity in *G. gentilis*. Ventral aspect of position of embryos within the abdomen of the female (modified according to ANDREESSEN 1984).

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Adults of several *Gyrophaena* species are found in many species of fungi, whereas the larvae appear to have a more limited host spectrum. Oviposition takes place only in a few species of young fungi when sporulation begins. Differences among *Gyrophaena* species have been noted in terms of the spectrum of their preferred mushrooms and the time of colonization (ANDREESSEN 1984, HENNEBERG 2004).

The development of the ovarioles and the maturation of the eggs seem to be induced only after the female comes into contact with the mushroom (HENNEBERG 2004). The rapid development of the ovaries and the larvae is correlated with the short persistence time of sporulating tissue in many mushrooms such as the agaricoid Basidiomycetes. The larvae feed almost permanently during the day and night. At 25°C, the development of larvae of *G. joyioides* can be finished in just one to two days (ANDREESSEN 1984). In the laboratory at temperatures of 16°C, the developmental time of *Gyrophaena joyioides* lasts 9 days from the egg to the third instar larva (Egg: 1 day, LI larva: 1.5 days, LII larva: 1.5 days, LIII larva including prepupa: 5 days (HENNEBERG 2004)). Pupation in the soil lasts about two to three weeks (ANDREESSEN 1984).

Eumicrota beetles, which prefer persistent polyporous fungi, have a longer larval development than *Gyrophaena* beetles, preferring fleshy gilled ephemeral mushrooms (ASHE 1987).

Oxyteline group

Scaphidiinae: *Scaphisoma castaneum* Motschulsky was collected and reared from the polypore *Auriporia aurea* (Peck) Ryvarden within a log of *Pinus ponderosa* Douglas. The approximate duration of the developmental stages at 22-24 °C were: egg: 4-6 days, LI: 1-2 days, LII: 2-4 days, LIII: 4-6 days, prepupa: 1-2 days, and pupa: 9-12 days. The complete developmental time of *S. castaneum* ranged from 21-25 days (mean 22) (HANLEY 1996).

Staphylinine group

Oxyporinae: *Oxyporus*: Some minutes after eclosion of the egg, the larva starts feeding. Larvae first feed gregariously but, later on, feed separately on gill and cap tissue. Larval feeding normally proceeds continuously during the night and day. HANLEY & GOODRICH (1994) have observed *Oxyporus* larvae using their mandibles to place small pieces of sliced fungus between the gills of the host mushroom, presumably to camouflage themselves while feeding within the excavated burrows.

In *Oxyporus occipetales* Fauvel, both the first and second larval instars at 22°C last about one day, whereas the third instar takes about six days. The third instar larva burrows into the soil and forms a pupal chamber. The pupal stage is of six days duration (HANLEY & GOODRICH 1993). The developmental time of *Oxyporus major* Gravenhorst from egg or early larval instar to the adult stage is 13-15 days at 21-23°C (GOODRICH & HANLEY 1995). In *O. stygicus* Say, the developmental time from the egg to the adult is 16-18 days, with 7-10 days being spent as pupae (HANLEY & GOODRICH 1994). The rapid development of the larvae of *Oxyporus* correlates well with the ephemeral habit of their mushroom habitat and its rapid decomposition (HANLEY & GOODRICH 1994).

Subsocial behaviour and parental care

In at least two groups of staphylinids, i.e. Aleocharinae: *Eumicrota* and Oxyporinae: *Oxyporus*, fungicoly is connected with subsociality involving parental care.

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Tachyporine group

Eumicrota: ASHE (1986b, 1987) has studied the parental behaviour in *Eumicrota* species. The adult female constructs an egg chamber at the ventral side of the hymenium of a mushroom. For its construction, the female enlarges a natural cavity in the hymenium surface such as a pore. Chewed fungus material is used to isolate the egg chamber internally from any adjacent open spaces. Mating takes place beside the egg chamber. The female guards and cares for her eggs and remains within her egg chamber before and during egg hatching. Before oviposition, the female grooms an area of the chamber with her mandibles, deposits an egg on the cell wall, picks up the egg with her mandibles and finally places it in the area that she has recently cleaned. This observation is consistent with TOPP's (1975) suggestion that aleocharine staphylinid females take their eggs with their mandibles and distribute them within the substrate. Within an egg chamber, eggs are arranged in an irregular cluster on the side and bottom of the cell. The number of eggs per chamber varies from 5 to 24.

The female is constantly active within her egg chamber. These activities include (i) grooming of the eggs and the chamber (eggs that are not groomed have only low hatching success rates, because the egg chamber is invaded by fungi), (ii) self-grooming and (iii) repelling older larvae, males and other females that attempt to enter the egg chamber. The repelling of intruders in a densely populated colony can occupy a substantial amount of the time budget of the female, which usually repels intruders by a simple body block or by attacking persistent intruders with her mandibles. If the larvae have left the mushroom, the females sometimes continue to prepare the egg chamber for a second egg cluster, providing the mushroom is not already in the process of decay (ASHE 1986b, 1987).

Females show high fidelity to their indivual chamber and will often remain in their cell even after disturbance. If they are forced to leave their chamber, they will usually take refuge nearby and return to the correct cell a short time after the disturbance. Females remain at least 5-6 days in the egg chamber. Under normal circumstances, females leave their chambers for occasional feeding tours. These occur in the vicinity of the egg chamber (1 cm) and last up to one minute (ASHE 1986b, 1987).

Gyrophaena and *Phanerota* beetles are related to *Eumicrota* but they neither construct egg chambers nor show the females protection of eggs as seen in *Eumicrota.* According to ASHE (1986b) the subsocial behaviour of *Eumicrota* is not a primitive condition that has been lost in *Gyrophaena* and *Phaenerota.* Instead, it has to be considered uniquely derived in the genus *Eumicrota.*

The unusual behavioural traits exhibited in mushrooms by females of *Eumicrota* are remarkably similar to those of the oxyteline staphylinids *Platystethus arenarius* (Fourcroy) (HINTON 1944) and *Oxytelus laqueatus* (Marsham) (LIPKOW 1982) in which adults and larvae can be found in an egg chamber within fresh cow dung.

Staphylinine group

Oxyporus: In *Oxyporus* beetles, feeding, courtship, mating and ovipositon take place on mushrooms. SETSUDA (1994) has reported subsocial parental care in the Oxyporinae. Adult females of *O. japonicus* Sharp have been observed to construct egg chambers within the stipe or cap of a mushroom (Agaricales). The female piles up material of chewed fungus at the opening of the chamber after oviposition. It covers her eggs with bits of chewed fungus and the young larvae are assumed to feed on this material. Females remain within the egg chamber after oviposition and also repel conspeci-

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fic females and possibly predaceous insects. Males have also been found in such chambers during the breeding season (SETSUDA 1994).

Most fruiting bodies contain only one egg chamber. The eggs are deposited in young mushrooms of small size and weight (on average 5 g in *Oxyporus japonicus*) (SETSUDA 1994). Corresponding observations of subsocial behaviour in *Oxporus* species have been made by HANLEY & GOODRICH (1995).

Staphylinidae as vectors for spores of Basidiomycetes

BENICK, as early as 1952, assumed a mutualistic relationship between Basidiomycetes and Coleoptera, in that Coleoptera feed on Basidiomycetes and, at the same time, disperse the spores of their host. HENNEBERG (2004) has investigated this hypothesis by washing the body surfaces of the beetles and searching the obtained solution for spores. According to his study, the mycetobionts *Oxypoda alternans*, *Gyrophaena joyioides* and *G. gentilis* do not have the potential for spore dispersal of their host mushrooms *Megacollybia platyphylla* (Pers. ex Fr.) Kotl. & Pouz. and *Marasmius alliaceus* (Jacqu. ex Fr.) Fr.. However, in the staphylinids *Lathrimaeum atrocephalum* (Gyllenhal) and *Atheta* sp. with unspecific relationships to fungal fruiting bodies such as *Pholiota* Fayod and *Armillaria* Karst., HENNEBERG (2004) has found appreciable numbers of germinable spores within the gut and attached to the body surface.

Meshwork-like canopies constructed by larvae of *Scaphisoma*

A peculiar behaviour of the larvae of *Scaphisoma castaneum* Motschulsky (Staphylinidae: Scaphidiinae) has been described by HANLEY (1996). Second and third larval instars have been observed to construct longitudinal meshwork-like canopies from digested food excreted from the anus. Larvae construct these retreats (a) by first excreting an elongated faecal pellet near the entrance of burrowed cavities, then reorienting themselves and (b) finally positioning the faecal pellets into place by using their mandibles (Fig. 9). The retreats are fragile and ephemeral, often decaying in about two days. The fecal pellets are held together with a viscous fluid and do not appear to be arranged in any definite pattern. Each retreat is approximately 2 cm long and is occupied by a single larva. Within the retreats, the larvae feed on the surface of the fungus and repair any damaged areas of their retreat. The function of the retreats remains unclear. However, they probably serve as an adaptation to hide the larvae from potential predators/parasitoids and/or to provide suitable microhabitats, perhaps to prevent dessication (HANLEY 1996). Similar retreat building has been observed in scaphidiine beetle of the genera *Scaphidium* and *Toxidium* LeConte (LESCHEN 1994b).

Mycophagy limits predation of aphids by Staphylinidae

Spores (conidia) of powdery mildew (*Erysiphe* spp.) were offered, together with the grain aphid *Sitobion avenae* (Fabricius), in food-choice experiments to determine the way in which fungal food affects feeding on aphids by some *Tachyporus* species and *Philonthus cognatus* (Stephens) (DENNIS et al. 1991). Results showed a preference for mildew conidia by *T. hypnorum* Fabricius, no preference by *T. chrysomelinus* Linné and *Tachyporus* spp. larvae and a preference for aphids by *T. obtusus* Linné and *P. cognatus* (adults and larvae). Mycophagy limited aphid predation and explained the numerical response of these Staphylinidae to areas of cereals with high aphid densities.

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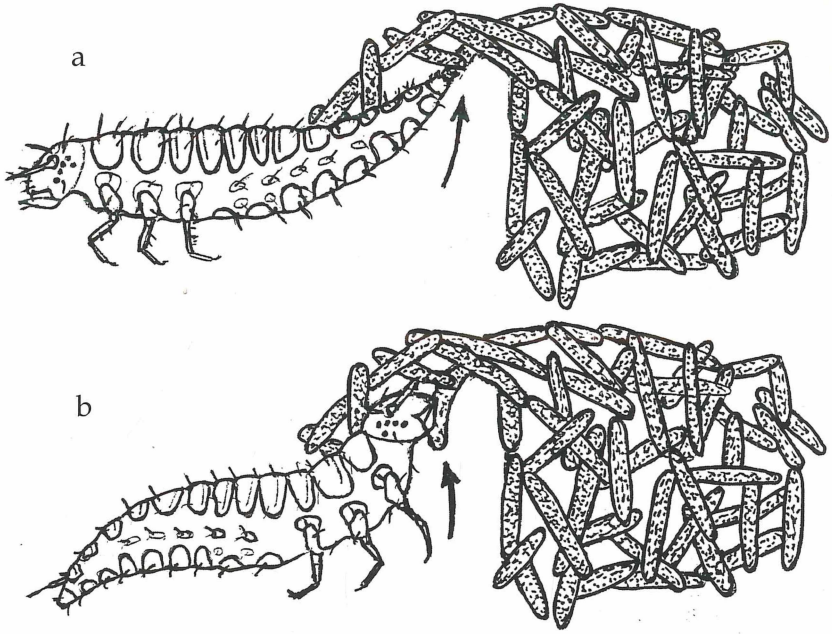

Fig. 9: Retreat construction behaviour of 2nd and 3rd larval instars of *Scaphisoma castaneum* Motschulsky. Modified from Hanley (1996). For further explanations see text.

Fungi as parasites in Staphylinidae

Ascomycete fungi of the order Laboulbeniales are obligate ectoparasites on the integument of their arthropod hosts such as Staphylinidae (ROSSI & SANTAMARIA 2000). Many Laboulbeniales are found in tropical forests (WEIR & HAMMOND 1997).

Zusammenfassung

Staphylinidae und Pilze

Assoziationen mit Pilzen haben bei der Evolution innerhalb der Staphyliniden eine bedeutende Rolle gespielt. So kommen in allen vier Unterfamilien-Gruppen Interaktionen mit Pilzen vor, sei es in Form direkter Mykophagie oder als Prädation von anderen pilzbewohnenden Organismen. In folgenden Unterfamilien treten mykophage/fungivore Arten auf: Micropeplinae, Neophoninae, Habrocerinae, Aleocharinae (z.B. *Gyrophaena* Mannerheim, *Phanerota* Casey, *Eumicrota* Casey, *Placusa* Erichson, *Homalota* Mannerheim, *Stictalia* Casey, *Pseudatheta* Cameron, *Pagla* Blackwelder, *Polylobus* Solier), Tachyporinae (*Sepedophilus* Gistel), Scaphidiinae (z.B. *Scaphisoma* Leach, *Cyparium* Erichson), Oxyporinae (*Oxyporus* Fabricius). In den folgenden Unterfamilien treten Arten mit zumindest fakultativer Mykophagie auf: Glypholomatinae, Omaliinae, Proteinae, Dasycerinae, Trichophyinae, Osoriinae. Das vorliegende Review fasst die Beziehung zwischen Käfern und Pilzen für verschiedene Unterfamilien der Staphylinidae zusammen und beleuchtet mögliche Anpassungen der Mundwerkzeuge an die Mykophagie (insbesondere Sporophagie). Ausgehend von einem mikro-

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phagen Grundplan haben die Mundwerkzeuge sporenfressender Staphyliniden in einigen Verwandtschaftsgruppen in konvergenter Weise besondere Abwandlungen erfahren, die sich als spezielle Anpassungen an diesen Ernährungstyp deuten lassen. Hierzu gehören bei den Maxillen besondere Rechen- und Bürstenstrukturen und bei den Mandibeln besondere Differenzierungen der molaren Mahlfläche. Verschiedene Staphyliniden innerhalb der Tachyporinen- und Oytelinengruppe mit primär reduzierten mandibulären Molae haben zudem sekundäre Mahlflächen (Pseudomolae) evolviert, was bei einigen Aleocharinen mit einer Umbildung des Labium-Hypopharynx einhergeht.

Andere in diesem Review behandelte Gesichtspunkte betreffen Art und Stärke der Bindung zwischen Staphyliniden und Pilzen sowie Besonderheiten von Larvalentwicklung, Brutpflege und Verhalten bei pilzbewohnenden Staphyliniden: junge Fruchtkörper von Basidiomyceten im Zustand der Sporulation werden von den mykophagen Staphyliniden *Gyrophaena, Eumicrota, Sepedophilus, Oxyporus* und den Prädatoren *Bolitobius* Mannerheim, *Aleochara* Gravenhorst bevorzugt. Ältere Fruchtkörper im Zustand der Fäulnis hingegen werden von Prädatoren wie *Tachinus* Gravenhorst, *Philonthus* Curtis, *Ontholestes* Ganglbauer, *Atheta* Thomson präferiert. In Anpassung an die fleischigen schnell vergänglichen Agaricales ist die Larvalentwicklung kurz. Bei 22-24°C kann sie drei (*Phanerota fasciata* (Say), *Gyrophaena joyioides* Wüsthoff) bis fünf Tage (*Oxyporus stygicus* Say) betragen (LI - LIII). Bei den festen und ausdauernden Polyporales dauert die Larvalentwicklung länger, z.B. 10 Tage bei *Scaphisoma castaneum* Motschulsky. Bei *Gyrophaena gentilis* Erichson tritt Ovoviviparie auf, was eine Anpassung an den schnell vergänglichen Fruchtkörper der Wirtspilze zu sein scheint. Bei den Gattungen *Eumicrota* und *Oxyporus* tritt Brutpflege auf.

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