

REVIEW ARTICLE

# External exoskeletal cavities in Coleoptera and their possible mycangial functions

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## Abstract

This paper reviews the occurrence of external exoskeletal cavities in beetles and provides critical reassessment of their possible mycangial function. In most reported cases, the decision to attribute mycangial function to exoskeletal cavities was based solely on the combination of two factors: (i) observation of these cavities on beetle's body; and (ii) knowledge that this particular beetle species uses fungi as a food source. Such reasoning resulted in the assumption, occasionally premature and not supported by other evidence, that exoskeletal pits in the following families may function as mycangia: Rhysodidae, Ptiliidae, Staphylinidae, Hybosoridae, Scarabaeidae, Derodontidae, Ptinidae, Jacobsoniidae, Boganiidae, Cryptophagidae, Endomychidae, Erotylidae, Latridiidae, Nitidulidae, Phloeostichidae, Silvanidae, Sphindidae, Pyrochroidae, Anthribidae, Attelabidae and Curculionidae. We conclude that only two beetle families include species with adequately documented cases of external exoskeletal mycangia: (i) Curculionidae (some Scolytinae and Platypodinae); and (ii) the structurally complex mycangia of Attelabidae (*Euops* females). One or more species of Sphindidae, Erotylidae, Silvanidae, and Latridiidae have likely functional mycangia. Exoskeletal pits with uncertain function are additionally reported from the following families: Cupedidae, Ommatidae, Lepiceridae, Carabidae, Histeridae, Hydraenidae, Leiodidae, Elmidae, Artematopodidae, Throscidae, Elateridae, Rhinorhipidae, Biphyllidae, Cerylonidae, Cyclaxyridae, Monotomidae, Mycetophagidae and Zopheridae. We also discuss the transport of fungal spores and conidia by waxy exudates or debris build up on beetle exoskeleton, as well as their passive attachment to the body.

**Key words:** Coleoptera, exoskeleton, fungal transmission, fungi, mycangia, mycetangia, morphology, spores.

## INTRODUCTION

Beetles (Coleoptera) are the largest order of living organisms characterized by a multitude of unparalleled natural histories. One of them is a remarkable dispersal alliance between fungi and beetles, wherein both organisms benefit from simultaneous colonization of new substrates. This strategy is often accompanied with pits or cavities on the beetle's body which are believed by many taxonomists to be used as a reservoir for fungi (spores or

conidia) to facilitate fungal dispersal. The diversity of these cavities and occurrence throughout Coleoptera, as well as their possible involvement in fungal dispersal, is the subject of this review.

The term "mycangium" (pl. "mycangia"; synonyms "mycetangium", "mycetangia") was proposed for insect exoskeletal cavities used as a storage place for fungal transport (Batra 1963; Francke-Grosmann 1963). Mycangia were originally discovered in, then repeatedly reported from, different species of bark and ambrosia weevils (Curculionidae: Scolytinae and Platypodinae; following the weevil classification of Kuschel *et al.* 2000). The mycangial function of these cavities in Scolytinae was demonstrated in a number of elaborate studies using Scolytinae as a model group (see Beaver 1989). These studies repeatedly suggest that if a deep exoskeletal cavity is discovered in a scolytine beetle, then it is likely to have a mycangial function.

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**Figure 1** Sap wood of White Fir *Abies concolor*, arrows showing beetle's galleries (likely those of *Scolytus ventralis* LeConte, 1868; Curculionidae: Scolytinae) and associated brown stain fungus; wood sample is deposited in the Scolytinae collection of the Field Museum of Natural History, Chicago. Figure reproduced with permission.

Intensive studies of mycangia in scolytine weevils have been particularly relevant to the forestry industry. Confirmed presence of a mycangium indicates dispersal-enhancing beetle/fungus co-adaptation, which, in turn, poses significant financial consequences. Economically important trees are killed by both beetles and fungi, and the quality of the timber is considerably degraded by penetration of beetle galleries and growing fungi (Fig. 1). Normally the food source is exhausted after one generation and adults therefore must disperse to new food sources resulting in more damage in trees and freshly logged timber (Beaver 1989).

Although publications on mycangia in bark and ambrosia beetles (Scolytinae) constitute the overwhelming majority of the literature available, isolated reports have claimed the presence of mycangia in other beetle families. Every case implicitly suggests the beetle's ability to transport fungi to a new host, which, in turn, might have economic consequences to humans. Most of these reports were scattered in the literature until Crowson (1981) attempted to summarize studies while introducing a number of new reports. No comprehensive treatment on mycangia in non-scolytine Coleoptera has been produced and new data on mycangia and mycangia-like structures in different beetle subgroups continues to be published.

Our interest in beetle mycangia outside of Scolytinae was raised by the discovery of peculiarly-shaped deep exoskeletal cavities on various body parts of some feather-wing beetles (Ptiliidae) by one of us (Grebennikov 2008, 2009). Given that the majority of these beetles are known to be exclusively mycophagous as

adults and larvae, and mycangia have already been reported in this family (Sörensson 1997), it seemed plausible to assume that these cavities might be mycangia. We experienced, however, significant difficulties in determining the true functional nature of these cavities in feather-wing beetles. Eventually it became evident that it is logically impossible to deduce their function in ptiliids. We concluded that assuming the function of a structure solely from its morphology resembling true mycangia of Scolytinae weevils could be deceptive and would lead to a false conclusion; thus, review of the literature is warranted.

The aims of this paper are: (i) to review reports on mycangia and mycangia-like structures throughout Coleoptera with particular emphasis on the taxa outside of the scolytine Curculionidae; and (ii) to critically evaluate these, trying to verify these structures as mycangia where possible.

We focus mainly on adults and in one case, Endomychidae larvae, which have setae that may function as mycangia. We do not review the mycangial pouches of adult female ovipositor in Lymexylidae, Ptinidae or Cerambycidae, and do not review studies of fungi contained in larval and adult midgut mycetomes in many different families of phytophagous and other beetles, other gut fungi (like Trichomycetes), and externally carried Laboulbeniales. Reviews of such cases of endo- and ectosymbiosis are provided by Buchner (1965), Weir and Hammond (1997), Lichtwardt *et al.* (1999) and elsewhere. Our overall goal is to promote a critical approach in attributing mycangial function to exoskeletal cavities.

## MATERIALS AND METHODS

The literature review is organized following the taxonomic structure of the order Coleoptera (Lawrence & Newton 1995; families of Cucujoidea follow Leschen *et al.* 2005). The superfamily Scarabaeoidea is the major exception being removed from its own series and included into the Staphyliniformia to reflect the growing evidence supporting such a placement (e.g. Caterino *et al.* 2005). Also the former family Scydmaenidae is treated as a subfamily of Staphylinidae (see Grebennikov & Newton 2009). The survey includes most families where exoskeletal mycangia were suspected to occur. In some cases, non-mycophagous groups were also mentioned (e.g. mainly predatory Histeridae and Elateridae) to illustrate the presence of similarly shaped exoskeletal pits not always linked to mycophagy. No entries were made for the families lacking exoskeletal cavities.

To gather other published records on mycangia and mycangia-like structures we relied heavily on our library-

ies, but checking the vast literature, especially strictly taxonomic papers that mention mycangia, fovea or related terms is an impossible task, so omissions are likely. We also performed an extensive literature search using the most recent reviews (Crowson 1981; Beaver 1989; Sörensson 1997) and online searches of Zoological Record (1864–2008) and “Google Scholar” using relevant keywords.

The initial assessment revealed that the records of mycangia and mycangia-like structures in the literature are reported for many distantly related beetle groups. The reports vary considerably in the authors’ degree of confidence in establishing the function of these cavities, as well as in the strength of supporting evidence. This necessitated a critical re-evaluation of this information based on the degree of confidence using the following criteria: (i) whether the particular beetle species is known to be associated with fungi in the adult or larval stage; (ii) whether fungal spores have been observed in, or in close proximity to, the cuticular pits; (iii) whether histological, scanning electron microscopy (SEM), or other fine morphological techniques were used to investigate the nature of the pits; (iv) whether other reports on mycangia are known for closely related groups of beetles; (v) whether direct biological observation supporting mycangial nature of the cavities was available; and (vi) when doubts were expressed by subsequent authors on the mycangial nature of these cavities. We also examined slide-mounted specimens contained in the RAB Leschen collection to confirm existing, or to report new, observations. Mycangial functions of exoskeletal cavities were critically reassessed and rated as “strongly supported” (if all criteria favored this conclusion), “likely” (one or two criteria were not met) and “inconclusive” when more than two criteria were not met.

While doing the literature search, we discovered records on mycangia-like exoskeletal cavities of unknown function. Owing to the overwhelming diversity of Coleoptera, it was deemed impossible to assemble all published records of such pit-shaped structures; however, an attempt to report at least some, preferably from the groups where no mycangia have ever been reported previously and/or when a cavity of unknown function was located on a body part known to support a mycangium in other beetles. We also queried specialists (see Acknowledgments) to check for additional records of mycangia.

We did not review mycangia-like structures, fovea or trichomes that exist in diversity in beetle inquilines associated with social insects, as these are likely to function in interspecies animal interactions and not in fungal spore transport, even in some lineages of mycophagous beetles that are associated with ants or termites (Kistner

1982). While we focus on external “visible openings”, passive fungal spore attachment to the cuticular surfaces of beetles may occur, as, for example, in Latridiidae (Blackwell *et al.* 1982). Spore attachment may also be facilitated by the presence of thick waxes and/or debris as in Priasilphidae (Fig. 28; see also Leschen & Michaux 2005; Leschen *et al.* 2005) that may confer protection (Lawrence & Hlavac 1979) and secondarily function in spore transfer. We discuss only one case of larval “mycangia”, that of Endomychidae.

## ORDER COLEOPTERA

### Suborder Archostemata

This suborder includes less than 50 extant species arranged in four or five families (Hörschemeyer 2005). No records on mycangia or mycangia-type cavities have been reported for Archostemata, although larvae of the majority of species are believed to be at least facultative mycophagous feeders on, and occurring in, old rotting wood (Hammond & Lawrence 1989; Lawrence 1989). All records on the exoskeletal cavities in Archostemata and accompanying SEM images reported below originate from unpublished material (T. Hörschemeyer, pers. comm., 2008).

#### *Cupedidae*

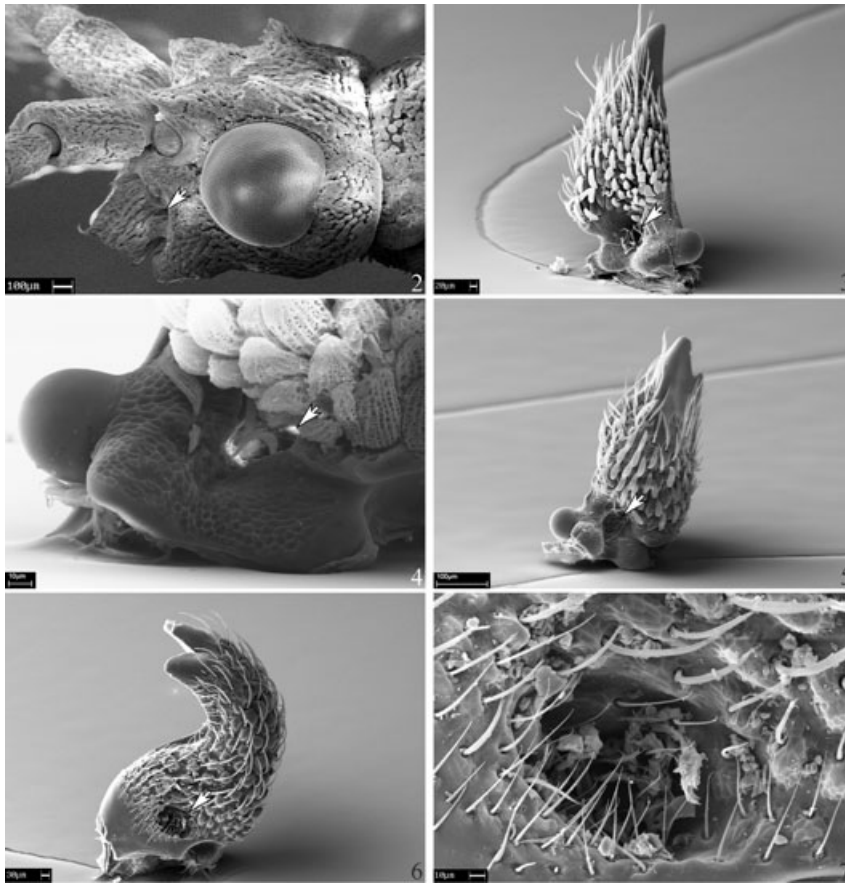
Adults of at least some members of this family have peculiar exoskeletal cavities opening on the lateral external surface of the mandibles between the dorsal acetabulum and ventral condyle. The species where such structures have been detected are *Distocupes varians* (Lea, 1902) (Figs 2,3); *Adinolepis youanga* (Neboiss, 1960) (Fig. 4); *Ascioplaga mimeta* Neboiss, 1984; *Cupes capitatus* Fabricius, 1801 (Fig. 5); and *Tenomerga moultoni* (Gestro, 1910). No fungal spores were detected in the cavities. Mycangial function of the mandibular exoskeletal cavities in Cupedidae is rated as inconclusive.

#### *Ommatidae*

*Omma stanleyi* Newman, 1839 has a wide opening on the dorsal surface of the mandible, mediad of the dorsal acetabulum (Figs 6,7). No fungal spores were detected in the cavity. This cavity appears structurally similar to those found in Cupedidae, although its location on mandibles is markedly different. No similar structure was found on the mandible of *Tetraphalerus bruchi* Heller, 1913. Mycangial function of the mandibular exoskeletal cavities in Ommatidae is rated as inconclusive.

### Suborder Myxophaga

This suborder comprises some 100 species in four families with both adults and larvae being aquatic (rarely



Figures 2–7 Exoskeletal cavities of Cupedidae and Ommatidae (Archostemata) indicated by arrows, scanning electron micrographs. 2,3 *Distocupes varians*, head, left laterodorsal (2) and right mandible, lateral (3); 4 *Adinolepis youanga*, base of left mandible, lateral; 5 *Cupes capitatus*, left mandible, lateral; 6,7 *Omma stanleyi*, right mandible, dorsal (6) and the same structure showing enlarged basal mandibular cavity (7). Figures 2–7 are courtesy and copyright of Thomas Hörnschemeyer, Göttingen, Germany; reproduced with permission.

riparian) and predominantly algae feeders; no reports on mycophagy are known for Myxophaga (Beutel 2005).

### *Lepiceridae*

The only two species of this family are almost certainly not mycophagous. Crowson (1981, p. 524) suggested that antennal cavities on the head capsule in *Lepicerus* Motschulsky, 1855 could be adapted for spore transport, while Anton and Beutel (2006) recently described these structures in detail. Mycangial function of this structure in Lepiceridae is rated as inconclusive.

### Suborder Adephaga

Adephagan beetles with some 34 000 species in 11 families (Beutel & Ribera 2005) account for some 10% of the overall beetle diversity. The great majority of the species are predators as adults and larvae, although mycophagy is suspected for two clades within this suborder: Rhysodidae and Carabidae: *Mormolyce* Hagenbach, 1825.

### *Rhysodidae*

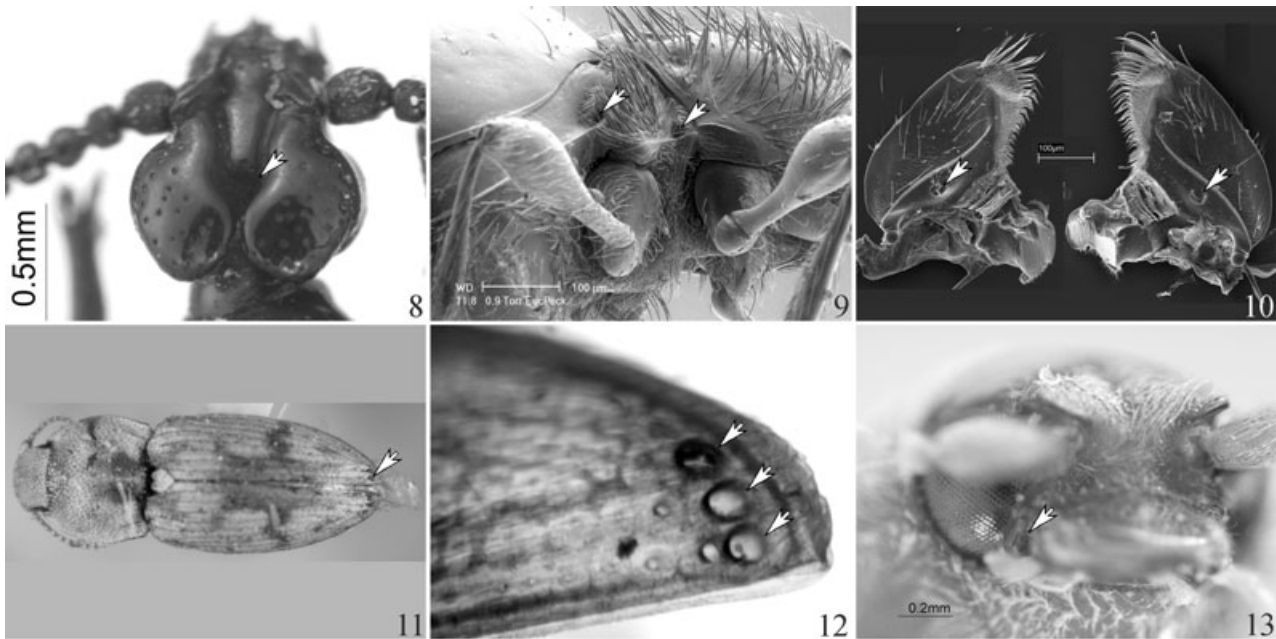
Larvae and adults of all Rhysodidae species inhabit rotten wood in association with Myxomycetes, while an

adult of *Omoglymmius hamatus* (LeConte, 1875) was observed feeding on a yellow plasmodium in a laboratory (Hlavac & Lawrence in Lawrence 1989). One of these authors (T.H.) saw a yellow slime mold plasmodium (a *Fuligo* probably) crawl up onto the elytra of an adult beetle and into the grooves on the elytra (J. Lawrence, pers. comm., 2008). This peculiar observation suggests that plasmodium can be carried to a new host by the beetle and become active again, without going through the process of sporulation (J. Lawrence, pers. comm., 2008). Crowson (1981, p. 522) also suggested that deep head grooves (Fig. 8) might be acting as mycangia; however, he did not elaborate on this hypothesis. Mycangial function of dorsal grooves in Rhysodidae is rated as inconclusive.

### *Carabidae*

No reports on mycangia have been published for Carabidae, although Bousquet (1996, fig. 145) illustrated peculiar cavities on the mesepisterna of the genus *Oodinus* Motschulsky, 1864. Since this taxon includes riparian and predatory species, it is almost certain that





Figures 8–13 Exoskeletal cavities of Coleoptera indicated by arrows, light microscopy (8–9, 11–13) and scanning electron micrographs (10). 8 *Omoglymmius hamatus* (LeConte, 1875), Rhysodidae, head, dorsal; 9 *Euconnus* sp., Staphylinidae: Scydmaeninae, pro- and mesothorax, right lateral; 10 *Oxymorostes riedeli* Ballerio, 2009, Hybosoridae: Ceratocanthinae, mandibles, dorsal; 11,12 *Agrypnella eburnean* Champion, 1895, Elateridae, habitus (11; body length: 3–4 mm) and apex of right elytron (12), dorsal; 13 *Blaiseus* sp. from Mexico, Chiapas, Elateridae, head, frontal. Figures reproduced with permission.

these cavities have no relation to fungi and their function, if any, remains unknown.

#### Suborder Polyphaga

This suborder comprises some 320 000 species (Beutel & Leschen 2005), or some 90% of the beetle extant diversity.

#### Series Staphyliniformia

### Superfamily Hydrophiloidea

#### Histeridae

Histerid beetles are mainly predators as larvae and adults, though some genera are mycophagous (Kovarik & Caterino 2005) and are known to possess markedly hardened exoskeletons with a diversity of grooves and pits. Myrmecophilous species of the subfamily Hetaerinae bear trichomes that are located on the mesoventrite and pronotum (Helava *et al.* 1985) and function in ant-beetle interactions. Peculiar mycangia-like exoskeletal cavities of unknown function are also known in some apparently non-myrmecophilous histerids. Species of *Plegaderus* Erichson, 1834 (Abareinae) have deep pits on the prosternum, while members of *Peploglyptus* LeConte, 1880 (Onthophilinae or Tribalinae) have cavities on both the pronotum and prosternum (M.

Caterino, pers. comm., 2008). Saproxylic species of the genus *Epiechinus* Lewis, 1891 (Onthophilinae) have rather large, setose cavities on the border between the meso- and metaventrite (A. Tishechkin, pers. comm., 2008). The variety of the exoskeletal cavities found in histerid beetles suggests that although they might be frequently found, they bear no single easily conceivable function.

### Superfamily Staphyloidea

#### Hydraenidae

Members of this family are aquatic and riparian, and are known to feed on algae. No reports on mycophagy or on mycangial cavities in Hydraenidae are known. It is worth mentioning that the remarkable degree of development of dorsal exoskeletal grooves and cavities is characteristic of the monotypic genus *Nucleotops* Perkins and Balfour-Browne, 1994 from South Africa. The depth and peculiar shape of these cavities in *Nucleotops* (see Perkins & Balfour-Browne 1994, fig. 2) resemble, and possibly even exceed, those exhibited by members of the family Rhysodidae (Fig. 8). This phenomenon might be seen as an example of the development of exoskeletal cavities with no apparent mycangial function.

### Ptiliidae

Ptiliidae are almost exclusively mycophagous (Hammond & Lawrence 1989). The only explicit reference to the occurrence of mycangia in adult Ptiliidae is that of Sörensson (1997) for mesocoxal cavities in the North European genus *Baranowskiella* Sörensson, 1997. This author reported these cavities having “a few sphaerules”, which were suspected to be fungal spores. There are at least two considerations, however, that make it difficult to accept that these mesocoxal cavities are indeed true mycangia. The first undermines the hypothesis of active fungal dispersal because, as outlined by Sörensson (1997), *Baranowskiella* wings are not adapted for flight. The second is the three- to five-fold size difference between the “sphaerules” observed in *Baranowskiella* mesocoxal cavities (about 1 µm diameter, as in Sörensson 1997, p. 265, fig. 18) and the reported spore size of its potential host fungus *Phellinus conchatus* (Persoon, 1796: Fries, 1821) Quélet, 1886 (5–6.5 µm × 4–4.5 µm; Ryvarde & Gilbertson 1994, p. 480; although the minimal measurement reported is as low as 3 µm; see references in Larsen & Cobb-Pouille 1990, p. 49). The inner diameter of mesocoxal cavities as depicted by Sörensson (1997, p. 265, fig. 18) is just about 7 µm, which can potentially permit a single spore inside, but not more than one in a row.

Sörensson (1997) further hypothesized that at least two other clades of the same ptiliid tribe Nanosellini might, in fact, possess previously unrecognized mycangia: those on the prothorax in the North American species *Hydnosella globitheca* Dybas, 1961 and those on the metaventrite of four *Nellosana* Johnson, 1982 species from New Zealand (Johnson 1982, p. 341, fig. 9). No further observations are available for these structures in both species.

Among non-nanoselline Ptiliidae, most members of the tribe Discheramocephalini possess two deep horizontally oriented cavities on both sides of the mesoventral keel (Fig. 15). In some cases the cavity bottoms almost reach each other inside, leaving only a thin diaphragm separating them (Fig. 19). Other genera of this tribe (*Fenestellidium* Grebennikov 2009) do not have this diaphragm and thus the mesoventral keel is completely penetrated (Grebennikov 2009, fig. 7G). Discheramocephalini species of the genera *Discheramocephalus* Johnson, 2007 and *Africoptilium* Johnson, 1967 possess additional deep cavities on the lateral portion of the mesoventrite (Figs 15, 19–21). At least some species of the genus *Skidmorella* Johnson, 1971 have a pair of peculiar pits between the eyes and on the scutellum (Grebennikov 2009). Moreover, all species of *Discheramocephalus* have between two and five pairs of pecu-

liar cavities on the eighth abdominal sternum (Figs 16, 22), and a deep and narrow transverse groove on the head posterior to eyes (Fig. 15, left arrow). Overall, members of *Discheramocephalus* are among the most peculiar beetles in terms of diversity of exoskeletal invaginations.

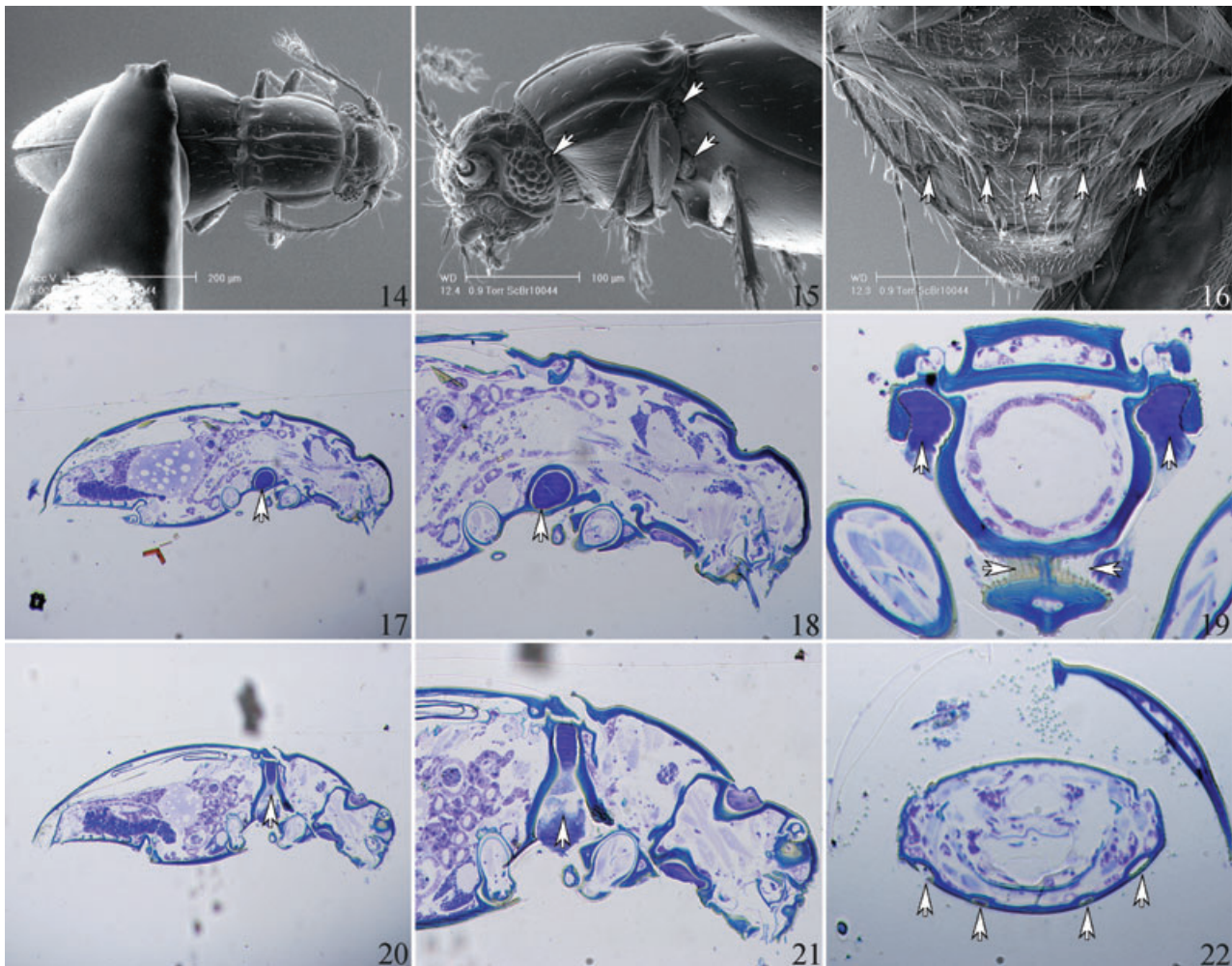
Detailed study of *Discheramocephalus* gave no indications to assume mycangial nature of these invaginations. No fungal spores were found in, or close to, exoskeletal cavities in Discheramocephalini based on examination using SEM (15 specimens, 12 species), euparal slide mounts (40 specimens, 15 species) or histological sectioning (2 specimens, 1 species). Structurally, with the exception of those on the abdomen of *Discheramocephalus*, these cavities resemble exoskeletal foveae of Staphylinidae: Pselaphinae (Chandler 2001), which are known not to have any relation to fungal transportation. It was also observed that at least one specimen of *Africoptilium* had fungal spores in its gut (Grebennikov 2009, fig. 11F), with a diameter roughly equal to or exceeding that of the exoskeletal pit on the mesoventrite. The latter observation does not support the role of these structures as mycangia. All these considerations led to an assumption that the mycangial nature of the discussed exoskeletal cavities in Ptiliidae, including those reported by Sörensson (1997), is inconclusive.

### Leiodidae

No reports on mycangia are known for Leiodidae, although the majority of the species are mycophagous (Hammond & Lawrence 1989). Newton (1998) reported deep setose cavities on the concealed part of the scutellum in Camiarinae Leiodidae, including *Eublackburniella* Jeannel, 1936, *Inocatops* Broun, 1893 and *Myrmicholeva* Lea, 1919, which also occur in undescribed forms as well as dorsoventrally paired cavities in *Afropelates* Jeannel, *Catopsolius* Sharp and other camiarines (A. Seago, pers. comm., 2008). The camiarine species *Baeosilpha rufescens* Broun, 1895 has peculiar epipleural foveae, similar to those found in Cyclaxyridae (see below). None of these cavities was observed containing spores and their function, if any, is unknown.

### Staphylinidae

Crowson and Ellis (1969) were the first to suspect the presence of the mycangia in the staphylinid subfamily Piestinae, which is partly mycophagous, at least in the larval stage. These authors reported characteristic mycangia-like cavities on the outer surface of the mandibles in species of three Piestine genera: *Siagonium* Kirby, 1815; *Prognathoides* Steel, 1950; and *Piestus* Gravenhorst, 1806. Later, Newton (1990) described a



**Figures 14–22** Exoskeletal cavities of *Discheramocephalus brucei* Grebennikov, 2008, Ptiliidae, indicated by arrows, scanning electron micrographs (14–16) and light microscopy of histological sections (17–22). 14 habitus, dorsal; 15 anterior part of body, left lateral; 16 abdomen, ventral; 17,18 longitudinal section close to midline, whole body (17) and anterior part of it (18); 19 cross-section through scutellum and mesothorax showing horizontal and vertical exoskeletal cavities; 20,21 longitudinal section about half-way between the midline and lateral edge of elytra, whole body (20) and anterior part of it (21); 22 cross-section through apical part of abdomen and cavities in sternum VIII. Scale bars: 200  $\mu\text{m}$  (14, 17, 20), 100  $\mu\text{m}$  (15, 18, 21), 50  $\mu\text{m}$  (16, 19, 22). Figures © Her Majesty the Queen in right of Canada; reproduced with permission.

new Australian monotypic genus from the subfamily Osoriinae and noted that the adults of this new genus, as well as some other Osoriinae, Oxytelinae and Piestinae possess rather characteristic mandibular cavities. He, however, did not indicate that they serve as mycangia. A peculiar subantennal cavity of unknown function is reported and illustrated for *Bledius bonariensis* Bernhauer, 1912 (see Herman 1986, fig 52), a species having no biological association with fungi.

A number of species of the tribe Scaphisomatini of the 100% mycophagous subfamily Scaphidiinae are known to possess a pair of setose cavities (also called “corbicula”) within the pronotal cavity occupying up to

75% of the pronotal volume (Leschen & Löbl 2005). Newton (1984) first reported the existence of these cavities, mentioning that they might be mycangia. No fungal spores were observed in these cavities and Leschen and Löbl (2005) doubted their mycangial function. These authors described the genus *Notonevtonia* Leschen and Löbl, 2003 and noticed the presence of weak hypomeral fovea on prothorax of unknown function.

Members of the subfamily Pselaphinae are well-known for their patterns of exoskeletal foveae on virtually any body part large enough to support such cavity (Chandler 2001). No pselaphines are known to be mycophagous, and such foveae have never been hypoth-



esized to play a role in fungal transport. These foveae resemble the ones found in the tribe Discheramocephalini (Ptiliidae) and in Scydmaeninae (see below), suggesting that similarly structured exoskeletal invaginations without any obvious function appear independently in various beetle groups.

Adults of the subfamily Scydmaeninae (treated previously as a separate family, Grebennikov & Newton 2009) prey predominantly on mites; no species are known to be mycophagous (O’Keefe 2005) and exoskeletal pits were not reported in the available literature. Such pits, however, seem to be rather common throughout this subfamily, as exemplified by those on the mesoventrite of an undescribed species of the North American *Euconnus* Thomson, 1859 (Fig. 9). Remarkable diversity of various exoskeletal modifications was also observed in the Asian species of the tribe Cephenniini, many of which remain undescribed (P. Jalszynski, pers. comm., 2008). Adults of one genus of Cephenniini, *Chelonoidum* Strand, 1935, have subcoxal pits on the metaventrite that is filled with waxy exudates, and contain no spores.

Overall, mycangial function of the discussed exoskeletal cavities in Staphylinidae is rated as inconclusive, and the general statement of mycangia presence in Staphylinidae by Bohac (1999, p. 361) appears groundless.

## Superfamily Scarabaeoidea Latreille, 1802

### *Hybosoridae*

Mandibular lobes of specimens belonging to two South America Anaidini genera, *Cryptogenius* Westwood, 1845 and *Callosides* Howden, 1971 have a peculiar cavity (Howden 2001, p. 201, fig. 4), which was called a “mycangium” and considered a synapomorphy for the clade consisting of these two genera (Ocampo 2006). Both are known from specimens taken from under the bark of dead standing trees normally infested with termites or from the forest leaf litter (Howden 2001). Ocampo (2006) reported observing fungal spores in gut contents of a species of *Cryptogenius*; however, no fungal spores have been reported from the mandibular cavities and their mycangial function is inconclusive.

The hybosorid subfamily Ceratocanthinae was reported to have mandibular mycangia-like cavities in all species (Nel & Scholtz 1990, p. 5). These cavities were called “mycangia” by Browne and Scholtz (1999) and optimized as a synapomorphy of the group. Although some depressions are present on the ventral mandibular surface in Ceratocanthinae adults (Fig. 10), there is no convincing evidence demonstrating that they are true mycangia (A. Ballerio, pers. comm., 2008). Fungal spores have not been observed in these cavities and their mycangial function is inconclusive.

### *Scarabaeidae*

Nel and Scholtz (1990) hypothesized a mycangial function of the mandibular cavities in the orphnine genus *Orphnus* MacLeay, 1891, the dynastine genus *Ancognatha* Erichson, 1847, and the ruteline genera *Anomala* Samouelle, 1819 and *Anoplognathus* Leach, 1819. Browne and Scholtz (1999) reported the presence of mandibular mycangia as a common character for the majority of the Scarabaeidae and optimized its occurrence as an autapomorphy of this clade. No further records of mycangia have been recorded for Scarabaeidae. None of these genera is known to be mycophagous and spores have never been observed in the mandibular cavities reported by Nel and Scholtz (1990). The status of the report on mycangia in Scarabaeidae is therefore rated as inconclusive.

Stebnicka (1999, p. 289, fig. 3) reported the presence of “pockets or cavities of possible mycangial function” on the mesoventrite in male specimens (females are unknown) of *Napoa peckorum* Stebnicka, 1999, an Ecuadorian aphodiine collected from termite nests. She further argues that “these structures are frequently found on the beetles that show much more pronounced burrowing adaptations” (Stebnicka 1999, p. 289). The number of these cavities is not stated, although the interpretation of figure 3 in (Stebnicka 1999) suggests that there is either one or three of them on each side of the mesoventrite. No fungal spores were observed in these cavities, and these beetles are not thought to be biologically associated with fungi. It is interesting to mention that this is second time where mycangia-like cavities are reported for the members of Scarabaeoidea presumably associated with termites (see Hybosoridae). The lack of supporting evidence suggests that the mycangial nature of the exoskeletal cavities reported on Aphodiinae *Napoa peckorum* Stebnicka, 1999 is inconclusive.

Remarkably deep exoskeletal cavities of unknown function have been observed on epipleura of both sexes in the scarabaeine genus *Cryptocanthon* Balthasar, 1942 (Howden 1973). Species of this genus are typical ball-making dung-beetles with no reported relation to fungal consumption or spore dissemination. It is reasonable to assume that these cavities in *Cryptocanthon* are not mycangia.

### *Series Elateriformia*

## Superfamily Dascilloidea

### *Elmidae*

Elmids are almost exclusively water dwellers and none are known to feed on fungi. Species of the genus *Dryo-*



*pomorphus* Hinton, 1936 possess peculiar cavities on the first visible abdominal sternum (Spangler 1985), which were previously mentioned by Crowson (1981, p. 524) as a possible adaptation for symbiotic relationships with algae.

## Superfamily Elateroidea

### *Artematopodidae*

Crowson (1973, p. 228) thought that deep pronotal pockets on the prosternum in *Artematopus* Petry, 1830, as well as sub-antennal pockets in his “Ctesibiinae” (now Artematopodinae), might serve as mycangia. Later, Crowson (1981, p. 523) and Lawrence (1995, fig. 3) noted a peculiar setose cavity in the fossil and extant species of the genus *Electribius* Crowson, 1973 located on the head beneath the antennae. Members of Artematopodidae are not recorded to feed on fungi and the mycangial function of these cavities is inconclusive.

### *Rhinorhipidae*

Lawrence (1987), when describing the type species and genus of this new Australian family, reported and illustrated a deep setose dorsal cavity at the base of the mandible, which is concealed beneath the clypeus when the mandibles are closed. These cuticular pits look remarkably similar to those found in some archostematan beetles (see above) and their function is unknown.

### *Throscidae*

Some members of the family Throscidae were thought to be mycophagous, although this biological association is not fully confirmed (Hammond & Lawrence 1989). Using SEM, Coffin (1993) observed and illustrated peculiar cavities on the head of members of the genus *Throscus* Latreille, 1796, which are rather similar in shape and location to those found on *Electribius* (Artematopodidae). This author did not suggest any function for these cavities; there are no credible reasons to assume that these cavities facilitate fungal transport.

### *Elateridae*

Like the elateroid families mentioned above, Elateridae also have some taxa possessing similarly shaped exoskeletal pits of unknown function on the head between the eyes and antennae. Hayek (1990, p. 42) noted the presence of these pits in the genus *Szombatya* Platia, 1986 and some species of *Melanotus* Erichson, 1829. A similar structure has been observed in adults of an undescribed species in the genus *Blaiseus* Fleutiaux, 1931 from Mexico (H. Douglas, pers. comm., 2008.; Fig. 13). Species of the genus *Agrypnella* Champion, 1895 possess peculiar cavities on the dorsal surface of the elytral apices (H. Douglas, pers. comm., 2008;

Figs 11,12). No credible evidence exists to link these cavities with fungal transport.

## *Series Bostrichiformia*

## Superfamily Derodontoidea

### *Derodontidae*

Crowson (1981, p. 522) reported two closely adjacent exoskeletal pockets at middle of second, third and fourth visible abdominal sterna on adults of mycophagous *Derodontus maculatus* Melsheimer, 1844, and assumed their mycangial function. This hypothesis, however, seems to be inconclusive because re-examination of these “cavities” showed that they are just shallow depressions between slightly elevated ridges (J. Lawrence, pers. comm., 2008). Moreover, Lawrence and Hlavac (1979) described surface features of Derodontidae adult beetles and concluded that most of these surface features (including deep exoskeletal pits on head and metaventrites) function in the storage, containment and distribution of secreted encrusted material to be mixed with detritus to form a defensive shield against macro- and micropredators.

### *Jacobsoniidae*

*Sarothrias eximius* Grouvelle, 1918 has a pit in the middle of the gula (Crowson 1981, p. 522, fig. 271), which was hypothesized by Crowson (1981) to be a possible mycangium. The feeding habits of this family are unknown and no detailed observations are available on the structure of this cavity. The assumption that this cavity is a true mycangium is inconclusive.

## Superfamily Bostrichoidea

### *Ptinidae* (=Anobiidae)

*Ptinus variegatus* Rossi, 1794 has a pit in the middle of the mentum, which Crowson (1981, p. 523, fig. 272) thought to be a mycangium. No detailed observation was made on the function of this cavity, and therefore Crowson’s (1981) hypothesis on their mycangial nature is inconclusive.

## *Series Cucujiformia*

## Superfamily Cleroidea

### *Acanthocnemidae*

Adults of the Australian species *Acanthocnemus nigricans* (Hope, 1845) have prothoracic exoskeletal cavities adjacent anteriorly to procoxae, which were demonstrated to serve as infrared receptor organs used in detection of forest fires (Schmitz *et al.* 2002). This beetle is hypothesized to be mycophagous in the larval stage, feeding on ascomycete fungi growing on wood or soil

immediately after fire (Wikars 2002). Besides Acanthocnemidae, infrared organs were found on the thorax and abdomen of some Buprestid species (Schmitz *et al.* 2000).

### Superfamily Cucujoidea

#### Boganiidae

When describing the pollen-feeding family Boganiidae (which at that time included all taxa currently attributed to the family Hobartiidae), Sen Gupta and Crowson (1966) reported that all its members have mandibular cavities opening dorsally or laterally with apparent mycangial function. These authors erroneously implied (although not clearly stated) that these beetles are mycophagous. No further observations are available on their function and their mycangial function is considered inconclusive.

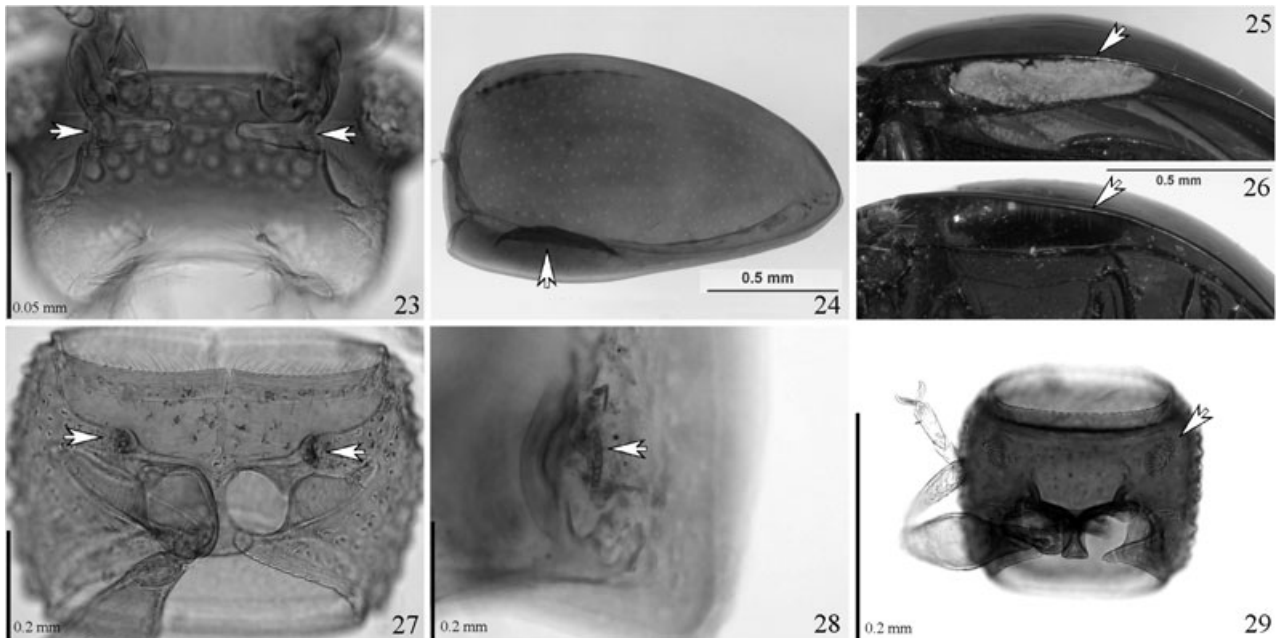
#### Sphindidae

Sen Gupta and Crowson (1966) and Crowson (1981, pp. 521, 546) reported that all species of the exclusively mycophagous family Sphindidae (see McHugh 1993; Lawrence & Newton 1980 on feeding habits) possess

dorsal cavities on the mandibles functioning as mycangia. McHugh (1990, fig. 21) illustrated slime mold spores in elytral punctures of *Carinisphindus isthmensis* McHugh 1990. In a later study he documented presence of slime mold spores in elytral punctures of *Eurysphindus hirtus* LeConte, 1878 (McHugh 1993, fig. 34) and *Genisphindus roxanneae* McHugh, 1993 (McHugh 1993, fig. 75) and concluded that these beetles are capable of spore transmission, although not necessarily in the exoskeletal cavities. He found such cavities located in different parts of beetles' body, including the dorso-proximal mandibular surface (McHugh 1993, fig. 11: *E. hirtus*) and lateral areas of mesoventrite (*Sphindiphorus natalensis* Sen Gupta et Crowson, 1977). Although McHugh (1993) was reluctant to corroborate mycangial nature of these cavities, we consider Sen Gupta and Crowson's (1966) hypothesis as likely.

#### Biphyllidae

Beetles of this family have deep setose pits on head below the eyes (Fig. 23); no spores have been observed in dissections, even though this family is associated with fungi in subcortical habitats (Lawrence 1991).



Figures 23–29 Exoskeletal cavities of Coleoptera indicated by arrows, light microscopy. 23 *Diplocoelus rudis* LeConte, 1863, Biphyllidae, head, ventral; 24–26 *Cyclaxyra politula* (Broun, 1881), Cyclaxyridae, disarticulated left elytron, ventral (24) and not disarticulated left elytron, ventro-lateral with (25) and without (26) whitish, waxy-appearing substance insoluble in water and alcohol; 27 *Corticaria* sp., Latridiidae, pronotum, ventral; 28 *Priasilpha obscura* Broun, 1893, Priasilphidae, posterior corner of prothorax, ventral; 29 *Nesolathrus* sp., Mycetophagidae, prothorax, ventral. Figures 23,24 Figures © Her Majesty the Queen in right of Canada; reproduced with permission.

### *Erotylidae*

Leschen (2003) documented the presence of ventral head cavities in many Erotylidae, although he did not observe spores. Van Zandt *et al.* (2003) reported two pairs of presumed mycangial pits on the ventral surface of the gena between the eyes and mandibles in adults of both sexes of a mycophagous erotylid beetle *Loberus impressus* (LeConte, 1863). These authors successfully documented germinated fungal spores growing from the pits. They further recorded colonies of both *Fusarium* sp. and *Cladosporium* sp. growing on inoculated agar plates. These authors noted that both genera of fungi found on *L. impressus* may be widely associated with other mycophagous beetles, and their conidia can be dispersed by air movement. This may suggest that the presence of the fungal spores in the cephalic pits of *L. impressus* might still be attributed to chance, strengthening Beaver's (1989) observation that *Fusarium* spp. spores were also found associated with other beetle species. Van Zandt *et al.*'s (2003) hypothesis of mycangial function of these cephalic pits is rated as likely.

### *Monotomidae*

Adult beetles of the New Zealand species *Lenax mirandus* Sharp, 1877 have large dorsal postocular lateral grooves that arise from deep asetose foveae on the head and central pits on the metaventrite and ventral process of abdominal segment 1, which are filled with debris and possibly spores. Like many other monotomids, *Lenax* is found under the bark of dead trees or fallen logs, but its exact diet is unknown. These data suggest that these pits are inconclusive as mycangia.

### *Cryptophagidae*

Hinton (1945) thought that the majority of Cryptophagidae associated with stored products feed principally on spores or hyphae of molds and are capable of internal or external transmission of spores. *Henoticus serratus* (Gyllenhal, 1808) has exoskeletal pits on each mesanepimeron and on each side of the metaventrite just behind and laterad of the mesocoxae, presumably acting as mycangia (Crowson 1981, p. 523, fig. 274). Leschen (1996) described and illustrated deep pits on prosternum, mesanepimeron and mesoventrite in various members of the family, although he neither observed spores in these cavities nor suggested that they function as mycangia. These data suggest that (Crowson's 1981) hypothesis is inconclusive.

### *Phloeostichidae*

Sen Gupta and Crowson (1966) implied a mycangial function of the mandibular cavities in the adults of the

Australian genus *Hymaea* Pascoe, 1869. The same authors noted the lack of such structures in the European *Phloeostichus* Redtenbacher, 1842, although they suggested that this function might be carried out by an emargination on the dorsal surface of the mandible. No further corroboration has been given to this hypothesis and the presence of mycangia is rated as inconclusive.

### *Silvanidae*

Crowson and Ellis (1969) reported mycangia on the mandibles of *Dendrophagus crenatus* (Paykull, 1799). These authors mentioned that mycangia-like cavities are regularly encountered in other Brontinae (=Hyliotinae), such as members of the genus *Cryptamorphia* Wollaston, 1854. These authors further reported "apparent spores" in these cavities, which once placed on agar produced the fungus *Ceratocystis radicola* (Bliss) Moreau, also known to be transmitted by bark beetles (Curculionidae: Scolytine). Crowson and Ellis (1969) further reported that some 20 larvae of this beetle were reared to adult stage on this fungus. The function of mandibular cavities as mycangia were supported by Thomas (1984, p. 49) and therefore this hypothesis is rated as likely.

### *Cyclaxyridae*

Adults of *Cyclaxyra* Broun, 1893 have widely open epipleural fovea (Figs 24–26) rather similar to those found in the leiodid genus *Baeosilpha rufescens*. These foveae are slightly deeper than their maximum width and they are lined with stiff, erect setae and frequently filled with a whitish, waxy-appearing substance insoluble in water and alcohol. Spores have never been found in association with the foveae, although these beetles feed on sooty-mold fungi (Ascomycota: Capnodiales) (Gimmel *et al.* 2009).

### *Nitidulidae*

Audisio and Jelínek (1993) were the first authors to report the presence of exoskeletal cavities on the ventral body surface of adult Nitidulidae as a characteristic feature of the "Axyroid-Group" of genera. They interpreted these structures as mycangia, although the only supporting evidence was the shape and location of these cavities, and that they both resemble mycangia-like cavities found in other cucujoid beetles. Kirejtshuk and Leschen (1998) mentioned "ovate or round" punctures on the abdominal ventrites in *Pocadionta dentipes* (Grouvelle, 1898) containing waxes and spores that were similar-looking to those structures in the Axyroid-Group. Kirejtshuk (2003) listed species transmitting fungal spores through the alimentary canal or on the body surface, suggesting that these beetles might be



important agents of weakening trees through fungal infection. He further referred to depressions on the mesoventrite in *Carpophilus* sp. (Kirejtshuk 2003, p. 5, fig. 6), possibly serving as mycangia. Other Nitidulidae beetles have pits, such as those on the mandibles of the predominantly phytophagous Meligethinae (Crowson 1995), and in *Meligethes* Stephens, 1830, which also have pits on the mesanepimera. In these meligethines we have not observed fungal spores or pollen. Therefore, hypotheses on presence of mycangia in Nitidulidae are considered as inconclusive.

### *Cerylonidae*

Ślipiński's (1990) review of Cerylonidae has references to, and illustrations of, deep exoskeletal cavities on pronotum of such genera as *Axiocerylon* Grouvelle, 1918, *Suakokoia* Sen Gupta et Crowson, 1973 and *Thyrododerus* Sharp, 1885. Although mycophagy appears to be the most plausible biology for the majority of Cerylonidae (Ślipiński (1990)), no published references suggest that these cavities might serve as mycangia.

### *Endomychidae*

Endomychidae are mostly mycophagous and many adults have fovea located on their bodies, in particular on the metaventrite (Tomaszewska 2000, 2005), but we have observed no spores contained in them.

Johnson (1986) reports a remarkable case of late-instar larva of *Xenomycetes laversi* Hatch, 1962 from Pacific North America possessing "mycangial setae". This is the second case in Coleoptera where the larval stage is assumed to be directly involved in the active transport of fungal spores. The first was reported by Pakaluk (1984) who suggested that larvae of *Lycoperdina* Latreille, 1807 which feed on Gasteromycetes may also be capable of spore dispersal. The spore-capturing structures of *X. laversi* are basket-shaped (=frayed) mycangial setae (Johnson 1986, p. 668: figs 1–3) that resemble (and are possibly homologous to) similar-looking setae of Coccinellidae and Corylophidae larvae. Figures 1 and 2 in Johnson's (1986) paper clearly show one of these abdominal setae holding spores of *Tapinella atrotomentosa* (Batsch) Šutara (= *Paxillus atrotomentosus*), "apparently the sole fungal host for both adults and larvae" of this species (Johnson 1986, p. 666). Johnson (1986) also reports (pp. 666, 668) that larvae of *Aphorista laeta* LeConte, 1852 "possesses basket-like mycangial setae very similar to those found on *Xenomycetes*" and further suggests (p. 169) that "similar setal formation may occur in *Aphorista vittata*, *Mycetaea birta*, *Endomychus coccineus*, and *E. biguttatus*". These beetles, however, feed on a variety of fungal types, which might also include plasmodia of Myxomycetes (J.

Lawrence, pers. comm., 2008), thus casting doubt on the assumption that the peculiarly shaped frayed setae of *X. laversi* larvae have specifically evolved to capture spores of their particular host fungus. Moreover, the presence of mycangia is expected to be found in a dispersal phase of a beetle's life cycle, while larvae of *X. laversi* can hardly be assumed to move out of the immediate vicinity of their food source (J. Lawrence, pers. comm., 2008). It is likely that the frayed or modified setae in Endomychidae are used primarily as a structural defense against predators, especially Hymenoptera, because most larvae of these groups feed on the surface of fungi and may be more susceptible to predation (e.g. Leschen & Allen 1987). These data suggest that the presence of mycangia in adults and larvae of Endomychidae is inconclusive.

### *Latridiidae*

Many species of *Corticaria* Marsham, 1802 have foveae on the prosternum that are anterior to the procoxae. Kullingsjö (1999) reported spores of eight fungal species isolated from specimens of *Corticaria rubripes* Mannerheim, 1844 and our observations corroborate this (Fig. 27). Other latridiid genera (e.g. *Enicmus* Thomson, 1859; *Cartodere* Thomson, 1859; many others) have differently located exoskeletal pits with waxy exudates, although these pits have never been reported to contain spores. Crowson (1981, p. 521, fig. 269) suggested that cavities of *Cartodere nodifer* (Westwood, 1839) on the mesoventrite and the first visible abdominal sternum might serve as mycangia. While the observations of Crowson (1981) require verification, we consider the mycangial function of the exoskeletal cavities in Latridiidae as likely.

## Superfamily Tenebrionoidea

There are many species in Tenebrionoidea that have foveae or mycangia-like structures, and also have waxy secretions that may serve a secondary function of spore dispersal (e.g. Zopheridae, Ślipiński & Lawrence 1999; Ulodidae, Leschen & Rhode 2002; bolitophagine Tenebrionidae, Matthews & Bouchard 2008, p. 131). We only list a few examples below due to the paucity of relevant information contained in the literature and the limits of our knowledge on these groups.

### *Mycetophagidae*

Mycetophagidae is a moderate-sized family composed of species that are mainly fungus feeding, but also contain species that feed on fern spores or on plant pollen. *Nesolathrus* Scott has lateral setose pockets on the prothorax (Fig. 29) which do not contain spores. Adults and larvae of *Nesolathrus* have been collected in

leaf litter and in association with the fronds of palms and other monocots, such as *Pandanus* (Pandanaeae; see Scott 1922).

### *Pyrochroidae*

Crowson (1981, p. 523) attributed a possible mycangial function to the lateral cavities on the visible abdominal ventrites 2–5 of adult *Cononotus sericans* LeConte, 1851. Natural history information is lacking for this genus, but larvae of *Cononotus bryanti* Van Dyke, 1939 have been taken from beneath dried cow dung while the adults appear to be adapted to dry habitats where they occur under rocks and in decaying vegetation (Doyen 1979). This is the only available published record on potential mycangia in Tenebrionoidea and the presence of mycangia in *Cononotus* is inconclusive.

## Superfamily Curculionoidea

### *Anthribidae*

Kuschel (1995, p. 33) indicated presence of a “mandibular mycetangial pocket” in the anthribid subfamilies Anthribinae and Choraginae, and optimized this character state as a synapomorphy for both subfamilies in his phylogenetic analysis of Curculionidae. Although many anthribid species with known biology are mycophagous, this report has apparently never been corroborated further; the presence of mycangia in Anthribidae is therefore rated as inconclusive.

### *Attelabidae*

Many attelabid species are remarkable for their sophisticated parental care, including preparing a leaf cradle for their progeny. Relatively recently, Sakurai (1985) and Sawada and Morimoto (1986) discovered that apparently all species of the genus *Euops* Schoenherr, 1839 developed symbiotic relationships with the fungi, which cover cradle leaves and are, presumably, beneficial to the larvae. Female mycangia in *E. splendidus* Voss, 1924 are formed by two deep cavities on the ventral surface of the body between the metathorax and abdomen, which are further covered by the metacoxae. Each mycangium in *Euops* consists of three separate chambers, each of which is believed to have a unique function in spore germination (Sakurai 1985): spore reservoir, spore incubator and spore bed. Such complex mycangia is unparalleled in Coleoptera (A. Riedel, pers. comm., 2008) and their function in fungal transport is strongly supported.

The nature of the association between *Euops* and its symbiotic mycangia fungi remains mysterious. In contrast to the predominant majority of similar phenomena, symbiotic fungi seem not to contribute to the process of decomposing plant tissue for beetle consumption (Koba-

yashi *et al.* 2007). These authors isolated two species of *Penicillium* Link, 1809 from the beetle mycangia and assumed that the fungi might be used in non-nutritive role; such is suppressing pathogenic bacteria or other fungi.

### *Curculionidae*

Weevil subfamilies Scolytinae and Platypodinae form presumably a clade (Kuschel *et al.* 2000) and include two large species groups with different biological scenarios of beetle–fungus mutualism. The first group, the so-called ambrosia beetles, includes all Platypodinae and some Scolytinae, known to feed on fungal gardens cultivated by the adults in deep burrows inside a tree’s xylem. The second group is bark beetles and includes most Scolytinae, which would normally attack trees by introducing a pathogenic fungal agent to kill the host and feed on the phloem of the dying tree. The majority of all reports on mycangia are restricted to species of these two subfamilies and the very concept of mycangia in Coleoptera originally evolved as a result of the study of Scolytinae and Platypodinae (Batra 1963; Francke-Grosmann 1963; many new studies are published annually and we will not attempt to reference them all here). Beaver (1989) recently summarized available data on the presence of mycangia in these two subfamilies. Other recent studies include that of Morales-Ramos *et al.* (2000), reporting an ergosterol-deficient ambrosia Scolytine beetle *Hypothenemus hampei* (Ferrari, 1867) using asperites and pronotal setae to carry *Fusarium solani* (Martius) spores to coffee beans. Beaver and Gebhardt (2006) revised the Scolytine genus *Scolytotrupis* Schaufuss, 1891, and provided detailed SEM and histological photographs of the pronotal mycangium for *S. blandfordi* Gebhardt, 2006. Farrell *et al.* (2001) performed a DNA-based phylogenetic analysis of Platypodinae and Scolytinae focusing on the origin of fungal gardening and concluded that this biology has evolved in weevils independently at least seven times (while in leaf-cutting ants, for example, fungal gardening has, apparently, evolved only once, according to Farrell *et al.* 2001).

All members of the weevil subfamily Raymondionyminae are small, blind and wingless depigmented dwellers of deep soil feeding on roots. Gilbert and Howden (1987, p. 148) questioned whether the metaventral cavity and ventral pits on the rostrum of their new species *Neoubychia mexicana* might serve as mycangia. It seems highly inconclusive that these features are mycangia, mainly due to the fact that these subterranean beetles are expected to have highly restricted dispersal capacity.

## RESULTS AND DISCUSSION

The critical reassessment of published reports on the presence of external exoskeletal mycangia in beetles indicates that this phenomenon is, apparently, less demonstrably widespread than assumed. It seems plausible to think that in most cases the authors' tendency to attribute mycangial function to exoskeletal cavities was based solely on the combination of two factors: (i) seeing cavities on beetle's body; and (ii) knowing that a particular species is mycophagous. Such reasoning resulted in assumptions of mycangial function of exoskeletal pits in Rhyssodidae, Ptiliidae, Staphylinidae, Hybosoridae, Scarabaeidae, Derodontidae, Ptinidae, Jacobsoniidae, Boganiidae (pollen-feeders apparently mistaken by Sen Gupta & Crowson 1966 as mycophagous), Cryptophagidae, Endomychidae, Erotylidae, Latridiidae, Nitidulidae, Phloeostichidae, Silvanidae, Sphindidae, Pyrochroidae, Anthribidae and Curculionidae. In most cases no further evidence was provided to corroborate these hypotheses, such as the presence of fungal spores in these cavities, their successful germination on artificial substrate or histological sections demonstrating glands normally associated with true mycangia, as found in Curculionidae (Scolytinae, Platypodinae). The only exceptions to this rule were the families Sphindidae, Erotylidae, Silvanidae and Latridiidae where additional supporting evidence was obtained. The Sphindidae review by McHugh (1993) provided strong evidence that at least some species, most notably *Eurysphindus hirtus* and *Genisphindus roxaneae*, do have functional mycangia, although the author was reluctant to make a firm statement to this effect. One species of Erotylidae (*Loberus impressus*) was documented to possess viable fungal spores in exoskeletal cavities, which produced colonies of *Fusarium* sp. and *Cladosporium* sp. on an artificial substrate (Van Zandt *et al.* 2003). These authors, however, were reluctant to make a firm statement on the mycangial nature of these cavities, mainly because an accidental occurrence of these easy-to-transport fungal spores in the pits of the beetle's exoskeleton was not excluded. Such caution indicates the difficulty and uncertainty faced by investigators when attempting to attribute function to a morphological structure. In Silvanidae, Crowson and Ellis (1969) similarly observed "apparent spores" in the cavities of *Dendrophagus crenatus* and succeeded in obtaining colonies of *Ceratocystis radicola*, which, however, does not offer as much convincing proof compared to that offered by Van Zandt *et al.* (2003) for Erotylidae. In Latridiidae, Kullingsjö's (1999) detailed results on ventral prothoracic pits containing fungal spores, further corroborated by our observations,

suggest the mycangial nature of these cavities. These considerations, however, do not convincingly demonstrate that true mycangia do indeed exist in any of these families, while in at least Ptiliidae our new histological data tend to reject, rather than corroborate, the mycangial hypothesis. Further testing of these assumptions might be a fruitful subject for future investigations, some of which will likely confirm the presence of mycangia in at least some of these beetle families.

Besides Curculionidae (Scolytinae, Platypodinae), only one beetle family has species with thoroughly documented cases of exoskeletal mycangial cavities firmly involved in fungal storage and likely dispersal: females of the genus *Euops* (Attelabidae) with structurally sophisticated mycangia between the metathorax and abdomen (Sakurai 1985). In all other previously reported cases of mycangia supportive documentation did not allow rating these instances as strongly supported. It is interesting to note that these strongly supported cases for mycangia are in groups of strictly phytophagous adult beetles, while the fungi are fed upon by the larvae. All other cases of mycangia-like structures in beetle lineages with mycophagous adults are rated as either inconclusive or likely and require further study.

Meanwhile, the true function of the mycangia-like structures or "pseudomycangia" is not clearly understood. These exoskeletal cavities and invaginations may function as body-strengthening devices in litter or subcortical species (e.g. Pselaphinae), as reservoirs for secretions (e.g. Cyclaxyridae) or for thermal sensing (e.g. Acanthocnemidae). Such "pseudomycangia" occur in Cupedidae, Ommatidae, Lepiceridae, Carabidae, Histeridae, Hydraenidae, Leiodidae, Elmidae, Armatopodidae, Throscidae, Elateridae, Rhinorhipidae, Acanthocnemidae, Biphylidae, Cerylonidae, Cyclaxyridae, Monotomidae and Mycetophagidae. In some taxa, like the rove-beetle subfamily Pselaphinae, or the feather-wing beetle genus *Discheramocephalus* (Figs 14–22), these pits are particularly numerous and diverse. It seems highly unlikely in the last examples that these pits are involved in fungal transport; yet often no credible explanation has been proposed to account for morphological complexity and overall diversity of these cavities often found on the exoskeleton.

Analogous exoskeletal pits among unrelated beetle lineages are often referred to as mycangia, but confirmation of their function in spore transport requires meeting several criteria based on histological, field or laboratory observations. Authors observing cavities in beetles should refrain from calling these structures "mycangia" without undertaking a detailed investigation of their function. The assumption that these structures are predominantly present in mycophagous



lineages is untrue, as we demonstrate that these occur mainly in taxa with phytophagous adults.

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