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Review of the Natural History of the Handsome Fungus Beetles (Coleoptera: Cucujoidea: Endomychidae)

F. W. Shockley

University of Georgia, Athens, GA

K. W. Tomaszewska

Polish Academy of Sciences, Wilcza 64, 00-679 Warsaw, Poland

J. V. McHugh

University of Georgia, Athens, GA

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Review of the Natural History of the Handsome Fungus Beetles (Coleoptera: Cucujoidea: Endomychidae)

F. W. Shockley

Department of Entomology
413 Biological Sciences Building
University of Georgia
Athens, GA 30602-2603 USA

K. W. Tomaszewska

Museum and Institute of Zoology
Polish Academy of Sciences
Wilcza 64, 00-679 Warsaw, Poland

J. V. McHugh

Department of Entomology
413 Biological Sciences Building
University of Georgia,
Athens, GA 30602-2603 USA

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F. W. Shockley

Department of Entomology
413 Biological Sciences Building
University of Georgia
Athens, GA 30602-2603, USA
E-mail: fws@uga.edu.

K. W. Tomaszewska

Museum and Institute of Zoology
Polish Academy of Sciences
Wilcza 64, 00-679 Warsaw, Poland
E-mail: wiolkat@miiz.waw.pl.

J. V. McHugh

Department of Entomology
413 Biological Sciences Building
University of Georgia
Athens, GA 30602-2603, USA
E-mail: mchugh.jv@gmail.com.

Abstract. The literature pertaining to natural history of Endomychidae (Coleoptera: Cucujoidea) is reviewed. One hundred fungal host records are provided for 32 endomychid species. Twenty-three records of endomychid yeast endosymbionts are compiled. Summaries are also presented for feeding preferences, interactions with natural enemies, non-lethal symbiotic relationships, and pest activity within the family. Unusual endomychid behaviors and habitats are reviewed, with particular attention to gregariousness and defensive strategies within Endomychidae.

Key Words: beetles, ecology, behavior, inquilinism, mimicry, symbiosis, mycophagy.

Introduction

The beetle family Endomychidae is classified within the Cerylonid Series of the superfamily Cucujoidea (Crowson 1955). The family currently includes approximately 130 genera and 1782 species and subspecies arranged among 12 subfamilies (Shockley et al. 2009). Endomychidae is represented in all major biogeographical regions, but species diversity is greatest in the tropical regions of Africa, Asia and the Americas. Most species are mycophagous, feeding on hyphae, spores and spore-bearing tissue and the supporting tissues of fungal fruitings; however, other feeding strategies and food sources are used by endomychids as well (e.g., phytophagy, predation, necrophagy and myxomycophagy).

While most endomychid publications are composed of isolated taxonomic descriptions, the limited published natural history information reveals a wide array of interesting behaviors and ecological relationships for this family. Although endomychids make up a significant part of the mycophagous entomofauna in many places and can become pests to humans under certain environmental conditions, relatively little is known about their natural history.

Little effort has been made to consolidate information about the natural history of this group into a single treatment. To complicate matters, notes about natural history and behavior are scattered widely throughout 172 years of scientific literature, making them difficult to compile and synthesize. This work represents the first attempt to review the known ecological interactions of Endomychidae and summarizes other interesting aspects of endomychid natural history.

Methods

The data presented in this review are largely the result of an extensive search of the literature. Some additional data are based on original observations made by the authors. More than 600 taxonomic treatments and 190 general ecological references were gleaned for biological data pertaining to Endomychidae. Two major databases, MYCOL database (Q. Wheeler *in litt.*) and BeetleBellyYeast project database (M. Blackwell *in litt.*; database presently accessible at the following URL: <http://lsb380.plbio.lsu.edu/beetlebellyfolder/beetlebelly.yeasts>), provided additional data for fungal host records and endosymbiotic yeast associations, respectively. Historical references to endomychid taxa have been updated with currently valid names. The names of most non-endomychid taxa have been updated by consulting a variety of references, but some are listed exactly as they occur in the source publications.

Records perceived to be uninformative, ambiguous, doubtful or incidental were ignored. For example, many older records list hosts as simply “fungus” or “bracket fungus” with inadequate information to allow accurate identification at even the highest taxonomic levels. An attempt was made to list only original published records. Subsequent iterations of these records were ignored. Host associations gleaned from the literature and from specimen label data must be viewed with some skepticism since many fungal host identifications were made by entomologists without confirmation by mycologists. This is a serious concern for the present study because many endomychid species feed on fungi that are very difficult or impossible to identify in the field.

Results

Feeding Strategies

Mycophagy. Some estimates suggest as many as 25 beetle families are primarily mycophagous and fully half of the known families may be indirectly mycophagous, (i.e., feeding on vegetative material that has been in some way altered by fungal enzymes) (Lawrence 1989). To date, few efforts have been made to consolidate the published fungal host records for Endomychidae. Even in comprehensive lists of beetle/fungus associations such as Benick (1952) and Leschen (1988), Endomychidae usually make up only a small fraction of the records, a reflection of the rarity of reliable records in the literature. Although the dangers of compiling a “complete” fungal host list have been discussed above, a single source list can be useful to researchers and naturalists (Table 1). Such resources encourage more diligent documentation of hosts and promote collaborations between entomologists and mycologists to make new host records more reliable.

Mycophagy generally refers to feeding on the softer hyphae and fruiting bodies of fungi. Most endomychids feed primarily on macro-Basidiomycetes (Hymenomycetes and Aphyllophorales). Within Endomychidae numerous species exhibit a special form of mycophagy known as sporophagy. In the case of sporophagy, the beetles have shifted from feeding on the hyphae of their fungal hosts to feeding on the spores. This condition may be facultative in taxa that feed on the mature fruiting bodies of basidiomycetes, but it may be obligate in some taxa. Obligate sporophagy has been hypothesized for all species of the subfamily Anamorphinae, at least in the larval stages (Pakaluk 1986, Leschen and Carlton 1993, Tomaszewska 2000), and sporophagy is the most common feeding strategy among taxa that feed on zygomycete molds.

Another specialized form of mycophagy known as lichenophagy has also been recorded within Endomychidae. Lichenophagy is defined as feeding on lichens during at least part of the life cycle. Lichens are the product of the symbiotic relationship between a fungus (the mycobiont) and a photosynthetic alga or cyanobacterium (the photobiont). Strohecker (1953) reported larvae of *Trycherus* Gerstaecker feeding on lichens. The feeding habits of adult *Trycherus* have not yet been recorded in the literature, but they are presumed to be truly mycophagous, as defined above, so it is unclear if this was a rare occurrence or typical for *Trycherus* larvae.

Species of Eupsilobiinae and Merophysinae, several of which are social insect inquilines, are known to feed on a combination of spores and hyphae of microfungi (Skelley and Leschen 2002). Specifically what these endomychids eat under the conditions within the nests of their social insect hosts is unclear, so the nature of these relationships remains unknown. Endomychids may be feeding directly on the fungal

gardens cultivated by their hosts (as nest parasites). Alternatively, they may be living mutualistically with their hosts and feeding on adventitious and destructive molds growing on these fungal gardens. Of course, the beetles may be feeding entirely on some other fungal substrate found only in these microhabitats.

Phytophagy. While many endomychid species are frequently observed on foliage (Fig. 1), phytophagy is rarely proposed as their primary mode of feeding. Endomychids, like many other mycophagous beetles, frequently wander onto and even nibble on any substrate, including plant tissue. Thus, it is not surprising that records of endomychids associated with plants typically lack specific information about a food source. Strohecker (1953) reported *Beccariola* Arrow associated with leaves of coffee plants. Arriaga-Varela et al. (2007) recorded *Anidrytus mexicanus* Strohecker from inside a bromeliad and *Catapotia laevis* Thomson from orchids. Blatchley (1910) collected specimens of *Rhanidea unicolor* (Ziegler) from thoroughwort flowers (Asteraceae). Stuntz (2001) found several endomychid species associated with epiphytes. Thornton (1957) recovered larvae, pupae and adults of a species of *Danae* Reiche from inside the umbels of papyrus sedge (paper reed), *Cyperus papyrus* L. (Cyperaceae). *Eumorphus quadriguttatus* (Illiger) was reported damaging betel pepper plants, *Piper betel* (L.) (Piperaceae) (Mondal et al. 2003). For all published accounts of plant feeding, facultative herbivory must be assumed because the endomychid species involved are known to be mycophagous.



Figure 1. *Eumorphus micans* Strohecker (smaller, brown specimens) and *Eumorphus fryanus festivus* (Arrow) (larger, black specimens) (Endomychidae: Lycoperdininae) resting on a *Piper* sp. (Piperaceae) in Borneo. Photo courtesy of D. Mann.

Endomychid associations with decaying plant material are difficult to interpret because it is often unclear whether the beetles are feeding on the decaying plant material itself, on the adventitious micro-fungi growing on that material, or on both. Arriaga-Varela et al. (2007) listed records of *Exysma laevigata* Gorham recovered from decaying pineapple and *Archipines intricata* (Gorham), *Epipocus punctatus* LeConte and *Epipocus tibialis* (Chevrolat) on banana debris. *Trochoideus desjardinsi* Guérin-Méneville is commonly collected from rotting coconut husks of the Coconut Palm (Arrow 1925). Many records associate endomychids with specific tree species (e.g., under bark of *Fagus* L.), but these records are generally vague and somewhat misleading. These associations are probably indirect, reflecting an association between the beetles' host fungus and specific tree species rather than between the beetles and the trees directly.

Predation: Entomophagy/Acariphagy. Only two genera of Endomychidae are known to contain predaceous species. The genus *Saula* Gerstaecker, which includes 26 species primarily from the Indomalaysian bioregion, is presumed to be entirely predaceous (Leschen 2000). This generalization, however, is based on published information about only two representative species. *Saula japonica* Gorham is a highly effective predator of arrowhead scale, *Unaspis yanonensis* (Kawana) (Hemiptera: Diaspididae) (Sasaji 1978, Takagi and Ogata 1985, Takagi 1999), but also feeds on cottony cushion scale, *Icerya purchasi* (Maskell) (Hemiptera: Margarodidae) (Leschen 2000), the citrus red mite, *Panonychus citri* (McGregor) (Acari: Tetranychidae) (Sasaji 1978), and the spiraling whitefly, *Aleurodicus dispersus* Russell (Hemiptera: Aleyrodidae) (Wen 1995, Chien et al. 2002). Another species, *Saula variipes* Arrow (as *Saura variipes*), was recorded as a predator of coconut bagworm, *Mahasena corbetti* Tams (Lepidoptera: Psychidae) (Mariau 2001).

Smirnov (1957) recounted observing "*Mycetaea tafilaetica*" feeding on Parlatoria date scale, *Parlatoria blanchardi* (Targioni Tozzetti) (Hemiptera: Diaspididae), at a Saharan oasis in northern Africa. *Mycetaea* Stephens is a small genus including five extant species that feed primarily on molds. Leschen (2000) suggested that the attraction to the molds growing in association with sternorrhynchan exudates may serve as an important step in the transition from mycophagy to predation. While the beetles could have been attracted to the black sooty mold growing on the honeydew produced by the scales, Smirnov noted that they were feeding directly on the scales. Smirnov (1958) later reported "*M. tafilaetica*" was successfully cultured on an artificial diet containing sucrose, honey, alfalfa flour, yeast, royal jelly and agar supplemented with dried pulverized prey. Unfortunately, Smirnov (1957) failed to formally describe this species. A search of the Zoological Record yielded no additional references to this species, so the name remains a *nomen nudum* (Shockley et al. 2009). Nonetheless, if Smirnov's generic determination was correct then this instance of *Mycetaea* preying on scale insects is still noteworthy.

Necrophagy. Watson (2004) recovered *Lycoperdina* Latreille (as "*Opadina* sp.") (*lapsus calami*, C. Carlton pers. comm.) from pitfall traps associated with wildlife carrion in Louisiana. *Lycoperdina ferruginea* LeConte is the only species occurring in North America and is frequently collected from inside puffball mushrooms and from leaf litter (Pakaluk 1984, Price and Young 2007). Interestingly, Kocarek (2003) recorded another species, *L. bovistae* (Fabricius), from pitfall traps associated with rat carrion in the Czech Republic. Although the proximity of two different *Lycoperdina* spp. to carrion independently makes their occurrences noteworthy, the presence of both species was likely incidental.

Aphorista vittata (Fabricius) and *Endomychus biguttatus* Say were found feeding directly on the putrefying flesh of pig carcasses during the advanced decay stage of decomposition (Payne and King 1970). *Mycetaea subterranea* (Fabricius) was collected in association with stored bones (Aitken 1975), so this species may also facultatively feed on carrion during the later, dry stages of decomposition. As with herbivory, necrophagy is assumed to be facultative since all of these endomychid species are known to be primarily mycophagous.

Myxomycophagy. Keller and Snell (2002) listed Endomychidae among beetle families that feed on myxomycetes. Similarly, Blackwell (1984) recorded Endomychidae feeding on myxomycetes representing three genera: *Fuligo* Haller, *Stemonitis* Roth and *Brefeldia* Rostaf. However, neither reference provided a specific list of the endomychid species involved. *Aphorista morosa* LeConte was found in association with

a yellow slime mold plasmodium (Lawrence 1991), but no direct evidence suggests that plasmodia are used as a food source by any endomychid species.

Interactions with other organisms

Predators of Endomychids. Erwin and Erwin (1976) reported larvae and adults of *Eurycoleus macularis* Chevrolat (Coleoptera: Carabidae) feeding on larvae, pupae and teneral adults of *Corynomalus* Chevrolat (as *Amphix* Laporte) (Fig. 2). A species of *Rhymbus* Gerstaecker (= *Bystus* Guérin-Ménéville) was listed as a potential prey item of the army ant, *Eciton hamatum* Fabricius (Hymenoptera: Formicidae) (Wheeler 1925); however, the beetles' presence was later questioned as incidental (i.e., they were already on the tree when the ants formed their bivouac) (Mann 1925). Denlinger (1994) noted reduviid nymphs feeding on aggregating adults of *Stenotarsus subtilis* Arrow on Barro Colorado Island in Panama, and unidentified pentatomid nymphs were observed feeding on late-instar larvae of *Corynomalus laevigatus* Gerstaecker in Costa Rica and *C. tarsatus* Erichson in Bolivia (F. Shockley pers. obs.). Wharton (1946) listed *Ascoschongastia indica* (Hirst) (Acari: Trombiculidae), an egg predator of *Tribolium castaneum* (Herbst), as a potential egg predator of endomychids.

Among vertebrate predators, only two bat species and one frog species have been recorded preying on endomychids, and all three are considered generalist insectivores. In each case, endomychids made up only a small fraction of the diet, and none were identified beyond family-level. Whitaker et al. (1999) recovered endomychids in scat of the Indian pygmy bat, *Pipistrellus mimus* Wroughton. Rajemison and Goodman (2007) found a single endomychid in the scat of an endemic Malagasy bat, *Myzopoda schliemanni* Goodman, Rakotondraparany and Kofoky. Johnson and Christiansen (1976) found a single endomychid among the stomach contents of Blanchard's cricket frog, *Acris crepitans blanchardi* (Harper), in Iowa.

Parasitoids attacking Endomychids. Only three parasitoids have been recorded thus far from endomychids, all targeting species of *Endomychus* Panzer. Walker (1836) described *Pteromalus endomychi* (Hymenoptera: Pteromalidae), reared from the larvae of *Endomychus coccineus* (L.). *Endomychobius* Ashmead was erected for the single species *Endomychobius flavipes* (Hymenoptera: Pteromalidae) (Fig. 3), reared from the larvae of *Endomychus biguttatus* (Ashmead 1896, Leschen and Allen 1987). *Pteromalus endomychi* Walker was later transferred to *Endomychobius* by Ruschka (1924). In addition, Reinhard (1958) reported larvae of *Endomychus biguttatus* parasitized by *Phyllophilopsis evanida* Reinhard (Diptera: Tachinidae).

Pathogens/Parasites of Endomychids. One of the most widespread pathogen groups infecting insects are bacteria of the genus *Wolbachia* Hertig which infect 16% of all insect species including representatives from all major insect orders



Figure 2-3. Natural enemies of Endomychidae. **2)** Larva of *Eurycoleus* sp. (Carabidae: Lebiinae) feeding on a pupa of *Corynomalus vestitus cinctus* (Endomychidae: Lycoperdininae) on Barro Colorado Island, Panama. Photo courtesy of N. Lord. **3)** *Endomychobius flavipes* (Hymenoptera: Pteromalidae), a host-specific parasitoid that attacks *Endomychus biguttatus* (Endomychidae: Endomychinae). Photo courtesy of M. Gates.

(Werren 1997, Kozek and Rao 2007). As many as 70% of insect species are potential hosts (Werren 1997, Kozek and Rao 2007). Werren et al. (1995) tested *Stenotarsus subtilis* for the presence of *Wolbachia*, but failed to recover the bacterium. To date, *S. subtilis* is the only endomychid species to be tested for the presence of *Wolbachia*.

The only ectoparasites reported for Endomychidae all belong to Laboulbeniales, a large order of ascomycete fungi containing many species that are obligate ectoparasites of insects. Weir and Hammond (1997) reported that, of 46 endomychid species collected in a 500 ha tract of lowland rain forest in Northern Sulawesi, only three were infected with Laboulbeniales (6.5%). Records of infection of endomychids by Laboulbeniales appear to be relatively rare, and known ectoparasites are restricted currently to species of the genus *Rickia* Cava.

Thaxter (1916) described eight species of *Rickia* attacking Endomychidae in two different subfamilies (Lycoperdininae and Stenotarsinae): *Rickia gracilis*, *Rickia latior* and *Rickia stenotarsi* from *Stenotarsus guineensis* Gerstaecker in Cameroon; *Rickia danaelis* from *Danae senegalensis* (Gerstaecker) in Cameroon; *Rickia ancylopi* from *Ancylopus bisignatus* Gerstaecker in Cameroon, *Rickia eumorphi* from *Eumorphus cyanescens* Gerstaecker in Mindanao (Philippines), *Rickia saulae* from a species of *Saula* Gerstaecker in Mindanao (Philippines), and *Rickia lycoperdinae* on a species of *Lycoperdina* in Madagascar. *Rickia eumorphi* was later found on *Eumorphus cyanescens* (Weir 1998) and has since been found on five additional species of *Eumorphus* Weber in Peninsular Malaysia, Thailand and Borneo: *E. festivus* Arrow, *E. macrospilotus* Arrow, *E. minor* Gerstaecker, *E. turritus* Gerstaecker and *E. tetraspilotus* Hope (Sugiyama and Mochizuka 1979, Sugiyama and Yamamoto 1982, Sugiyama and Phanichapol 1984). Kaur and Mukerji (1996) reported the first collection of *Rickia ancylopi* on *Ancylopus* Costa in India, and it has since been found in Japan, Peninsular Malaysia, Taiwan and Korea (Sugiyama 1973, Terada 1978, Lee and Lee 1981, Sugiyama and Majewski 1985, Majewski 1988).

Endosymbionts of Endomychids. The only known endosymbionts of endomychids are yeasts located primarily in the gastric caecae (Table 2). McHugh et al. (1997) speculated that endosymbionts in another mycophagous beetle, *Megalodacne heros* (Say) (Coleoptera: Erotylidae), might serve a function in the digestion of fungal tissue. A recent series of studies (Suh and Blackwell 2004, Suh et al. 2004, Suh et al. 2005) isolating, culturing and identifying endosymbiotic yeasts occurring in the gut of mycophagous beetles has led to the description of six new species of yeast endosymbionts from endomychids. However, many additional yeast endosymbiont species remain undescribed (Ganter 2006).

Phoresy on Endomychids. Phoresy on endomychids is rare compared to other taxa of similar habits (i.e., erotylids, tenebrionids), perhaps due to differences in grooming or defensive chemistry (addressed elsewhere). Aguiar and Buhrnheim (1998) listed the pseudoscorpion *Paratemnoides minor* (Balzan) (Atemnidae) riding phoretically on endomychids, but the beetles were left undetermined beyond the family-level. Phoretic pseudoscorpions are often found in association with rotting wood where they are predaceous on other small invertebrates.

Most known phoretics of endomychids are mites. Crawford (2005) noted the presence of undetermined phoretic mites on the venter of *Aphorista laeta* LeConte. Mites from two undescribed genera of Rhizoglyphinae are phoretic on *Lycoperdina koltzei* Reitter and *Mycetina marginalis* (Gebler) (Klimov 2000). Wheeler and Blackwell (1984) mentioned another phoretic rhizoglyphine occurring on *Lycoperdina ferruginea*. Masan (2001) recorded the uropodine mite *Oodinychus ovalis* (Koch) (as *Trichouropoda ovalis*) (Acari: Mesostigmata: Uropodina) associated with *Endomychus coccineus*. Both rhizoglyphines and uropodines are obligate mycetophagous inhabitants of decaying wood and are commonly phoretic on mycophagous beetles (Bloszyk et al. 2006).

Endomychids as Inquilines. Endomychidae includes a number of species closely associated with social insects, particularly ants and termites (Table 3). Wasmann (1894) listed 11 endomychids associated with ants. Price and Young (2007) noted the close proximity of adults of *Rhanidea unicolor* to a colony of *Lasius* Fabricius ants, although no direct association was inferred. Myrmecophily is the most common form of social insect inquilinism among endomychids; however, termitophilous and melittophilous species are also known. Endomychids have also been recovered from birds' nests. Hicks (1959) generated a checklist

of insects found in bird nests, including three species of Endomychidae: *Symbiotes gibberosus* (Lucas), *Holoparamecus caularum* (Aubé), and *Mycetaea subterranea* (Table 4).

Habitat, habits and behavior

Habitat Specialization. Two types of habitats are preferred by many endomychid species: 1) the subcortical region of standing or fallen dead trees where they are closely associated with the fruiting bodies of macrofungi, and 2) leaf litter where they feed on the spores and hyphae of microfungi (Lawrence 1991, Price and Young 2007). However, endomychids are commonly found in many other habitats, reflecting the behavioral diversity of the family. Dajoz (1966) listed *Symbiotes gibberosus* and *Mycetaea subterranea* among beetles collected from tree holes, suggesting possible dendrolimnetophily. However, this condition has not been formally proposed for any other endomychid species, and even Dajoz questioned their presence as merely accidental. Price and Young (2007) recently reported *Phymaphora pulchella* Newman from damp tree-hole litter.

No endomychids are known to be obligately xylophagous (i.e., feeding directly and exclusively on wood), so the presence of subcortical and dendrolimnetophilic species is more likely linked to other ecological processes active in stressed, dying or dead trees. Shockley et al. (2008) speculated that *Micropsephodes lundgreni* Leschen and Carlton may orient to turpentine (a monoterpene released after tree wounding), verbenone (bark beetle anti-aggregation pheromone) and frontalin (bark beetle aggregation pheromone). Likewise, Skelley and Burgess (1995) reported collecting *Trochoideus desjardinsi* from ethanol/turpentine traps suggesting it may also orient to wounded trees. Price and Young (2007) recovered *Phymaphora pulchella*, *Rhanidea unicolor*, *Endomychus biguttatus*, *Danae testacea* (Ziegler) and *Symbiotes gibberosus* from Lindgren funnels baited with ipsdienol, though none were collected in large numbers and may be incidental.

Collection data for endomychids show a strong bias for habitats close to the ground (e.g., fallen logs, stumps, leaf litter, etc.). To date, no work has focused on endomychid diversity at heights above three meters, but several large-scale ecological studies have recovered endomychids from the canopy. Ulyshen and Hanula (2007) collected substantial numbers of *Micropsephodes lundgreni* from the canopy of a temperate deciduous forest, leading them to propose it may be a canopy specialist. Hammond (1994) reported 7 of 41 endomychid species (~17%) collected from the Sulawesi canopy were exclusive canopy specialists, and canopy specialization by some endomychids is further supported by other surveys of canopy beetles (e.g., Allison et al. 1997, Stork 1991). Marques et al. (2006) found endomychids to be the dominant fungivores in the Brazilian rainforest canopy at one site.

Cave-dwelling Endomychids. Very few endomychid species exhibit cavernicolous or troglodytic habits. Some species may be associated with bat guano, as with *Holoparamecus gabrielae* Rücker (Rücker 2003), but for most, the natural history remains unknown. Jeannel (1926) recorded *Mycetaea subterranea* (as *M. hirta*) from inside the mouth of a cave in France. This species is known to occur in dark cellars and grain bins where it feeds on mold so it is not unreasonable to speculate similar habits in caves. Jeannel (1934) described a new anamorphine, *Cereaxina troglodytes* (later synonymized under *Reitteria escherichi* Wasmann [Merophysiinae]) from a cave in Asia Minor. Reddell and Veni (1996) collected a species of *Anamorphus* LeConte in a cave in Belize. Hoffman et al. (2004) listed a species of *Rhymbus* (= *Bystus*) collected in a cave in the Yucatan Peninsula. Moulds (2004) recorded an unidentified endomychid from Ashford Cave, New South Wales, Australia.

Endomychids as Pests. Chen and Cheng (2000) recorded a species of *Idiophyes* Blackburn as a nuisance pest in homes in China. Chuter (1999) noted that *Endomychus coccineus* facultatively colonized old, decaying particle/chip board. Endomychids are not usually considered pests of cultivated fungi since most species prefer hard bracket or shelf fungi to the more commonly cultivated agarics. *Symbiotes* Redtenbacher, however, includes several species that feed on oyster mushrooms, *Pleurotis ostreatus* Fries, a commonly harvested fungus for human consumption (Cline and Leschen 2005). *Mycetaea subterranea* was documented infesting stored caches of research-grade fungal pathogens (ergot sclerotia) (Singh and Tripathi 1990). In most cases where endomychids are considered pests, the beetles infest stored food products that have spoiled, feeding primarily on molds and secondarily on the product itself.

All recorded stored product pests within Endomychidae belong to four genera—*Holoparamecus* Curtis and *Merophysia* Lucas (Merophysiinae), *Mycetaea* (Mycetaeinae) and *Trochoideus* Westwood (Pleganophorinae) (Table 5). Commercial exportation of stored products has resulted in multiple introductions of pest species throughout the world, and many have become established. *Holoparamecus* species are the primary endomychid pests with at least six species known to infest stored products. The three remaining genera each include a single stored product pest species: *Merophysia letourneuxi* Pic, *Mycetaea subterranea* and *Trochoideus desjardinsi*.

Aggregation/Diapause. Endomychids often cluster together in small groups in the field (F. Shockley pers. obs.), but this may be an artifact of the patchiness of their host fungi. Within Endomychidae, only two species have been documented as regularly forming larger non-feeding aggregations, both members of *Stenotarsus* Perty. Roubik and Skelley (2001) noted *Stenotarsus latipes* Arrow sometimes forms aggregations, but Arriaga-Varela et al. (2007) argued this species never forms aggregations in Mexico. Denlinger (1996) noted *Stenotarsus* spp. form aggregations, but it was unclear if he was referring to *S. latipes* or other *Stenotarsus* spp. that also aggregate.

Much work has been done on the aggregation behavior and diapause of *Stenotarsus subtilis* (frequently misidentified in the literature as *S. rotundus* Arrow, a junior synonym of the non-aggregating species *S. ovalis* Arrow) (Roubik and Skelley 2001). Adults of *S. subtilis* form large aggregations of up to 70,000 individuals (Denlinger 1994) in association with diapause, which may last up to 10 months per year (Tanaka 1988, Wolda and Denlinger 1984). These beetles do not fly during diapause, but migrate up and down the base of the tree on which they are aggregating based on humidity cues (Denlinger 1986). While other beetles often aggregate for reproduction, aggregations of *S. subtilis* consist of sexually immature virgin females and sexually mature males (Nedved and Windsor 1994a, Roubik and Skelley 2001, Tanaka 1986). Males abstain from mating until triggered by the first wet season rains (Tanaka et al. 1987b, c; Wolda 1992).

On Barro Colorado Island, Panama, where many of these studies were conducted, known aggregations of *S. subtilis* form at the base of two trees, an *Oenocarpus panamanus* Bailey (Arecaceae) and a *Tetragastris panamensis* (Engler) (Burseraceae). Interestingly, the beetles often aggregate on the exact tree used the previous year, despite aggregations consisting exclusively of newly eclosed, naïve univoltine adults (Tanaka et al. 1987b). Aggregating beetles do not feed and so must conserve water (Tanaka 2000, Yoder et al. 1992), relying upon fat reserves stored during larval instars (Wolda 1989, Nedved and Windsor 1994b). Dormant beetles are resistant to suboptimal temperatures due to accumulated glycerol and glucose in the hemolymph (Pullin and Wolda 1993, Nedved 2000). A variety of factors can influence the beetles' metabolic rates and the timing of diapause termination such as daylength and humidity (Tanaka et al. 1987a, c; 1988b), size of the aggregation (Tanaka et al. 1988a) and disturbance (i.e., handling the beetles) (Tanaka et al. 1987b).

Defensive Strategies. Endomychids have a variety of physical and chemical defenses that help them ward off or evade potential predators. Endomychids have been suggested as participants in mimicry complexes with beetles from a variety of families including Carabidae (Arrow 1925, Brown 1985), Chrysomelidae, Coccinellidae (Donisthorpe 1901, Crowson 1981), Erotylidae (Marshall 1902) and Tenebrionidae (Brown 1985). Whether the mimicry proposed was Batesian or Müllerian remains unclear. In complexes involving predators, the mimicry may also be aggressive on the part of the predator. Leschen and Carlton (1993) described a special case of crypsis (mimicking inanimate objects) in the larvae of *Bystus decorator* Leschen and Carlton in which the larvae cover themselves with frass and pieces of bark and fungi to blend into their surroundings and shield themselves from predation. Females of *Endomychus biguttatus* often use the tough hyphae of their obligate reproductive host, *Schizophyllum commune* Fries, to camouflage their eggs (Leschen 1994).

In addition to the mimicry described above, a few taxa may exhibit Wasmannian mimicry (a social insect parasite/inquiline mimicking its host). Escherich (1911) described a larva associated with the termite *Eutermes ceylonicus* Holmgren. Arrow (1925) later identified this larva as that of *Trochoideus desjardinsi*, noting that the larva so strongly resembled the host that dorsally it was difficult to differentiate the two. Lawrence and Reichardt (1969) list *Trochoideus* spp. as potential ant mimics based on their highly modified antennae, a common feature of myrmecophiles. The myrmecophile *Cholovocera maderae*

(Wollaston) readily detects and follows the trail pheromone of its host ant, *Paratrechina longicornis* (Latreille). Interestingly, beetles are completely unmolested by workers, suggesting possible chemical mimicry of nest–mate recognition pheromones (Kistner 1982). This endomychid species also has a morphological adaptation in the pronotum that allows each beetle to be lifted by the ants without injury and transported along with the eggs when the host nest is disturbed (Kistner 1982).

Dettner (1987) and Skelley and Leschen (2002) suggested that some endomychids are likely to have chemical defenses, but few defensive chemicals have been identified. The terpenoid stenotarsol was recently isolated from *Stenotarsus subtilis* (Laurent et al. 2005), and *sec*-butyl 2-methoxy-3-alkylpyrazine was isolated from *Eumorphus tetraspilotus* (Moore et al. 1990). Numerous endomychid species have evolved the ability to reflexively bleed hemolymph in response to agitation, particularly from the femoro-tibial joints (Dettner 1987, Laurent et al. 2005, Skelley and Leschen 2002). This behavior has been documented in species of *Endomychus* (Endomychinae), *Lycoperdina* (Lycoperdininae), *Rhanidea* Strohecker (Leiestinae), *Corynomalus* (Lycoperdininae) and *Eumorphus* Weber (Lycoperdininae) (Skelley and Leschen 2002, F. Shockley pers. obs., Z. Simmons pers. comm.). Once secreted, beetles immediately begin to fastidiously clean the appendage from which the hemolymph cocktail was exuded (Z. Simmons pers. comm.). In some *Eumorphus* spp., beetles can selectively bleed from the leg or legs closest to the stimulus source, suggesting that the compounds may be costly to produce. If beetles are continuously stimulated without a recovery period, the amount of exudate released is reduced with each agitation until the beetles eventually cease to exude droplets altogether (Z. Simmons pers. comm.).

Whether the compounds exuded by endomychids are produced internally or sequestered from external sources (e.g., their fungal hosts) and then chemically altered for exudation remains unclear. In some cases, endomychids may actively seek out alternative defensive compounds not internally produced or externally acquired from their primary hosts. For example, several endomychid species are attracted to the biologically active deterrent compound cantharidin. *Aphorista laeta*, *A. vittata*, *Lycoperdina ferruginea*, *Danae testacea* and *Xenomycetes morrisoni* Horn preferentially orient to pitfall traps baited with cantharidin (Dettner 1987, 1997; Hemp and Dettner 2001; Price and Young 2007; Young 1984a, b; Young 1989). Since many insect species respond to cantharidin, sensitivity to it or interspecific acquisition of it may be widespread throughout insects. Although a role in chemical defense of endomychids was explicitly implied in the studies referenced above, no specific mechanism was proposed for how endomychids might acquire cantharidin, why they would prefer it to other more readily available compounds, and whether or not they can even sequester it or chemically modify it prior to exudation.

Non-chemical Communication. Endomychids also have several mechanisms for communication via stridulation. In the field, stridulation by females of *Corynomalus* spp. has been observed to “corral” larvae, but more often serves as a distress signal encouraging conspecifics to move away from the area (F. Shockley pers. obs.). Gorham (1885) was the first to note the presence of a stridulatory apparatus on *Encymon ruficollis* Gorham, attributing it to be a sexually dimorphic feature of males. Gahan (1900) rejected this assertion and discussed the form and function of the stridulatory apparatus in Endomychidae. The stridulatory organ is composed of a file located dorsally on the posteromedial region of the head and a membrane on the anterior margin of the pronotum which move in opposition to produce sound. This feature is a synapomorphy of the subfamily Lycoperdininae.

Arrow (1924) also described a stridulatory alar organ consisting of a set of modified patches on the posterior margin of the dorsal surface of the hind wing and a complimentary file on the inner surface of the medial margins of the elytra. The alar organ is present in many endomychids, albeit sometimes in highly modified or reduced form, and has specifically been observed within Anamorphinae (*Bystus*), Endomychinae (*Endomychus*), Epipocinae (*Epipocus* Germar), Lycoperdininae (*Amphisternus* Germar, *Eumorphus*, *Corynomalus*, *Cymbachus* Gerstaecker), and Stenotarsinae (*Stenotarsus* and *Danae*).

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Table 1. Known fungal hosts of Endomychidae.

		Host Fungus ¹	
Endomychid Taxon	Family	Genus/Species	Ref ²
Anamorphinae			
<i>Bystus</i> sp.	Pleurotaceae	<i>Pleurotus</i> sp.	32
	Polyporaceae	<i>Favolus brasiliensis</i>	32
	Polyporaceae	<i>Favolus</i> sp.	32
	Polyporaceae	<i>Polyporus</i> sp.	32
	Polyporaceae	<i>Poria</i> sp.	32
	Xylariaceae	<i>Daldinia</i> sp.	32
	Xylariaceae	<i>Hypoxylon</i> sp.	32
	Xylariaceae	<i>Xylaria</i> sp.	32
	<i>Symbiotes duryi</i> Blatchley	Pleurotaceae	<i>Pleurotus ostreatus</i>
<i>Symbiotes impressus</i> Dury	Pleurotaceae	<i>Pleurotus ostreatus</i>	8
<i>Symbiotes latus</i> Redtenbacher	Hymenochaetaceae	<i>Inonotus hispidus</i>	36
<i>Symbiotes</i> sp.	Pleurotaceae	<i>Pleurotus ostreatus</i>	19
Endomychinae			
<i>Endomychus biguttatus</i>	Auriculariaceae	<i>Auricularia auricula-judae</i>	23
	Auriculariaceae	<i>Auricularia mesenterica</i>	23
	Fomitopsidaceae	<i>Piptoporus betulinus</i>	32
	Schizophyllaceae	<i>Schizophyllum commune</i>	35
<i>Endomychus coccineus</i>	Auriculariaceae	<i>Auricularia mesenterica</i>	11
	Boletaceae	<i>Boletus suberosus</i>	12
	Lycoperdaceae	<i>Bovista</i> sp.	34
	Polyporaceae	<i>Panus conchatus</i>	28
	Polyporaceae	<i>Polyporus</i> sp.	36
	Polyporaceae	<i>Trametes hirsuta</i>	30
	Polyporaceae	<i>Trametes versicolor</i>	28
Epipocinae			
<i>Epipocus longicornis</i> Gerstaecker	Boletaceae	<i>Boletus edulis</i>	2
	Sirobasidiaceae	<i>Sirobasidium sanguineum</i>	2
<i>Epipocus tibialis</i>	Auriculariaceae	<i>Auricularia mesenterica</i>	2
<i>Epipocus unicolor</i> Horn	Boletaceae	<i>Fistulinella</i> sp.	2
	Polyporaceae	<i>Coriopsis gallica</i>	10
Leiestinae			
<i>Leiestes seminigra</i> (Gyllenhal)	Fomitopsidaceae	<i>Piptoporus betulinus</i>	36
<i>Phymaphora pulchella</i> Newman	Meruliaceae	<i>Climacodon pulcherrimus</i>	7, 32
	Fomitopsidaceae	<i>Piptoporus betulinus</i>	24, 32
<i>Rhanidea unicolor</i>	Steccherinaceae	<i>Irpex lacteus</i>	7, 32
Lycoperdininae			
<i>Aphorista laeta</i>	Ganodermataceae	<i>Ganoderma applanatum</i>	4
<i>Aphorista morosa</i>	Gomphaceae	<i>Gomphus floccosus</i>	4
	Crepidotaceae	<i>Crepidotus mollis</i>	4
	Paxillaceae	<i>Paxillus</i> sp.	4
	Pluteaceae	<i>Pluteus cervinus</i>	4
	Polyporaceae	<i>Coriopsis gallica</i>	10
	Coniophoraceae	<i>Coniophora arida</i>	15
<i>Aphorista vittata</i>	Russulaceae	<i>Lactarius argillaceifolius</i>	22
	Russulaceae	<i>Russula</i> sp.	22

Table 1. cont'd.

Endomychid Taxon	Host Fungus ¹		Ref ²
	Family	Genus/Species	
Lycoperdininae			
<i>Aphorista vittata</i>	Marasmiaceae	<i>Armillaria mellea</i>	22
	Marasmiaceae	<i>Armillaria tabescens</i>	22
<i>Eumorphus marginatus</i> Fabricius	Polyporaceae	<i>Polyporus</i> sp.	3
<i>Eumorphus</i> sp.	Ganodermataceae	<i>Ganoderma</i> sp.	20
<i>Lycoperdina bovistae</i>	Boletaceae	<i>Boletus</i> sp.	36
	Geastraceae	<i>Geastrum fimbriatum</i>	28
	Geastraceae	<i>Geastrum rufescens</i>	28
	Lycoperdaceae	<i>Langermannia gigantea</i>	13
	Lycoperdaceae	<i>Bovista</i> sp.	14
	Lycoperdaceae	<i>Handkea excipuliformis</i>	28
	Lycoperdaceae	<i>Handkea utriformis</i>	5, 17
	Lycoperdaceae	<i>Lycoperdon bovista</i>	5
	Lycoperdaceae	<i>Lycoperdon gemmatum</i>	28
	Lycoperdaceae	<i>Lycoperdon perlatum</i>	17
	Lycoperdaceae	<i>Lycoperdon pyriforme</i>	5
	Lycoperdaceae	<i>Lycoperdon verrucosum</i>	29
	Russulaceae	<i>Lactarius piperatus</i>	28
	Russulaceae	<i>Russula delica</i>	28
	Marasmiaceae	<i>Armillaria mellea</i>	28
	Tricholomataceae	<i>Clitocybe nebularis</i>	28
	Tricholomataceae	<i>Gymnopus fuscipes</i>	28
	Tricholomataceae	<i>Lepista flaccida</i>	27
<i>Lycoperdina ferruginea</i>	Hydnaceae	<i>Hydnum</i> sp.	22
	Lycoperdaceae	<i>Calvatia cyathiformis</i>	25
	Lycoperdaceae	<i>Langermannia gigantea</i>	25
	Lycoperdaceae	<i>Lycoperdon molle</i>	25
	Lycoperdaceae	<i>Lycoperdon perlatum</i>	25
	Lycoperdaceae	<i>Lycoperdon pyriforme</i>	35
	Lycoperdaceae	<i>Lycoperdon subvelatum</i>	25
	Lycoperdaceae	<i>Lycoperdon umbrinum</i>	25
	Lycoperdaceae	<i>Lycoperdon</i> sp.	1
	Pezizaceae	<i>Peziza</i> sp.	25
	Pluteaceae	<i>Pluteus cervinus</i>	22
<i>Lycoperdina penicillata</i> Marseul	Lycoperdaceae	<i>Bovista plumbea</i>	26
	Lycoperdaceae	<i>Lycoperdon gemmatum</i>	26
<i>Lycoperdina succincta</i> (L.)	Geasteraceae	<i>Geastrum triplex</i>	33
	Lycoperdaceae	<i>Bovista nigrescens</i>	16
	Lycoperdaceae	<i>Lycoperdon gemmatum</i>	11
<i>Mycetina cruciata</i> (Schaller)	Pleurotaceae	<i>Pleurotus</i> sp.	9
	Polyporaceae	<i>Trametes suaveolens</i>	21
	Polyporaceae	<i>Polyporus</i> sp.	36
<i>Mycetina idahoensis</i> Fall	Polyporaceae	<i>Polyporus</i> sp.	36
<i>Mycetina perpulchra</i> (Newman)	Coniophoraceae	<i>Coniophora arida</i>	15
	Meripilaceae	<i>Meripilus giganteus</i>	22
Mycetaeinae			
<i>Mycetaea subterranea</i>	Coniophoraceae	<i>Serpula lacrymans</i>	5, 21
	Polyporaceae	<i>Polyporus squamosus</i>	36
	Polyporaceae	<i>Laetiporus sulphureus</i>	9
	Polyporaceae	<i>Polyporus</i> sp.	6
	Polyporaceae	<i>Trametes pubescens</i>	31

Table 1. cont'd.

Endomychid Taxon	Host Fungus ¹		Ref ²
	Family	Genus/Species	
Pleganophorinae			
<i>Trochoideus desjardinsi</i>	Auriculariaceae	<i>Auricularia</i> sp.	20
Stenotarsinae			
<i>Stenotarsus circumdatus</i> Gerst.	Russulaceae	<i>Russula</i> sp.	2
<i>Stenotarsus latipes</i>	Russulaceae	<i>Russula</i> sp.	2
	Russulaceae	<i>Lactarius deliciosus</i>	2
	Russulaceae	<i>Lactarius</i> sp.	2
	Sirobasidiaceae	<i>Sirobasidium sanguineum</i>	2
<i>Stenotarsus marginalis</i> Arrow	Russulaceae	<i>Russula mexicana</i>	2
	Russulaceae	<i>Lactarius</i> sp.	2
<i>Stenotarsus</i> sp.	Polyporaceae	<i>Favolus tenuiculus</i>	2
Xenomycetinae			
<i>Xenomycetes laversi</i> Hatch	Paxillaceae	<i>Paxillus atrotomentosus</i>	18

¹ Host fungus family and species names verified using the electronic Index Fungorum, <http://www.indexfungorum.org/>. Last accessed 9 February, 2009.

² References: 1) Ackerman & Shenefelt 1973; 2) Arriaga-Varela *et al.* 2007; 3) Arrow 1925; 4) J.S. Ashe *pers. comm.*; 5) Benick 1952; 6) Bercio 1930-31; 7) Burakowski & Ślipiński 2000; 8) Cline & Leschen 2005; 9) Dajoz 1966; 10) Dajoz 1996; 11) Donisthorpe 1935; 12) d'Orbigny 1846; 13) Fowler 1887-1891; 14) Ganglbauer 1899; 15) Hoebeke *et al.* 1987; 16) Horion 1961; 17) Hyman & Parsons 1992; 18) Johnson 1986; 19) Lawrence 1991; 20) Lawrence & Milner 1996; 21) Lentz 1879; 22) Leschen 1988; 23) Leschen & Carlton 1988; 24) Majka 2007; 25) Pakaluk 1984; 26) Peyerimhoff 1915; 27) Rapp 1934; 28) Rehfous 1955; 29) Rouget 1858; 30) Scheerpelz & Höfler 1948; 31) Selonen *et al.* 2005; 32) F.W. Shockley *pers. obs./museum specimens*; 33) Sunhede 1974; 34) Weiss 1924; 35) Weiss & West 1920; 36) Q.D. Wheeler *in litt.*, MYCOL database.

Table 2. Yeast gut endosymbionts of Endomychidae.

Endomychid Taxon	Yeast Isolate	Ref ¹
Anamorphinae		
<i>Bystus piceus</i> (Gorham)	<i>Candida ambrosiae</i>	4
	<i>Candida barrocoloradensis</i>	4
	<i>Candida boleticola</i>	4
	<i>Candida homilentoma</i>	4
Epipocinae		
<i>Epipocus tristis tristis</i> Guérin-Ménéville	<i>Candida athensensis</i>	4
Lycoperdininae		
<i>Corynomalus laevigatus</i>	<i>Ambrosiozyma monospora</i>	3
	<i>Candida amphixiae</i>	4
	<i>Candida endomychidarum</i>	3
	<i>Candida sinolaborantium</i>	3
	<i>Candida michaelii</i>	3
<i>Corynomalus vestitus cinctus</i> (Fabricius)	<i>Candida emberorum</i>	1
	<i>Candida halonitratophila</i>	4
	<i>Pichia nakazawae</i>	3
	<i>Trichomonoascus petasosporus</i>	4
<i>Lycoperdina ferruginea</i>	<i>Asterotremella humicola</i>	4
Stenotarsinae		
<i>Stenotarsus lemniscatus</i> Gorham	<i>Candida cylindracea</i>	4
	<i>Candida haemulonii</i>	4
	<i>Candida panamensis</i>	4
	<i>Pseudozyma rugulosa</i>	4
<i>Stenotarsus obtusus</i> Gerstaecker	<i>Candida panamensis</i>	4
<i>Stenotarsus validicornis</i> Gerstaecker	<i>Candida nodaensis</i>	4
Endomychidae (Undetermined)		
Larva	<i>Candida athensensis</i>	4
Larva	<i>Candida smithsonii</i>	2

¹ References: 1) Suh *et al.* 2004; 2) Suh & Blackwell 2004; 3) Suh *et al.* 2005; 4) M. Blackwell *in litt.*, BeetleBellYeast Project Database.

Table 3. Published records for endomychid inquilines of social insects.

Endomychid Taxon	Assoc ¹	Specific Host Taxon (if known)	Ref ²
Anamorphinae			
<i>Rhymbillus hospes</i> Reich.	A	No specific host listed	7, 14
<i>Symbiotes latus</i>	A	<i>Lasius brunneus</i>	4, 7, 18
Eupsilobiinae			
<i>Chileolobius convexus</i>	A	<i>Pachycondyla</i> sp.	13
<i>Eidoreus minutus</i> Sharp	A	<i>Pheidole punctulata</i>	2, 9
<i>Evolocera championi</i> Sharp	A	No specific host listed	16
<i>Evolocera</i> sp.	B	<i>Ancyloscelis apiformis</i> , <i>Melitoma marginella</i>	19
<i>Microxenus laticollis</i> Woll.	A	No specific host listed	1
Merophysiinae			
<i>Cholovocera attae</i> (Kraatz)	A	<i>Messor barbara</i> , <i>M. structor</i>	6
<i>Cholovocera beloni</i> (Wasmann)	A	<i>Holcomyrmex scabriceps</i> , <i>Pheidole sulcaticeps poonensis</i> , <i>Ph. wroughtoni</i> , <i>Ph. latinoda</i> , <i>Paratrechina longicornis</i>	6, 8
<i>Cholovocera fleischeri</i> Reitter	A	<i>Atta</i> sp.	6
<i>Cholovocera formicaria</i> Motsch.	A	<i>Aphaenogaster testaceopilosa</i> , <i>Messor barbara</i> , <i>M. structor</i> , <i>Pheidole pusilla</i> , <i>Ph. megacephala</i>	4, 18
<i>Cholovocerida ecitonis</i> (Wasm.)	A	<i>Eciton praedator</i> , <i>E. omnivorum</i>	18
<i>Cholovocerida maderae</i> (Woll.)	A	<i>Paratrechina longicornis</i>	8, 18
<i>Holoparamesus</i> spp.	A	<i>Atta mexicana</i>	12, 15
<i>Merophysia carinulata</i> Rosenh.	A	<i>Aphaenogaster testaceopilosa</i> , <i>Pheidole pusilla</i> , <i>Ph. megacephala</i>	18
<i>Merophysia carmelitana</i> Saulcy	A	<i>Messor barbara</i>	6
<i>Merophysia formicaria</i> Lucas	A	<i>Messor barbara</i> , <i>A. testaceopilosa</i> , <i>Pheidole pusilla</i> , <i>Ph. megacephala</i>	18
<i>Merophysia oblonga</i> Kisenwetter	A	<i>Aphaenogaster testaceopilosa</i> , <i>Pheidole pallidula</i> , <i>Tetramorium caespitum</i>	6, 18
<i>Reitteria escherichi</i>	A	<i>Pheidole pallidula</i> , <i>Camponotus aethiops</i>	6
Mycetaeinae			
<i>Mycetaea subterranea</i>	B	No specific host listed	5, 11
	A	<i>Formica rufa</i> , <i>F. protensis</i> , <i>F. exsecta</i> , <i>Lasius niger</i> , <i>L. fuliginosus</i>	4, 18
Pleganophorinae			
<i>Pleganophorus bispinosus</i> Hampe	A	<i>Lasius brunneus</i>	18
<i>Trochoideus desjardinsi</i>	A	<i>Plagiolepis longipes</i>	7, 10, 18
<i>Trochoideus desjardinsi</i>	C	<i>Eutermes ceylonicus</i> , <i>Termes gilvus</i>	3
Stenotarsinae			
<i>Stenotarsus secticollis</i> Strohecker	C	No specific host listed (implied only)	17

¹ Associations: A = Myrmecophilous, B = Melittophilous, C = Termitophilous.² References: 1) Arriaga-Varela *et al.* 2007; 2) Arrow 1922; 3) Arrow 1925; 4) Bernard 1968; 5) Ganglbauer 1899; 6) Hetschko 1926; 7) Hölldobler & Wilson 1990; 8) Kistner 1982; 9) Kolbe 1910; 10) Lawrence & Reinhardt 1969; 11) Marseul 1867-68; 12) Navarette-Heredia 2001; 13) Pakaluk & Ślipiński 1990; 14) Reichensperger 1915; 15) Rojas 1989; 16) Sharp 1891; 17) Skelley 1999; 18) Wasmann 1894; 19) Yanega & Leschen 1994.

Table 4. Published records for endomychids as nest associates of birds. Modified from Hicks (1959).

Endomychid Taxon	Host		Ref ¹
	Scientific Name	Common Name(s)	
Anamorphinae			
<i>Symbiotes gibberosus</i>	<i>Picus viridis</i> L.	Pic vert, Green Woodpecker	1, 2
Merophysiinae			
<i>Holoparamesus caularum</i>	<i>Ciconia ciconia</i> L.	White Stork	6, 7
Mycetaeinae			
<i>Mycetaea subterranea</i>	<i>Buteo buteo</i> L.	Common Buzzard	4
	<i>Corvus monedula</i> L.	Choucas, European Jackdaw	2
	<i>Riparia riparia</i> (L.)	Sand Martin	5
	Species not identified	Owl	3, 8

¹ References: 1) Leleup 1947a; 2) Leleup 1947b; 3) Linsley 1944; 4) Roubal 1929; 5) Stadler 1948; 6) Székessy 1944; 7) Székessy 1950; 8) Walker 1896.

Table 5. Endomychid species known to infest stored products.

Endomychid Taxon	Stored products infested	Ref ¹
Merophysiinae		
<i>Holoparamesus caularum</i>	rice, grain	6
	grain	7
	flour, barley, grain, cacao, spices	3
<i>Holoparamesus depressus</i> Curt.	rice, dried mushrooms, chocolate bars, bone sacks, flour, ginger	6
	Indian ground-nuts, wine vats	7
	Brazil nuts, oils seeds, carobs, illipenuts	1
	flour, barley, grain, cacao, spices	3
<i>Holoparamesus ellipticus</i> Woll.	Unknown (not provided)	4
<i>Holoparamesus ragusae</i> Reitter	wine vats, chocolate	7
<i>Holoparamesus signatus</i> Woll.	Unknown (not provided)	4
<i>Holoparamesus singularis</i> (Beck)	rice	6
	wine vats	6
	flour, barley, grain, cacao, spices	3
<i>Holoparamesus</i> spp.	licorice apricots, dried bamboo leaves, bean curd, betel, dried chili pods, dried black pepper and dry soup mix	8
<i>Merophysia letourneuxi</i>	flour, barley, grain, cacao, spices	3
Mycetaeinae		
<i>Mycetaea subterranea</i>	wine corks, hay refuse, mouldy sacks, flour, oats, beer drippings, corn, grain, mouldy wood	7
	hay	5
	palm kernels, stored bones	1
Pleganophorinae		
<i>Trochoideus desjardinsi</i>	coconut husks	2
	kapok seeds	1

¹ References: 1) Aitken 1975; 2) Arrow 1925; 3) Attia & Kamel 1965; 4) Biodiversity New Zealand 2007; 5) Buchelos & Athanassiou 1998; 6) Hinton 1941; 7) Hinton 1945; 8) Zimmerman 1990.