A review of myrmecophily in ant nest beetles (Coleoptera: Carabidae: Paussinae): linking early observations with recent findings

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Abstract Myrmecophily provides various examples of how social structures can be overcome to exploit vast and well-protected resources. Ant nest beetles (Paussinae) are particularly well suited for ecological and evolutionary considerations in the context of association with ants because life habits within the subfamily range from free-living and predatory in basal taxa to obligatory myrmecophily in derived Paussini. Adult Paussini are accepted in the ant society, although parasitising the colony by preying on ant brood. Host species mainly belong to the ant families Myrmicinae and Formicinae, but at least several paussine genera are not host-specific. Morphological adaptations, such as special glands and associated tufts of hair (trichomes), characterise Paussini as typical myrmecophiles and lead to two different strategical types of body shape: while certain Paussini rely on the protective type with less exposed extremities, other genera access ant colonies using glandular secretions and trichomes (symphile type). We compare these adaptations with other taxonomic groups of insects by joining contemporary research and early sources and discuss the possibility of an attracting or appeasing effect of the secretion. Species that are ignored by their host ants might use chemical mimicry instead. Furthermore, vibrational signals may contribute to ant–beetle communication, and chemical signals have proven to play a role in host finding. The powerful defense chemistry of paussines as "bombardier beetles" is not used in contact with host ants. We attempt to trace the evolution of myrmecophily in paussines by reviewing important aspects of the association between paussine beetles and ants, i.e. morphological and potential chemical adaptations, life cycle, host specificity, alimentation, parasitism and sound production.

Introduction

A great diversity of arthropods live together with ants and profit from ant societies being well-protected habitats with stable microclimate (Hölldobler and Wilson 1990; Wasmann 1913; Wheeler 1960). The concentrated brood and accumulated food items in ant nests constitute valuable resources, readily exploitable by associated organisms. Ant nests, however, are well-fortified, and due to their numerousness and chemical defence, ants are able to overwhelm intruders of large body size. Thus, the question of how ant-associated arthropods (myrmecophiles) freely roam an ant colony and develop in the nest has received broad interest. The mechanisms of some ant–myrmecophile interactions, which can be termed "symbioses" due to the close spatial association, have become fairly well understood, as chemical ecology has grown into an own discipline. On the other hand, the enormous advances in ecological understanding of ant colonies as super-organisms have given a new paradigm for assessing the underlying proximate and ultimate processes (Bourke and Franks 1995; Crozier and Pamilo 1996; Hölldobler and Wilson 1990). Sociobiological characteristics of an ant colony are

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of elementary importance for the question as to whether a myrmecophile can successfully intrude an ant colony. The pre-adaptation for being infiltrated differs between colonies of one species because some features may be displayed facultatively (Crozier and Pamilo 1996; Hölldobler and Wilson 1990). One such characteristic is the queen number, which can range from one (monogyny) to multiple (polygyny). Because of the high degree of relatedness among individuals and the sophisticated nestmate recognition, monogynous colonies are suspected to be less prone to intrusion. Aggressiveness, however, seems to be more pronounced in polygynous colonies (Hölldobler and Wilson 1977). Polygyny may be combined with occupation of multiple nest sites by one colony (polydomy). Recognition mechanisms in polydomous colonies differ from those in monodomous colonies based on the lack of constant nest odour exchange (Soroker et al. 2003), and connecting trails might further enhance colony finding by intruders. Additionally, colony movement frequency, colony size, habitat choice and nesting materials can be variables that influence the suitability of an ant colony for a particular myrmecophile.

Formerly, myrmecophiles had been categorised by the degree of acceptance in the ant colony as synechthrans, synoeketes, symphiles and true parasites (Wasmann 1890, 1896). This nomenclature is now considered as outdated because several organisms fit in more than one category. Today, it is common to distinguish myrmecophiles, which are only occasionally tended by ants (facultative interaction), from those that invariably depend on ants, at least during some life-stages (obligate association). Relationships may range from mutual benefaction (mutualism) to unidirectional impairment (parasitism), and taking lycaenid butterflies (Lepidoptera: Lycaenidae) as an example, we find the whole span of interaction types from mutualism (Fiedler and Saam 1995) to obligate parasitism (Wardlaw et al. 2000) within one taxon (Pierce and Young 1986; Pierce et al. 2002).

Since the extensive work of Wasmann (e.g. Wasmann 1903, 1913; Wasmann and Brauns 1925), many myrmecophiles have been described, and among them are numerous beetle species (e.g. Kistner 1993; Päivinen et al. 2002). Recent investigations involve, for example, the families Staphylinidae, Pselaphidae (Akino 2002), Scarabaeidae (Vander Meer and Wojcik 1982) and Coccinellidae (Orivel et al. 2004).

Associations of paussine beetles (Carabidae: Paussinae) with ants have been reported early in literature (Dohrn 1851; MacLeay 1838) and were most thoroughly studied by Wasmann and his contemporaries (e.g. Eidmann 1937; Escherich 1898, 1899b, 1907; Reichensperger 1924; Van Emden and Wasmann 1925; Wasmann 1890, 1903, 1906, 1913, 1920, 1929, 1934). Afterwards, investigation of the behavioural aspects of the taxon diminished.

Investigating ant guests is particularly interesting, as they can help to understand recognition mechanisms and their deception. Among myrmecophilous arthropods, Paussinae deserve special attention, as the origin of myrmecophily in the group is still unclear, and Paussini combine conspicuous adaptations, which are displayed by diverse other groups of myrmecophiles.

While the taxonomy and biogeography of paussines are fairly well examined (e.g. Ball and McCleve 1990; Darlington 1950; Deuve 2001a, b; DiGiulio et al. 2003; Luna de Carvalho 1989; Nagel 1986b, 1987b; Stork 1985), reports of behaviour and ant–paussine interactions are scarce and often were by-products of taxonomic investigations. We provide a comprehensive review of the known facts about the association of ant nest beetles and their hosts to spark interest in these rare beetles and encourage field observations. Beyond this, we want to contribute to the understanding of myrmecophily—not only in paussines—by discussing ant nest beetle biology in the context of other myrmecophilous arthropod groups.
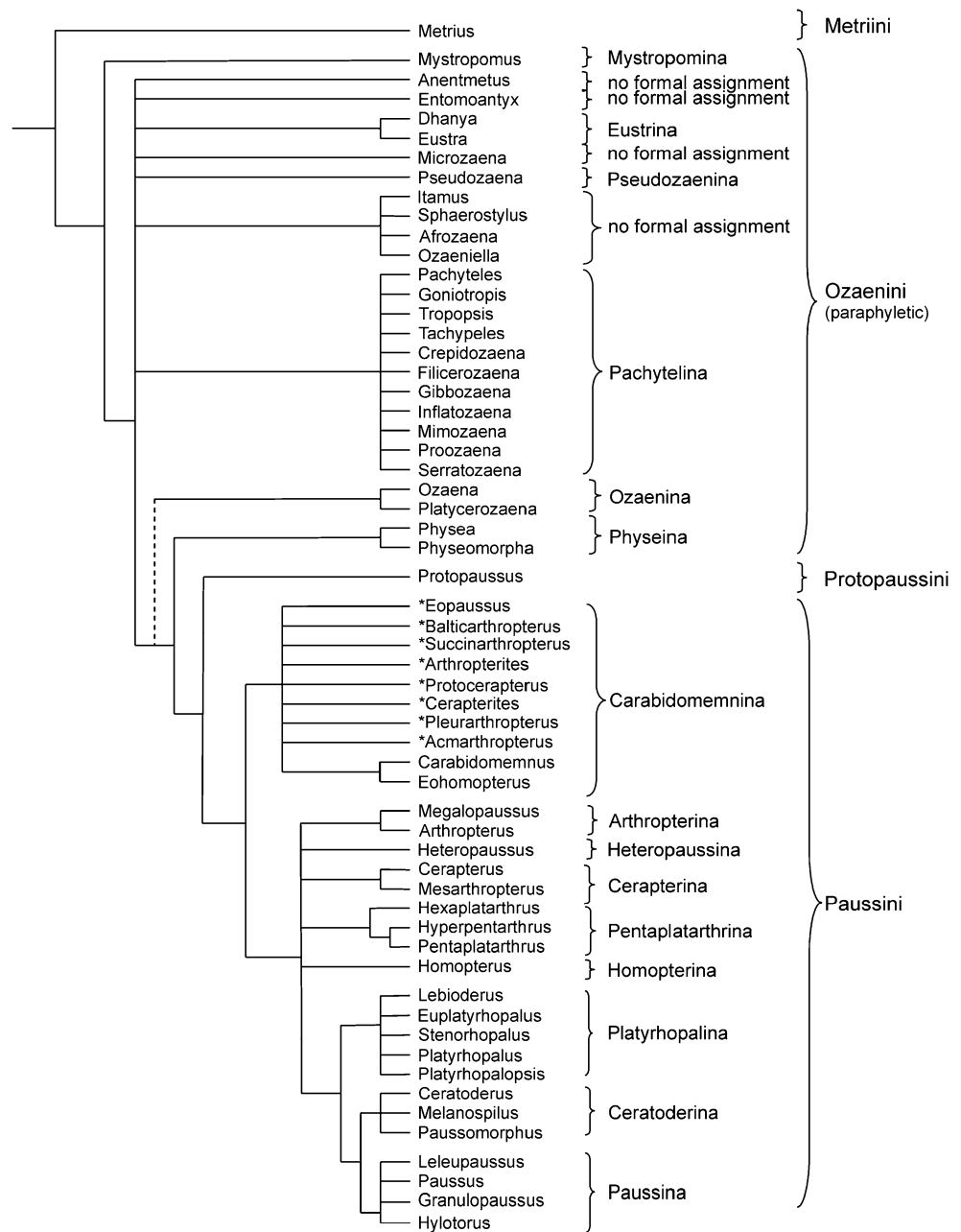
General morphology

The subfamily Paussinae comprises Metriini, Ozaenini, Protopaussini and Paussini (Fig. 1), which are small or medium sized (2.8–22.0 mm) and predominantly brownish. The body shape of Metriini and Ozaenini (Fig. 2) is similar to those of other carabids, but some genera display characters that call to mind myrmecophilous adaptations of other beetles, such as crassate antennae, reduction in tactile setae or flattened body and legs. The body shape of Protopaussini and Paussini is either slender or compact and reflects two different morphological strategies of integration in host colonies, which will be described later on. Many species of the tribe Paussini are characterised by enlarged antennae (Fig. 2). Like most nest-inhabiting myrmecophiles, paussines are not shaped like an ant, i.e., are not myrmecomorphic. Morphological ant-resemblance—although frequent in ant guests—seems to be restricted to species wandering near ant trails outside the nests (Cushing 1996; McIver and Stonedal 1993; Taniguchi et al. 2005; Wasmann 1925; Wheeler 1960).

Distribution and activity pattern

Paussines are found in all continents except Antarctica, but their main distribution is restricted to subtropical and tropical areas, with the highest diversity in the paleotropics (see Appendix). The Nearctic Metriini are extratropical, while a few Ozaenini, Protopaussini and Paussini reach the southernmost parts of the Nearctic and Palearctic regions.

Fig. 1 Hypothesised phylogenetic relationships of Paussinae genera based on the current knowledge of adult and larval structural characters (amended from DiGiulio et al. 2003). Fossil genera are marked in *asterisks*
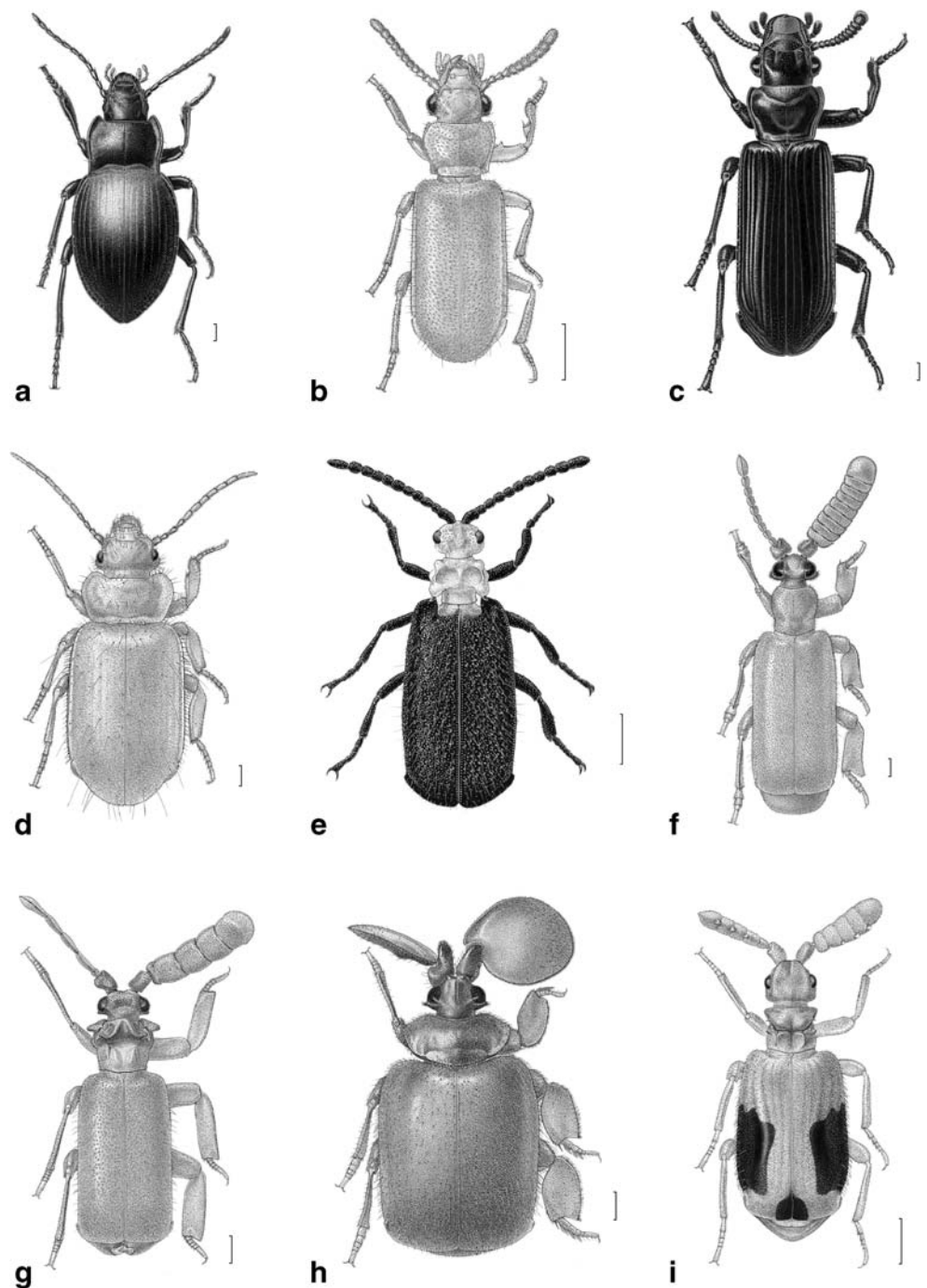

Amber fossils from the European Baltic and the North Sea area and fossils from lacustrine deposits from Germany document that Paussini once were distributed in areas where they are extinct today (Nagel 1987b; Wappler 2003; Wasmann 1929).

Dominican (West Indian Island of Hispaniola) and Mexican amber fossils (Chiapas) originated in similar settings and document an early Tertiary distribution at the southern edge of West Laurasia (Nagel 1987b, 1997; Solorzano Kraemer 2006). The ranges of some *Paussus* species correspond to specific vegetation zones, thus indicating an association with large-scale climatic and ecological conditions (Nagel 1986a, 1987a). An ecore-gional, rather than a host ant-related dependency of the beetles' distribution, is furthermore indicated by the northern distribution limit of *Paussus favieri* in southern France, which is situated further South than the distribution limit of its main host ant (Le Masne 1961a).

Metriini and Ozaenini are found under stones, fallen trees and bark and in rotten wood, leaf litter and humus. Paussini are usually found in the ground level zone of the vegetation and were mostly collected from subterranean ant nests. The presence of paussines on trees, however, is indicated by sporadic observations so that one can assume Paussini to settle in their host ants' nest, irrespective of its location (Keller 1892; Wasmann 1892, 1915). Apart from

Fig. 2 Habitus of adult Paussinae. **a** *Metrius contractus* Eschscholtz 1829; **b** *Pachyteles gyllenhali* (Dejean 1825); **c** *Platycerozaena* sp.; **d** *Physea hirta* LeConte 1853; **e** *Protopaussus almorensis* Champion 1923; **f** *Arthropterus* sp.; **g** *Pentaplatarthrus gestroi* Kolbe 1896; **h** *Platyrhopalopsis picteti* (Westwood 1874); **i** *Melanospilus bensoni* Westwood 1845. *Scale bar* 1 mm. All beetles are displayed with the right legs and antennae at their broadest view and the left extremities at their narrowest view. Drawings by E. Weber, except *Protopaussus* (by S. Flachsmann)

ant nests, male Paussini are captured at light traps, whereas females are rarely collected in this manner. Various other trapping methods yielded only low numbers of Paussini, which, however, frequently represented species not normally recorded at light traps (Nagel 2004; Wagner 2000).

The activity of ant nest beetles (presence outside ant nests) depends on seasonal climatic conditions. Direct triggers might be humidity, temperature or day length, which also influence ant colonies, and thus indirectly affect paussine activity. The extratropical Metriini are active during the spring and summer periods in California (Larochelle and Larivière 2003). In winter rain areas, subtropical or tropical seasonal climates, very few, if any, Paussini are observed during the dry season, whereas they become more abundant with thundery atmosphere and rain (Dohrn 1851; Escherich 1898; Kaupp and Rödel 1996; Kistner 1982; Leston 1978; Nagel 1986a, 1987a; Reichensperger 1948). In the inner tropics of Africa, Paussini are active throughout the year but with peaks of abundance (Reichensperger 1948). Regarding the circadian

activity, most paussines are crepuscular or nocturnal, although diurnal species exist as well (Batelka 2000).

Myrmecophily in the taxon Paussinae

Since the first comprehensive taxonomic treatments of ant nest beetles had been written (De Chaudoir 1868; Westwood 1833), almost 800 species have been assigned to the subfamily (Deuve 2004, 2005; Lorenz 2005; Nagel 2003, 2006). Similar to what is observed in the New World Scarabaeinae tribe Phanaeini (Philips et al. 2004), myrmecophily has only evolved in the derived groups of the taxon Paussinae, i.e. Paussini, Protopaussini, and the ozaenine Physeina, which are presumed to be the sister-group of the Paussini (DiGiulio et al. 2003; DiGiulio and Moore 2004; see Appendix). The Physeina are intermediate between the basal Ozaenini and the Paussini in terms of behaviour and morphology. While the association of *Physea* with *Atta* Fabricius 1804 (Myrmicinae) is a derived character, the burrowing ability of the larvae and the adults' prey spectrum are basal ozaenine features (DiGiulio and Vigna Taglianti 2001; DiGiulio et al. 2003; Eidmann 1937; Van Emden 1936). Protopaussini are proposed to be myrmecophilous because of the form of body and mouthparts and the presence of trichomes[1] on the body (Nagel 1997). Other paussines are thought to be free-living predators of arthropods, and a specialised larval trapping behaviour in the ozaenine genus *Pachyteles* (see paragraph "The life stages of paussines") indicates that obligate myrmecophily in paussines may have evolved from this independent lifestyle. Structural traits, such as the larval terminal disk of the common ancestor of all Paussinae, suggest multiple evolution of myrmecophily from pre-adapted ancestors in the tribes Ozaenini, Protopaussini and Paussini (DiGiulio and Vigna Taglianti 2001). Multiple evolution is also considered as the best explanation for myrmecophily in Ptininae (Coleoptera: Bostrichoidea), but in contrast to the Paussinae, myrmecophilous genera are basal in the Ptininae (Philips 2000). The current knowledge on phylogenetic relationships in Paussinae, however, does not contradict a monophyletic origin of myrmecophily (Ball and McCleve 1990; DiGiulio et al. 2003), as it is presumed for the scarabaeine Phanaeini (Philips et al. 2004).

Fossils of Protopaussini and Paussini date from the Paleogene and Neogene [Baltic amber, Eocene, 40–50 Ma; German lacustrine sediments, Eocene, 44–45 Ma; Dominican amber, Miocene to Eocene, 15–45 Ma; Mexican amber, Miocene-Oligocene border, 22–26 Ma; Poinar (1992);

Solorzano Kraemer (2006); Wappler (2003); Weitschat and Wichard (2002)] and their structural similarity with recent taxa suggest that myrmecophily in paussines already existed in the Early Tertiary. This assumption is supported by the presence of myrmecophilous structures, such as trichomes, crassate antennae, cephalic horn, or lack of tactile setae[2] in fossils (see Appendix). Furthermore, the display and close contact of a *Formica flori* worker with *Eopaussus balticus* in a piece of amber is similar to the positioning of recent ants and Paussini at contact and might indicate some kind of association, especially when considering the boat-shaped, trichome-bearing antennal club of the latter. The presence of mold particles (remnants of rotten wood typically found in ant nests) and an ant larva in amber pieces containing paussines further indicates an early association (Wasmann 1929).

Paussini are most frequently associated with Myrmicinae and Formicinae, which derived from a common ancestor during Early to Mid-Cretaceous, 125 to 75 Ma (Moreau et al. 2006). The oldest fossils of myrmecophilous Paussini date from the Early Eocene (50 to 45 Ma, see above), but the common ancestor of the Paussini and Protopaussini must have been present earlier. Thus, it seems reasonable to assume its existence concurrently with the highest diversification period of the main ant lineages, which occurred 100 to 60 Ma.

The life stages of ant nest beetles

In this section, we deal with the different life stages of ant nest beetles: adults, eggs, larvae and pupae. As only few investigations of paussine larvae are available, we merge morphological and behavioural data in one section and focus on adult ant nest beetles in the remaining chapters.

In the seasonal tropics, adult Paussini occur outside ant nests in increased numbers at the beginning of the rains, simultaneous with ant swarming. Thus, Paussini move to a new host colony when ant worker activity is increased, which might enhance adoption at the entrance of the colony. A similar activity pattern has been observed in North American *Cremastocheilus* beetles (Scarabaeidae), which disperse from the host colonies with the first summer rains to form large aggregations for mating (Alpert 1994). As males of certain paussine species may be abundant at light traps at dispersal time, whereas

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[1] Specialised tufts of hair on some insects that serve to dispense chemical secretions from underlying glands (Resh and Cardé 2003).

[2] Setae are defined as hollow, often slender, hair-like cuticular projections (Gordh and Headrick 2001), which include the bristle-shaped mechanosensory *sensilla chaetica* and chemosensory *sensilla basiconica*.

females are not, one may infer different distribution practices for the two sexes, and considering that other capturing techniques yielded insignificant numbers of beetles, female Paussini might only rarely, or not at all, leave their natal colonies. Copulation has been observed at the end of the dry season and during the transition period between dry and wet season inside or in front of ant nests (Escherich 1907; Fairmaire 1903; Nagel 1987a) and in springtime in the Spanish winter rain area (Rosenhauer 1856). In captivity, a single male copulated with up to five females (Péringuey 1883). The mechanism of mate location remains unknown, but based on the recovery of more than 100 Pentaplatarthrus gestroi from one colony and similar records, Reichensperger (1948) suggested aggregation in the so-called central or mating colonies, where increased numbers of individuals converge for mating. Male ant nest beetles are likely to die shortly after mating and females after oviposition (Reichensperger 1948). The maximum recorded survival time of non-feeding beetles in captivity was 60 days, which, however, does not indicate natural life spans.

Paussine eggs have been investigated by several authors (DiGiulio and Vigna Taglianti 2001; Kaupp et al. 2000a, b; Luna de Carvalho 1959, 1989; Moore and DiGiulio 2006). Captive female Goniotropis kuntzeni started to lay eggs about 1 month after the onset of summer rains in Arizona (Moore and DiGiulio 2006), and Pentaplatarthrus getroi deposited eggs at the end of the rainy season in Zimbabwe (P. Nagel, personal observations). The number of eggs recovered from preserved or freshly caught specimens of several paussine genera roughly corresponds to the egg numbers of other carabids (Kaupp et al. 2000a; Thiele 1977). External egg morphology has been studied and compared to other carabids, using shell thickness, mesh sizes, and shapes of the chorion grid layer to characterise the eggs. An internal, spongy air-filled layer surrounds the eggs of several Ozaenini and Paussini. This structure may be favourable under distinct dry and wet conditions, respectively, by buffering water loss and adsorption (Kaupp et al. 2000a).

Paussini and Physeina spend their entire juvenile stages inside ant nests (DiGiulio and Vigna Taglianti 2001; DiGiulio and Moore 2004; Nagel 1987a). The larvae of Paussini are blind and physogastric with reduced legs (Fig. 3). This probably constitutes an adaptation to life within ant colonies, where mobility is of marginal importance. Physogastry has also been observed in termitophilous staphylinids, where the bloated abdomen imitates the habitus of a termite worker (Wilson 1971), and myrmecophilous paussine larvae might deploy the same mechanism. Further myrmecophilous adaptations in larval Paussini are the bristled third antennal segment and mouthparts, the development of a terminal disk from the last three segments plus the urogomphi[3], which is also present in larvae of Metriini and Ozaenini, and its equipment of various sensilla types (Arndt and Beutel 1994; Arndt 1998; DiGiulio et al. 2000, 2003; DiGiulio and Moore 2004; Luna de Carvalho 1959, 1992; Reichensperger 1948; Van Emden 1922; Vigna Taglianti et al. 1998; Wasmann 1910; Fig. 3b).

In the ozaenine Physea setosa, the terminal disk apparently only serves for fixing the larva, which is ready for pupation, to the ground (Eidmann 1937). In contrast, in the non-myrmecophilous genus Pachyteles, the behavioural importance of the terminal disk is well-documented by laboratory experiments: Pachyteles larvae live in self-dug burrow chambers, facing inwards and closing the entrance with the terminal disk (phragmosis). Small arthropods are strongly attracted by a secretion on the terminal disk, approach and touch the disk and are grabbed by the closing disk. The larva then quickly leaps backwards with the anterior part of the body, seizing the prey with the mandibles and dragging it into the burrow to feed on it (DiGiulio and Vigna Taglianti 2001).

Anterio-dorsal structures in larvae of Lycaenidae, the dorsal nectary organs, which also secrete ant-attracting liquids, have been identified as myrmecophilous organs, which are frequently licked by the host ants, and contribute to the adoption and tending of the larva (e.g. Pierce et al. 2002). The behavioural observations of Pachyteles suggest an analogous function of the terminal disk in myrmecophilous paussines, and thus indicate the evolution of myrmecophily in ant nest beetles from predatory ancestors (Wasmann 1910, 1918a).
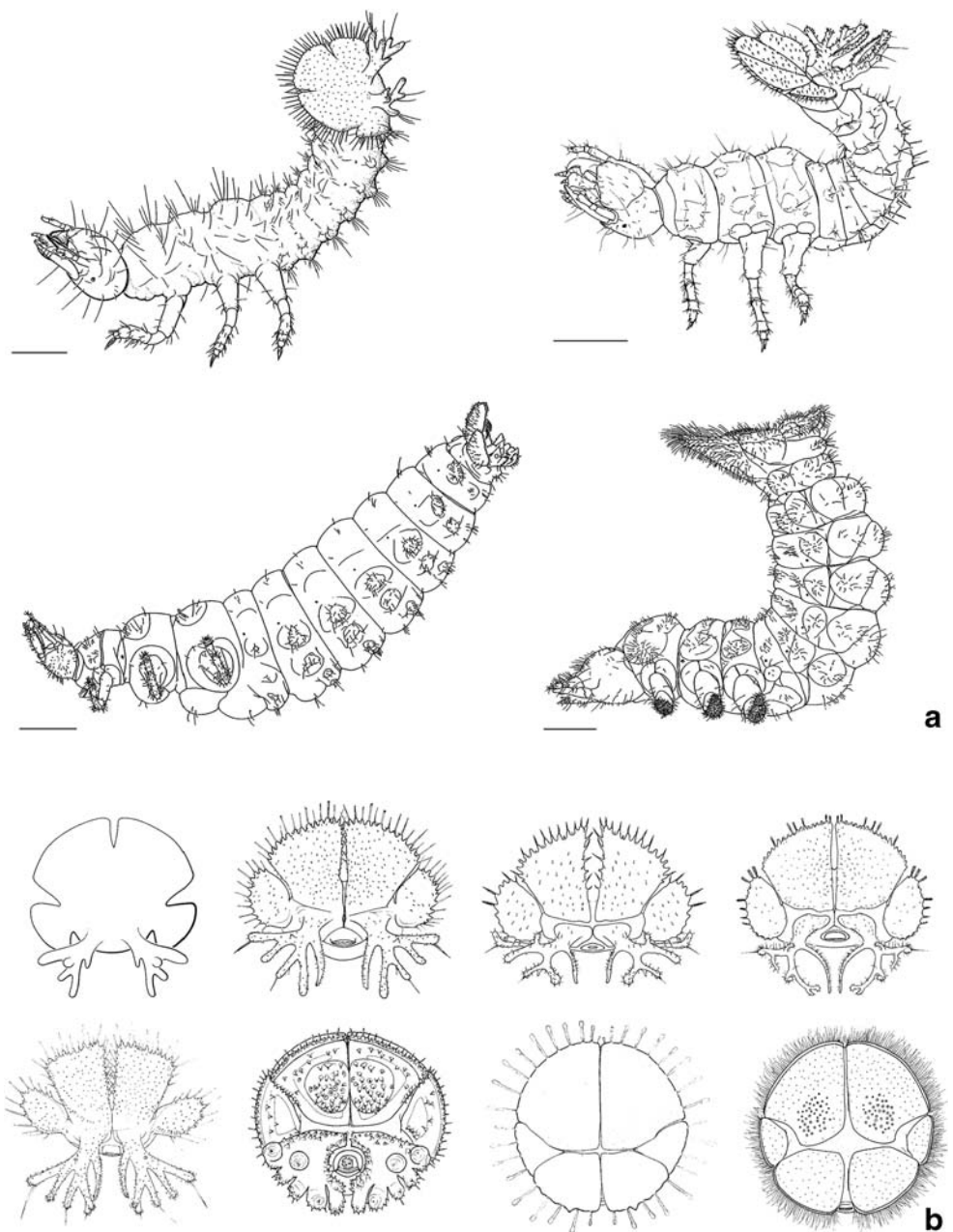
Pupal chambers with Physea pupae were found in the soil between fungus gardens of Atta ants (Eidmann 1937; Van Emden 1936), and recently, Pachyteles pupae were also recorded from subterranean pupal cells (DiGiulio and Vigna Taglianti 2001). Detailed descriptions of Pachyteles, Physea, Paussus and Platyrhopalopsis pupae have confirmed their general shape of ground beetle pupae (pupa exarata; Böving 1907; Luna de Carvalho 1951, 1959, 1977a), but differences between basal and derived taxa are useful for phylogenetic reconstruction (DiGiulio et al. 2007).

Alimentation

All members of the subfamily Paussinae are predators, but an obligate dependence on ant prey is only found in the tribe Paussini. Species of the ozaenine genera Pachyteles and Goniotropis are not associated with ants and their

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[3] Paired dorsal processes that project from the posterior margin of the ninth larval tergite (Resh and Cardé 2003).

Fig. 3 a Habitus of larvae of Paussinae. *Top left*: *Metrius contractus* Eschscholtz 1829; *top right*: *Pachyteles digiulioi* Deuve 2000; *bottom left*: *Physea setosa* Chaudoir 1868; *bottom right*: *Platyrhopalopsis melleii* (Westwood 1933). *Scale bar* 1 mm. b Terminal disks of larvae of Paussinae. *Top, left to right*: *Metrius contractus*, *Pachyteles digiulioi*, *Pachyteles mexicanus* (Chaudoir 1848), *Itamus cavicola* (Moore 1978). *Bottom left to right*: *Goniotropis kuntzeni*, *Physea setosa*, *Arthropterus* sp., *Platyrhopalopsis melleii*. All drawings provided by Andrea DiGiulio

larvae trap small invertebrates with the terminal disk (DiGiulio and Vigna Taglianti 2001). In contrast, *Physea* larvae probably prey on ants and ant brood inside the brood chambers of *Atta* nests, whereas adult *Physea* feed on ant-guests in the waste chambers of the nest (Eidmann 1937).

The present knowledge on alimentation in Paussini only refers to adults (Le Masne 1961a, b, c). The beetles do not devour the whole ant prey but extract liquid and tissue by piercing the integument with the mandibles and mangling the body (Le Masne 1961a, c). The mouthparts of Paussini and Protopaussini are highly adapted for fluid feeding (Evans and Forsythe 1985). M.E.G. Evans (personal communication) described a highly developed cibarial-pharyngeal sucking pump in two *Paussus* species and noted that pre-oral digestion might not be necessary.

Adult Paussini feed on ant larvae (Escherich 1907; Le Masne 1961a, c; Péringuey 1886), ant eggs (Escherich 1899b) and live adult ants (Le Masne 1961a, b, c). The observed beetles inserted their slender, acute mandibles into the abdomen of the ant and sucked the body dry. Kistner (1982) misinterpreted this report, writing that the beetle bit

off a piece of the gaster and, after freeing the ant, fed on the contents of the retained piece. Ants that were attacked by paussines never reacted aggressively. During suction, the beetle's mandibles remained inserted in the body without moving, and the maxillary and labial palpes stayed in contact with the ant body. In different species of ant nest beetles, these mouthparts are very diverse in shape, and therefore possibly contribute to the success of prey capture. After being released, the tortured ants stayed close to the beetle and finally died within a few days.

The beetles feed neither on the ants' stored food nor on their waste material (Le Masne 1961c). Food exchange between ants and their guests—although frequently observed in other myrmecophiles (Hölldobler and Wilson 1990)—is not reported for paussines. The beetles also do not steal from ants engaged in trophallaxis, as certain staphylinids or silverfish do (Le Masne 1961a, c; Wasmann 1898).

Due to the rarity of ant nest beetles, only few authors observed live specimens in the laboratory and all attempts at captive breeding have been unsuccessful, as most beetles did not accept food (Escherich 1898; P. Nagel, personal observations). Successful feeding is only reported for few species (Escherich 1898; Le Masne 1961a, c; Péringuey 1886).

Parasitism

Although paussines are accepted and integrated in their host ant colony, they are detrimental to the colony preying in ants and their brood. Such a symbiosis, in which one partner lives at the expense of the other—in this case, a paussine affecting an ant colony—is referred to as parasitism (Hölldobler and Wilson 1990).

Paussini, however, provide a secretion to the ants, which Wasmann (1903) considered as sufficient compensation for the loss of brood to make the relationship mutually beneficial.

This kind of mutualism, where ants are sufficiently rewarded for their tending, is realised in caterpillars of non-parasitic myrmecophilous lycaenid species, which supply their hosts with a highly nutritive secretion (Fiedler and Maschwitz 1988; Pierce et al. 2002). Predatory lycaenid species, in contrast, provide only vestigial rewards to the ants, and not only prey heavily on the colony, but also compete with the ant larvae for worker attention. In these species, the secretion provided is only a means of deception, not a true reward (Wardlaw et al. 2000). A similar situation is assumed for ant nest beetles because the degree of predation seems to exceed the advantage, the ants take from the secretion (Escherich 1898). As mutualistic relationship requires that both partners receive a net benefit from the interaction (Bronstein 2001; Hoeksema and Bruna 2000), we thus consider Paussini as ant parasites and not as mutualists.

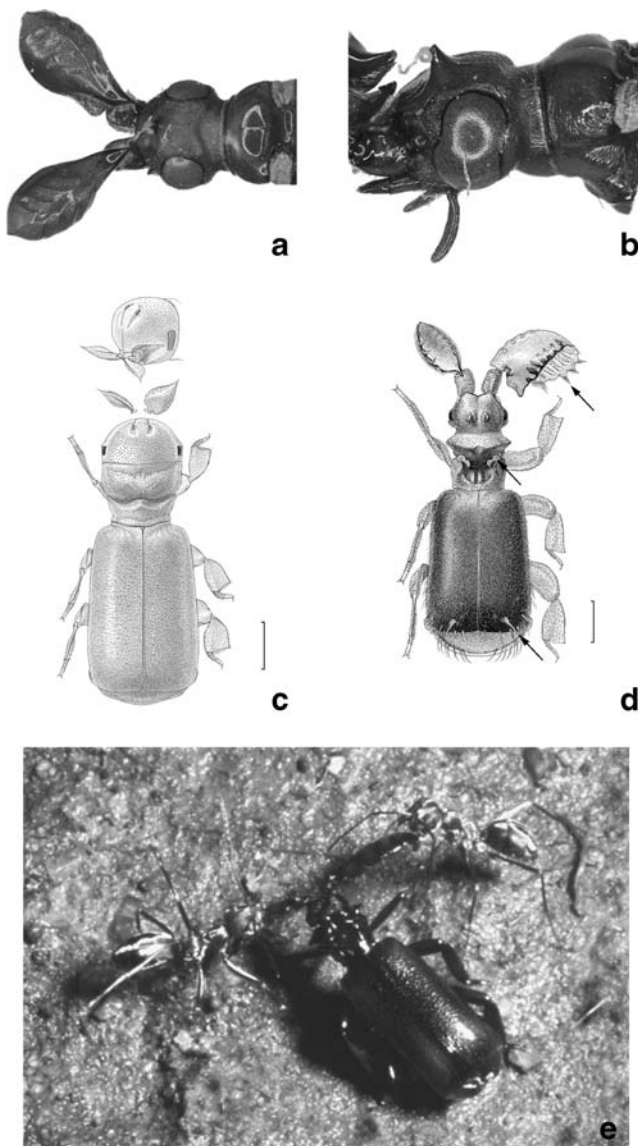## Adaptations to myrmecophily

Myrmecophilous organs and other morphological adaptations

It is crucial for ant parasites to avoid triggering aggression in ants. Several ant parasites secrete appeasement allomones that are ingested by the ants (Fiedler and Maschwitz 1989; Hölldobler 1970). Due to the observation of ants frequently licking Paussini, it was presumed that these also secrete appeasement substances (Wasmann 1890). However, there is no evidence for the ingested secretion to be derived from certain glands so that the terming of "myrmecophilous organs" is based on a combination of behavioural and morphological data and an analogy with other myrmecophiles.

Complexes of unicellular, epidermal secretory glands are situated on antennae, front, prothorax and on the tip of the abdomen of ant nest beetles (Wasmann 1903; Yung 1938). These gland complexes seem to be consistent with the epidermal gland types described for other insects, for some of which a myrmecophilous character is assumed, too (Alpert 1994; Cammaerts 1974; Noirot and Quennedey 1974, 1991).

Inside the antennal club of *Paussus cucullatus* Westwood 1850 are six segmentally organised secretory ducts, which lead to a uniform gland complex. Thickened antennae with glands were also reported from the myrmecophilous beetle *Claviger testaceus* Preyssler 1790 (Pselaphidae; Cammaerts 1974), and within carabids, *Platynus assimilis* (Paykull 1790) and the myrmecophagous *Siagona europaea* Dejean 1826 possess gland complexes as well (Giglio et al. 2005; Weis et al. 1999). Suggestions about the function of the antennal gland secretion in these species include lubrication and protection of sensillae and cuticle as well as a pheromonal relevance, but no evidence for an ant-related role is provided (Giglio et al. 2005). Within Hymenoptera, *Solenopsis invicta* Buren 1972 females pour a paste-like secretion of unknown function from antennal glands (Isidoro et al. 2000), and a similar secretion was recently revealed to contain symbiotic *Streptomyces* bacteria in *Philanthus* Fabricius 1790 females (Crabronidae), by means of which the cocoons are protected from fungal infestation (Kaltenpoth et al. 2005). It is doubtful, however, if myrmecophilous paussines provide their host ants or own clutch with a brood-protecting secretion.

Fig. 4 **a**, **b** Head of *Paussus cridae* Gestro 1916 with frontal secretion horn connected with the frontal gland, to which a strand of dried-up secretion is attached. **a** dorsal view, **b** lateral view. **c**, **d** Different types of body shape in myrmecophilous Paussini. Right extremities are displayed at their broadest view, left extremities are displayed at their narrowest view. *Scale* 1 mm, drawing: Eva Weber. **c** *Hylotorus blanchardi* Raffray 1882 representing the protective type with smooth body and short, retractable extremities. **d** *Paussus paulmuelleri* Nagel 1983 representing the symphile type with long extremities and trichome tufts (indicated by *arrows*). **e** Two *Anoplolepis custodiens* (F. Smith 1858) ants yanking the antennae of a *Pentaplatarthrus gestroi* Kolbe 1896

Besides the antennal glands, a paired frontal gland connected to a paired, sometimes fused pore on the vertex is present in many derived Paussini (Paussina; Fig. 4a–d). A similar frontal gland has also been observed in some ant-associated *Cremastocheilus* beetles, and in both taxa, the organ is suggested to be relevant in the context of myrmecophily (Alpert 1994; Escherich 1898).

Prothoracal myrmecophilous glands in Paussini are located at a transversal cleft equipped with trichomes and discharge the secretion through a cribellum into the cavity or into the trichomes. In *Pentaplatarthrus*, the abdominal myrmecophilous organs are situated laterally from the eighth abdominal segment to the pygidium, and their ducts meet the surface at the base of the pygidial trichomes (Yung 1938). Additionally, in several ant nest beetle species, the elytra are filled with secretory glands and thus may be further myrmecophilous organs, which would constitute a progress in myrmecophilous adaptation (Yung 1938).

The described epidermal gland complexes in ant nest beetles call to mind the Pore cupola organs and Dish organs, which aid in mediating myrmecophily in lycaenid caterpillars (Pierce et al. 2002). In both cases, the composition of the appeasing secretion is unknown (Fiedler and Maschwitz 1989; Wasmann 1896). In lycaenids, a relation with the honeydew-like secretion of the dorsal nectary organs (Fiedler and Maschwitz 1988, 1989; Pierce et al. 2002) might be supposed. In contrast, the paussine myrmecophilous secretion has been assumed to be a fatty compound that may contribute to the shiny russet or dark auburn colour of Paussini, which characterises many myrmecophiles (Wasmann 1896, 1920). Possibly a protein fraction may also be present (Kistner 1982), as it is the case in *Lomechusoides strumosus* (Fabricius 1775; former generic assignment to *Lomechusa* Gravenhorst 1806) adoption gland secretion (Hölldobler and Wilson 1990) and in the dorsal nectar organ secretion of myrmecophilous lycaenids. In the latter, the amount and mixture of amino acids seems to reflect the intimacy of the association with attendant ants, and interspecific differences in the composition are thought to allow for the gustatory preferences of the major host (Daniels et al. 2005).

While some lycaenid larvae are able to regulate the number of attending ants by varying the rate of secretion exoposition (Axén et al. 1996; Leimar and Axén 1993), there are no hints for such a mechanism in ant nest beetles.

Distinct trichomes, which are arranged in close vicinity of the myrmecophilous glands (Yung 1938), are common in paussine and staphylinid ant-guests. In Protopaussini and Paussini, trichomes may be present in all body parts, except the ventral abdomen, but are most obvious on the antenna, prothorax, metasternum, elytra and pygidium. In Metriini, Ozaenini and other Carabidae, trichomes are lacking (Darlington 1950). The long bristles on the surface of *Physea* may consist of several bristles sticking together and are likely to be trichomes, too. The function of the trichomes is to enlarge the surface to be wetted with the secretion and furthermore to protect the beetles from damage caused by the ants, as these gnaw the hairs and glandular openings and occasionally bite off secretion-impregnated trichomes (Reichensperger 1924; Wilson 1971; Yung 1938).

Adult Ozaenina, Physeina and Paussini lack most of the basic ground beetle equipment with "fixed" tactile setae[4] (Darlington 1950) but still possess various sensilla, most of which are presumably chemoreceptive (Nagel 1979). A large apical antennal sensory field of high sensilla density is discernible in several Ozaenina and all Paussini studied (Ball and McCleve 1990; Ball and Shpeley 1990; Nagel 1979). Most probably, these sensilla are crucial, not only for mate finding but also for the association of Paussini with ants.

On the basis of myrmecophilous organs and other morphological criteria, Paussini can be assigned to two different defensive strategies: the protective type and the symphile type (Wasmann 1913, 1925; Fig. 4c,d). The protective type (Trutztypus; Wasmann 1913, 1925; Fig. 4c) combines two or more of the following characters: compact, hard body, broad, retractable legs and crassate, broad or small, retractable antennae. These beetles, which bear few or no trichomes, an undivided pronotum and often protective mouthparts, usually are larger in size and belong to the less derived taxa within the Paussini (Nagel 1979, 1987a; Reichensperger 1948; Wasmann 1913), although strongly derived genera include small species of the protective type, too. This body shape provides effective protection against attacks and is used by other coleopteran social parasites as well (Rasa 1996). In contrast, the symphile type (Symphilentyp; Fig. 4d) is characterised by a slim body with long, slender extremities, a crenate or cleft pronotum, a flanged pygidium and numerous trichome tufts on various body parts. Paussini of the symphile type often have a more or less boat-shaped antennal club, numerous, yellow trichomes and secretion pores on the cephalus (Nagel 1979, 1987a; Reichensperger 1948).

The evolutionary sequence of myrmecophilous adaptations cannot be reconstructed with the currently known fossil record. All striking adaptations are already present in the oldest known Baltic amber fossils. However, phylogenetic evidence suggests that the loss of tactile setae, the tendency for crassate antennae and the development of an increased apical antennal sensory field formed part of the first morphological structures developed with myrmecophily. These characters are already present in the Ozaenina, which probably are the most basal myrmecophilous Ozaenini. Myrmecophagy in the form of fluid feeding with specialized mouthparts is suggested to have evolved in the next step, and it is an apomorphic feature of Protopaussini+Paussini. A reduced and wedged pedicel (antennomere 2) in the ancestor of the Paussini allowed for the extremely increased size of the antennal flagellum and the development of gland-bearing, heavy antennomeres. The

partial or complete fusion of antennomeres 3 to 11 occurred several times independently within the Paussinae, representing a typical parallelism (Nagel 1979).

Chemical mimicry

Myrmecophiles may imitate the habitus of their host as well as behavioural features, for example, characteristic antennation movements, by which staphylinid ant guests induce the feeding reflex of their host ant (Hölldobler and Wilson 1990; Wasmann 1898). Except for elytral colour patterns of few Paussina allegedly shaped like the body of an ant, none of these mechanisms are deployed by ant nest beetles (Wasmann 1925), which consequently are bound to use another mode of deception.

The most important recognition character in social insects is their pheromonal signature (Singer 1998; Vander Meer et al. 1998). By means of trophallaxis and grooming, members of an ant colony constantly exchange their recognition cues, thus forming a gestalt colony odour, which is used to distinguish nestmates from non-nestmates (Lenoir et al. 2001). Using chemical mimicry (sensu Dettner and Liepert 1994), parasites can move freely within their host colony and steal food or prey on the ant brood (Stowe 1988). Parasites may either acquire host-specific substances by means of physical contact (beetles: Vander Meer and Wojcik 1982; hymenopterans: D'Ettorre et al. 2002; Vander Meer et al. 1989) or consumption of host larvae (spiders: Allan et al. 2002; beetles: Dinter et al. 2002; ants: Liang and Silverman 2000) or synthesise the host specific substances by themselves (beetles: Geiselhardt et al. 2006b; syrphid flies: Howard et al. 1990). Furthermore, both strategies may be combined (butterflies: Akino et al. 1999; Schlick-Steiner et al. 2004; Schönrogge et al. 2004). Organisms, which—like Paussini—use different host species, are likely to adopt surface chemicals of the respective host (D'Ettorre et al. 2002; Vander Meer and Wojcik 1982), whereas self-production of compounds is frequently observed in host-specific cleptoparasites (Geiselhardt et al. 2006b; Howard et al. 1980). Chemical insignificance, however, may also help parasites to intrude host nests (ants: Lenoir et al. 2001). Preliminary chemical investigations revealed species-specific hydrocarbon patterns for a few Paussus species (authors, unpublished). A possible congruency with ant hydrocarbon patterns, as well as the origin of the chemicals, however, remains to be investigated. Such a congruency has been shown for another myrmecophilous carabid, Siagona europaea Dejean 1826, which has certain cuticular hydrocarbons in common with its prey ant. Furthermore, volatiles from different ant glands have been found on the beetle's cuticle after contact and consumption of ants, which are indicative of yet another mechanism of chemical defence and integration (Zetto Brandmayr et al. 2005)

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[4] The elytral series umbilicata of tactile setae is present in most species, and some Carabidomemnus display single tactile setae on the antennal scape (Luna de Carvalho 1966; Nagel 1983).

Table 1 Records of ants associated with Paussinae

Ant subfamily	Ant taxon	Paussinae taxon	Region
Dolichoderinae: Dolichoderini	*Dolichoderus bispinosus* (Olivier 1792) (also reported as *Monacis* Roger 1862, sp.)	*Homopterus steinbachi* Kolbe 1920 (6)	Neotropical
Dolichoderinae: Dolichoderini	*Iridomyrmex rufoniger* (Lowne 1865)	*Arthropterus* sp. (7)	Australian
Dolichoderinae: Dolichoderini	*Tapinoma erraticum* (Latreille 1798) or *T. simrothi* Krausse 1911 (reported as *T. erraticum* inclusive of *T. simrothi*)	*Paussus thomsonii* Reiche 1860 (reported as *P. verticalis* Reiche ssp. *cymbalista* Alluaud) (5)	SW Palaearctic
Dolichoderinae: Dolichoderini	*Technomyrmex foreli* Emery 1893 (reported as *T. albipes* Smith 1861 or *T. albipes* ssp. *foreli*)	*Paussus cochlearius* Westwood 1838 (4)	Afrotropical
Formicinae: Lasiini	*Anoplolepis* Santschi 1914 spp. (reported as *Plagiolepis* Mayr 1861, spp.)	*Pentaplatarthrus* spp., *Cerapterus concolor* Westwood 1850	Afrotropical
Formicini: Lasiini	*Lasius* Fabricius 1804, sp. (doubtful record)	*Paussus turcicus* Frivaldsky von Frivald 1835	Palaearctic
Formicinae: Plagiolepidini	*Lepisiota* Santschi 1926, spp. (mostly reported as *Acantholepis* Mayr 1861, spp.)	*Paussus* spp., *Carabidomemnus pallidus* (Raffray 1885), *Mesarthropterus wasmanni* (Reichensperger 1915), *Paussomorphus chevrolati* (Westwood 1852)	Afrotropical
Formicinae: Plagiolepidini	*Paratrechina* Motschoulsky, 1863, spp. (recorded as *Prenolepis longicornis* Latreille,1802, and *Paratrechina ellisii* Forel, 1891)	*Melanospilus bensoni* Westwood 1845, *Paussus* spp.	Oriental, Madagascan
Formicinae: Camponotini	*Camponotus* Mayr 1861, spp.	*Arthropterus* spp., *Paussus* spp.	Australian, SW-Palaearctic, Madagascan
Formicinae: Camponotini	*Camponotus ocreatus* Emery 1893 (a)	*Goniotropis kuntzeni* Bänninger 1927 (a)	SW Nearctic
Formicinae: Camponotini	*Polyrhachis bihamata* (Drury 1773) (b)	*Cerapterus herrei* Schultze 1923 (b)	Oriental
Formicinae: Notostigmatini	*Notostigma* Emery 1920, sp.	*Megalopaussus amplipennis* Lea 1906	Australian
Formicinae: Formicini	*Formica flori* Mayr 1868[a]	*Eopaussus balticus* Wasmann 1926[a]	Baltic amber
Formicinae: Formicini	Ant larva, probably of *Formica flori* Mayr 1868[a]	*Protocerapterus incola* Wasmann 1927[a]	Baltic amber
Dorylinae: Dorylini	*Dorylus* Fabricius 1793, sp. *Dorylus brevipennis* Emery 1895	*Paussus cridae* Gestro 1916 (8), *Paussus fallax* Péringuey 1892 (10)	Afrotropical
Ponerinae: Ponerini	*Hypoponera* aff. *truncata* (F.Smith 1860) (reported as *Ponera* aff. *truncata*)	*Platyrhopalus westwoodii* Saunders 1838 (3)	Oriental
Ponerinae: Ponerini	*Ponera* Latreille 1804, sp.	*Paussus favieri* Fairmaire 1851 (9)	SW Palaearctic
Ectatomminae: Ectatommini	*Rhytidoponera metallica* (F.Smith 1858) (reported as *Ectatomma metallicum*)	*Arthropterus brevis* Westwood 1850 (1, 2)	Australian
Myrmicinae: Attini	*Atta sexdens* (Linnaeus 1758)	*Physea setosa* Chaudoir 1868	Neotropical
Myrmicinae: Solenopsidini	*Pheidologeton diversus* (Jerdon 1851)	*Platyrhopalopsis melleii* (Westwood 1833)	Oriental
Myrmicinae: Solenopsidini	*Monomorium junodi* Forel 1910 (recorded as *M. delagoensis pretoriensis* Arnold 1944)	*Leleupaussus tetramerus* Luna de Carvalho 1962	Afrotropical
Myrmicinae: Solenopsidini	*Solenopsis geminata* (Fabricius 1804)	*Platyrhopalus acutidens* Westwood 1833	Oriental, S-Palaearctic
Myrmicinae: Tetramoriini	*Tetramorium* Mayr 1856, spp. (also recorded as *Xyphomyrmex* sp.)	*Paussus* spp.	Afrotropical, Oriental
Myrmicinae:	*Aphaenogaster swammerdami* Forel 1886	*Paussus* spp.	Madagascan

Table 1 (continued)

Ant subfamily	Ant taxon	Paussinae taxon	Region
Pheidolini	(sometimes reported as *Stenamma* [*Ischnomyrmex*] *swammerdami*)		
Myrmicinae: Pheidolini	*Messor* Forel 1890, spp. (also reported as *Atta barbara* Linnaeus 1767, *Aphaenogaster barbara capensis* Mayr 1862)	*Pentaplatarthrus* spp., *Carabidomemnus pallidus* (Raffray 1885), *Paussus* spp.	Afrotropical
Myrmicinae: Pheidolini	*Pheidole* Westwood 1839, spp. (early records also as *Oecophthora* Heer 1852, spp.)	*Paussus* spp., *Platyrhopalus denticornis* (Donovan 1804), *Hylotorus* spp., *Granulopaussus* spp.	Palaearctic, Madagascan, Afrotropical, Oriental
Myrmicinae: Cremato-gastrini	*Crematogaster* Lund 1831, spp.	*Paussus spinicola* Wasmann 1892, *Ceratoderus venustus* Hisamatsu 1963	Afrotropical, E-Palearctic
Myrmicinae: Myrmicariini	*Myrmicaria* Saunders 1842, spp.	*Heteropaussus* spp., *Cerapterus* spp., *Pentaplatarthrus gestroi* Kolbe 1896	Afrotropical, Oriental

The sequence of taxa and their nomenclature is based on Bolton (1995, 2003) for ants and Nagel (2003) and Lorenz (2005) for beetles. The original records are given in brackets whenever they differ from the current valid names. In most cases, the records refer to findings of beetles in the ants' nest. The records are basically taken from Reichensperger (1948); Van Emden and Wasmann (1925); Wasmann (1894, 1904, 1911), and supplemented by further literature data, unpublished data from museum specimens, and the authors' own records. References of the rare records of Dolichoderinae, Ponerinae and Ectatomminae as host ants and findings with *Dorylus* sp. are given in the following: (1) Lea (1910), (2) Wasmann (1911), (3) Gestro (1892), (4) Van Emden and Wasmann (1925), (5) Hellmann (1985), (6) Darlington (1950), (7) Sloane (1933), (8) Luna de Carvalho (1989), (9) Alonso Zarazaga (1980); Murria (1994), (10) Specimen in Bulawayo Natural History Museum, *teste* Nagel. The ant and paussine species marked (a), (b) were found simultanuously on the same tree, but a possible association remains speculative.
[a] Fossil taxa

Host specificity and host location in ant nest beetles

Ant-guests frequently choose ecologically dominant ant species with long-lived colonies as their hosts (Fiedler 2001). Like lycaenid caterpillars (Fiedler 2001), Paussini are most frequently associated with ants belonging to the subfamilies Myrmicinae and Formicinae (Nagel 1987a; Table 1). Associations of ant nest beetles with Dolichoderinae, Ponerinae and Ectatomminae have rarely been reported. Within Myrmicinae, Formicinae and Dolichoderinae, trophobiosis is widely distributed and might constitute the basis for the development of ant–myrmecophile interactions, as these ants are more likely to accept rewarding secretions (Fiedler 2001). Ant nest beetles do not seem to have species-specific relationships with ants (DiGiulio and Vigna Taglianti 2001; Nagel 1987a). Some species are found in nests of several different ant species, e.g. *Paussus favieri* has been reported to be associated with *Pheidole pallidula*, *P. megacephala* Fabricius 1793, *Messor barbarus*, *Camponotus lateralis* and *Ponera* sp. (Alonso Zarazaga 1980; Kistner 1982; Wasmann 1894). On the other hand, a single ant species may host several different paussine species (Table 1). On the genus level, species of the myrmicine genus *Pheidole* have been reported most frequently as hosts of ant nest beetles.

Besides the myrmecophilic life habit with apparent adaptations to deceive the communication of ants, in some arthropods like the aleocharines (Staphylinidae), species of the same taxonomic group have also gained access to termite nests. Regarding microclimate, social behaviour and brood amount, termite nests provide conditions, which are similar to those found in ant nests. The only indication for an association of paussines with termites (Kistner 1982; Luna de Carvalho 1977b), however, is likely to be accidental because this particular species usually lives with *Pheidole* ants (Wasmann 1918b). Other records of Paussini with termites are spurious, as ants occasionally occupy parts of termite mounds (Nagel 1987a). As Paussini prey on the brood and do not depend on food items of the colony, which in termite nests are plant-derived, one wonders why these beetles have not found their way into termite colonies. One possible explanation may be the different pre-adaptations of the communication systems of ant nest beetles and termites.

Adult Paussini might use ant-derived olfactory signals for locating host-ant colonies (Reichensperger 1948), and host trail pheromones or other airborne semiochemicals are likely candidates.

Numerous guests of army ants, as well as larvae of the carabid *Anthia* (*Termophilum*) *sexmaculata* Fabricius 1787 follow chemical trails laid by their host (Dinter et al. 2002; Wilson 1971), and *Paussus favieri* adults show this behaviour, too. In the laboratory, the beetles followed trails of the host ant *Pheidole pallidula*, but ignored trails of the non-host genera, suggesting that ant nest beetles are able to discriminate the trail pheromones of host from non-host ant

species (Cammaerts et al. 1989, 1990; Cammaerts and Cammaerts 1992).

Paussus favieri is less sensitive to the trail pheromone of its host ant than the ants themselves: The optimal pheromone concentration to make the beetle follow a trail is four to ten times higher than for ant workers. Beetles, however, avoid even higher concentrations, which is interpreted as protective evasion of accumulations of aroused ants (Cammaerts et al. 1990). In addition, *Paussus favieri* follows trails of its host ant further than ant workers do, which was also observed in a staphylinid ant-guest (Quinet and Pasteels 1995). The beetle, thus, is more likely to find the respective host colony due to reduced risk of trail loss. Ants possess various glands, which may be involved in trail laying (Billen and Morgan 1998). In the investigation of Cammaerts et al. (1990), artificial trails were laid using isolated poison glands of *Pheidole pallidula*, which already have been shown to contain active trail components in ponerine and formicine ants (Janssen et al. 1997; Kohl et al. 2003). In contrast, *Paussus favieri* does not respond to trails laid with mandibular glands or freshly isolated Dufour glands (Cammaerts et al. 1990). The only component of *Pheidole pallidula* trail pheromone that has been identified so far is 3-ethyl-2,5-dimethylpyrazine. This component does not elicit trail following behaviour in *Paussus favieri* (Cammaerts and Cammaerts 1992, 1994) but might be part of a physiologically active pheromone blend.

The observation of a *Pentaplatarthrus gestroi* in Zimbabwe landing near the entrance of an *Anoplolepis custodiens* (Smith 1858) ant nest (Formicinae) and the subsequent adoption of the beetle (P. Nagel, pers. observations) might indicate further nest-finding cues, such as volatile nest odour components, or volatile compounds which are derived from the ant–ant communication. Such a mechanism has proven to be highly effective in a South African darkling beetle which finds subterranean burrows of its host using olfactory cues from the host's defensive secretion (Geiselhardt et al. 2006a).

Interactions of ant nest beetles and their host ants

In ant nest beetles, the adults invade ant nests, and thus, both adults and larvae need to avoid ant-aggression. In contrast, larvae of other myrmecophiles, such as lycaenids and some carabid species, enter the colony by themselves so that the adult forms require protective mechanisms only for the short time of eclosion (Dinter et al. 2002; Pierce et al. 2002). Whereas it is well known how lycaenid caterpillars are adopted by ants (e.g. Akino et al. 1999; Hölldobler and Wilson 1990), only few coincidental

observations indicate the adoption procedure in Paussini. In all cases, extensive licking and pulling of the beetle was involved (Escherich 1898; P. Nagel, personal observations). Similarly, *Myrmica* Latreille 1804 ants lick the adoption gland secretion of adult *Lomechusa* Gravenhorst 1806 (former *Atemeles* Dillwyn 1829) beetles and consecutively carry the beetles into the brood chambers (Hölldobler and Wilson 1990).

Once within an ant colony, adult ant nest beetles seem to exhibit different levels of integration (Reichensperger 1948), which will be shown using three exemplary *Paussus* species (symphile type) that are associated with *Pheidole* ants: *Paussus arabicus* move slowly within ant colonies and frequently face aggressive reactions of the ants. The ants grasp the beetles' antennae or legs and pull it out of the brood chambers or along the tunnels of the nest. If the ants do not succeed in keeping *P. arabicus* away from the brood, they carry the larvae and eggs away (Escherich 1898, 1907; Péringuey 1883; Raffray 1886). However, Escherich (1907) observed a *P. arabicus* that approached the brood chambers again and was subsequently ignored when feeding on the larvae. A similar change of reaction has also been observed in *Cremastocheilus* scarabs (Alpert 1994). In both cases, however, the trigger of the alteration remains obscure.

In contrast, after short initial aggression, *Paussus turcicus* is intensely groomed by its *Pheidole* host ants, which seem especially attracted to the antennal cavities and always surround or even cover the slowly moving beetle (Escherich 1898, 1899b). Nevertheless, *P. turcicus* is dragged along the tunnels of the nest like *P. arabicus*. Altogether, the treatment which *P. turcicus* experiences in the ant colony is very similar to the tending of the host ant queen. Thus, morphological deception might be involved, as both the paussine and the ant queen are similar in size and surface structure (Escherich 1898).

The association of *Paussus favieri* with its facultatively polygynous host ant *Pheidole pallidula* is strikingly different from the above-mentioned cases. The beetles are usually ignored by the ants, moving quickly and undisturbed within the tunnels and touching ants and objects with the antennae. Although *Paussus favieri* may also be faintly attacked and licked during adoption, the ants only very rarely touch, quickly groom or drag the beetle later on (Escherich 1899b; Le Masne 1961b). There is no difference between the adoption procedure in colonies with or without prior experience with *Paussus favieri* (Le Masne 1961b).

The extensive care of *Paussus turcicus* and occasional licking of *P. favieri* call to mind *Lomechusoides* adults, which are continuously tended by their host ants, although the beetles heavily prey on the ant brood (Hölldobler and Wilson 1990). In contrast, licking in *Cremastocheilus*

scarabs mainly occurs when the beetles feed on ant larvae while they are otherwise ignored or attacked (Alpert 1994). The benefits myrmecophiles gain from inducing grooming or licking may thus differ widely between species, depending on the degree of attraction. Whereas *Lomechusoides* and *P. turcicus* profit from clearance of fungi and parasites and maybe transfer of communicational cues, it is assumed that *Cremastocheilus* distracts the ants to feast on ant brood without being disturbed (Alpert 1994), and for most myrmecophilous paussines, the truth might lie in between.

From an evolutionary point of view, the integration type of *Paussus arabicus* can be considered as the most basal, as attacks occur, but cease during the contact with the ants. A possible explanation would be that the beetle adopts the colony odour during the interaction with the ants. In contrast, *P. turcicus* provides a reward in the form of a myrmecophilous secretion, which may or may not entail a nutritive benefit for the ants. Nevertheless, the production certainly is costly for the beetle, as the secretion is not derived from waste material, like aphid honeydew (Stadler and Dixon 1999), but rather a product of specialised glands. This is why we consider the integration type of *P. favieri* as the most derived. These beetles are allowed to move freely among the ants without apparent costs, and one may assume advanced chemical mimicry as the mediating mechanism in this association.

Ant nest beetles are "bombardiers"

Within the Carabidae, a typical pygidial defensive gland containing a variety of noxious chemicals is observed. 1,4-Benzoquinone and its derivatives have evolved several times independently within the homologous gland (Schildknecht et al. 1968b). The bombardier beetles (Brachinini, Crepidogastrini, Ozaenini, Protopaussini and Paussini) are known for their exploding mechanism, which has been described together with the chemical reactions for different species of bombardiers (Aneshansley et al. 1969; Dean et al. 1990; Eisner and Aneshansley 1999; Eisner et al. 1977, 2000, 2001a, b; Peschke et al. 1986; Schildknecht and Koob 1969). The authors found a complex, paired defensive organ composed of secretory tissue, a reservoir and a vestibule, also called reaction chamber (Eisner et al. 2000). In the reservoir, hydroquinones and hydrogen peroxide are present, and in the wall of the vestibule, secretory glands are situated, which produce a mixture of enzymes (Schildknecht et al. 1968a).

The ability of paussines to spray defensive secretion has been described early (Lacordaire 1833; Westwood 1833), and a general similarity of the pygidial defence

glands and discharge mechanism in Paussini and Brachininae has been shown (Dierckx 1901; Escherich 1899b; François 1899; Raffray 1892). The discharge is hot and audible in most bombardiers including Paussini, but while Crepidogastrini emit a non-pulsed mist and Brachinini emit a precisely aimed pulsejet (Eisner and Aneshansley 1999; Eisner et al. 2001a), this is not true for Paussini because of their immobile abdomen. Instead, a subapical elytral fold (flange of Coanda) at the opening of the defence gland allows directional spraying (Arrow 1931; Eisner 1980; Eisner and Aneshansley 1982; Eisner et al. 1992). This fold is missing in Metriini, which do not explosively discharge a spray, but excrete their defence chemical as froth (Eisner et al. 2000, 2001b). 1,4-Benzoquinones are substantial ingredients of the secretion in all species investigated. Furthermore, *n*-alkanes were found (Table 2). The suggestion of free iodine as a defensive secretion component of ant nest beetles is based on chemical reactions probably elicited by benzoquinones, which were misinterpreted due to the early state of knowledge (Dohrn 1851; Escherich 1899a; Hieke 1994; Loman 1887; Paulian 1988).

The convergence of the paussine and brachinine defensive mechanism is striking, as several details in morphology and chemistry are identical. These homoplasies, however, are likely, as compartmentation of the secretory apparatus and biosynthesis of benzoquinones are widespread phenomena in arthropods.

The combination of tanning chemicals and heat (Aneshansley et al. 1969) makes the defensive system of bombardiers an effective weapon, and by this means, Paussini are able to deter attacking non-host ants and even geckos (Karny 1923; Nagel 1987a). Yet, ant nest beetles do not emit defensive secretion to appease or disperse attacking host ants. This is particularly surprising, as ants occasionally kill intruding paussines during these attacks (Escherich 1898; Péringuey 1883), but clearly indicates that Paussini are able to distinguish host ants from non-host ants.

Among myrmecophilous beetles, the aleocharines have a conspicuous tergal defensive gland, which also stores benzoquinones in various lipid solvents (Blum et al. 1971; Brand et al. 1973; Peschke and Metzler 1982; Steidle and Dettner 1993). These oozing secretions have been reported to protect the beetles against attacks of arthropod predators and especially ants. Astonishingly, in derived groups of myrmecophilous and termitophilous aleocharines, the glandular reservoir and producing cells are reduced. Apparently, those species are integrated in a way into the ant colony that defence is not necessary in their whole life cycle, and so they were able to save the costs for the expensive chemicals. In contrast, species with a loose contact to ants (*Pella* Stephens 1835, *Drusilla* Leach 1819) still keep their ability of chemical defence

Table 2 Defensive secretion components of different species of paussines

Tribe	Species	Benzoquinones (BQ)					n-Alkanes			
		1,4-BQ	2-methyl-1,4-BQ	2-ethyl-1,4-BQ	2,3-dimethyl-1,4-BQ	2-methoxy-3-methyl-1,4-BQ	n-tridecane	n-tetradecane	n-pentadecane	not specified
Metriini	*Metrius contractus* Eschscholtz 1828[a]	x					x	x	x	
Ozaenini	*Goniotropis nicaraguensis* Bates 1891[b]	x	x		x		x	x	x	
	Pachyteles Perty 1830 spp.[a, b]	x	x		x		x	x		
	Physea hirta LeConte 1853[b]	x	x		x					
	Platycerozaena magna (Bates 1874)[a] (sub *Ozaena magna*)	x	x		x		x			
	Platycerozaena panamensis (Bänninger 1949)[b]	x	x	x	x					
Paussini	*Homopterus arrowi* Reichensperger 1938[a,b]		x			x				
	Arthropterus MacLeay 1838 sp[c]		x	x						
	Pentaplatarthrus gestroi Kolbe 1896[d]		x	x						x
	Paussus favieri Fairmaire 1851[e]	x	x							

[a] Eisner et al. (1977)
[b] Roach et al. (1979)
[c] Moore and Wallbank (1968)
[d] Krüger and Nagel (unpublished)
[e] Schildknecht and Koob (1969)

(Steidle and Dettner 1993). In basal paussine groups (Metriini, Ozaenini), which may have contact to ants and other arthropod predators, the benefits of chemical defence are easy to understand; but even in the highly derived Paussini (*Paussus*), the exploding gland is still operating (crepitation during molestation). However, as it has never been observed to operate during contact with host ants, it might only be needed during dispersal or in the short period of invading an ant nest, when beetles are likely to encounter a variety of enemies. The duration of stay outside ant nests may vary considerably between paussine species. Moreover, one should consider in further investigations that males and females may have a different need for chemical defence and that there might be a sex-specificity in morphology and chemistry.

Sound production

Three general types of stridulatory organs are present in Paussini. The alary–elytral type is widespread in beetles (Dumortier 1963), also present in carabids (Freitag and Lee 1972) and was found in virtually all Paussini with fully developed hind wings (Nagel 1987a). The abdomen–femur type with passive *pars stridens* at the proximal abdominal sternite and active file-shaped *plectrum* at the proximal part of the hind femur is present in all Paussina (except *Leleupaussus*; Darlington 1950; Escherich 1898; Luna de Carvalho 1949; Nagel 1987b). In *Euplatyrhopalus* and *Platyrhopalopsis*, a stridulatory organ of the thorax–femur type is located at the metasternum and mesofemur. Structural details, however, differ considerably (Luna de

Carvalho 1951; Westwood 1874). Larvae of myrmecophilous riodinid and lycaenid butterflies possess stridulatory organs of completely different structure: In riodinids, for example, anteriorly directed papillae on the edge of the prothorax strike the epicranial surface, thus producing substrate-borne sounds (DeVries 1988, 1991). While *Paussus* species apparently only stridulate in response to molestation (Nagel 1987a), caterpillars stridulate at initial contact with ants and, while stridulating, are more frequently attended by ants then when silent (DeVries 1988; Travassos and Pierce 2000).

While it seems reasonable for riodinid and lycaenid caterpillars to attract and maintain a high number of ant workers to protect them while feeding on plants, Paussini do not necessarily profit from attracting ants, as—once within the nest—the principal enemies are the ants themselves. Thus, one may assume that acoustic signals emitted by paussines might rather imitate vibrational ant signals and possibly aid in appeasing attending ants. Airborne components of paussine calls, furthermore, are likely to be intraspecific signals, as these are not perceivable for ants (Roces and Tautz 2001).

Conclusions

Myrmecophily in paussines seems to have evolved from a free-living predatory life habit. Morphological features, such as trichomes and specific glands, clearly classify Paussini as characteristic myrmecophiles, and their mouthparts are highly specialised for ant prey.

Paussini appear to deploy the same mechanisms of integration in host colonies, which are used most frequently by other myrmecophiles. While some species benefit from their protective body shape and withstand ant attacks without being hurt, other species seem to reward or chemically deceive their host ants to exploit the resources of the ant nest and prey on the brood. The use of myrmecophilous secretions may be most effective if the respective ant species is engaged in trophobiotic interactions, and exploiting non-trophobiotic ant species as hosts thus would necessitate alternative integration mechanisms. As ant nest beetles have multiple host species, a rather general mechanism of chemical integration, such as chemical insignificance and mimicry by means of adoption of components, seems likely. Additional vibrational signals might complement ant–paussine communication.

Paussini may use chemical cues to recognise host ants, as host trail following has been observed. The ability of host recognition, however, is clearly demonstrated by the fact that Paussini never spray their powerful defensive secretion on host ants but readily deter non-host ants by this means.

To characterise the recognition mechanisms involved in ant–paussine interactions, future research will have to centre on the identification of chemical patterns of Paussini and their comparison with ant recognition cues. Furthermore, molecular systematics will have to enlighten the evolution of myrmecophily in the Paussinae, and more behavioural data need to be collected. Along with this, thorough investigation of host ant biology is required to enable comparative statements on specific host–parasite pairs. Research on ant nest beetles then may give new insight in the co-action of chemical and morphological features deployed to avoid ant aggression in a phylogenetic context and enable scientists involved in ant–parasite research to revert to another specialised myrmecophile for comparison and construction of models.

With this review, we aim to reintroduce ant nest beetles in recent research on myrmecophiles and animate observation and discussion of these conspicuous beetles.

Appendix

Table 3 Genera of Carabidae: Paussinae, their classification as used in the present paper, distribution, number of species, and association with ants

Tribe, subtribe, genus	Distribution	Number of species	Life form and relationship to ants
Metriini LeConte, 1853 (2 extant species)			
Metrius Eschscholtz 1829	W-Nearctic	2	Adults of ordinary caraboid groundplan, feed on millipedes in the field; larvae free-living, moveable terminal disk, not associated with ants
Ozaenini Hope 1838 (205 extant species) (N.B.: this tribe is not monophyletic, the classification is provisional)			
Ozaenini: Mystropomina Horn 1881			Most larvae unknown, the rare field data characterize adults as predators without indications of any kind of association with ants; mouthparts of adults basically of ordinary caraboid groundplan, probably mixed feeders (fluids, mush, and fragments); beetles mostly found in rotten wood, on or under tree bark, under stones, in leaf litter and humus; some genera show crassate antennae and flattened or broadened body, which are structures sometimes associated with myrmecophily
Mystropomus Chaudoir 1848	Australian	2	
Ozaenini: no formally established subtribe			
Anentmetus Andrewes 1924	Oriental	2	
Ozaenini: no formally established subtribe			
Entomoantyx Ball and McCleve 1990	Neotropical (Central America)	1	
Ozaenini: Eustrina Jeannel 1946			
Dhanya Andrewes 1919	Oriental, *SE Palearctic*	6	
Eustra Schmidt-Goebel 1846 (incl. *Ozaenaphaenops* Deuve 1986)	Oriental, *SE- E- Palearctic*	24	
Ozaenini: no formally established subtribe			
Microzaena Fairmaire 1901	Madagascan	4	
Ozaenini: Pseudozaenina Sloane 1905			
Pseudozaena Laporte de Castelnau 1834	Oriental, Australian (New Guinea and surroundings)	2	
Ozaenini: no formally established subtribe			
Itamus Schmidt-Goebel 1846	Oriental, Australian (Bismarck Archipelago)	4	*Mystropomus* with pit above the coxa of prothorax, *Dhanya* with large cavity medially to the coxa, both structures of unknown function
Sphaerostylus Chaudoir 1848	Madagascan	4	Known larvae (*Itamus, Afrozaena, Pachyteles, Goniotropis*) hyperprognathous, with moveable terminal disk, which has been demonstrated in *Pachyteles* and *Goniotropis* to be used for closing entrances of burrows (phragmosis) and for trapping small insects; no demonstrated association with ants
Afrozaena Jeannel 1946	Afrotropical, Madagascan	10	
Ozaeniella Basilewsky 1976	Afrotropical	1	
Ozaenini: Pachytelina Jeannel 1946			
Pachyteles Perty 18305	Neotropical, *SW-Nearctic*	49	
Tachypeles Deuve 2001	Neotropical	17	
Goniotropis Gray 1832 (inclusive of *Scythropasus* Chaudoir 1854)	Neotropical, *S-Nearctic*	31	
Tropopsis Solier 1849	Neotropical	2	
Crepidozaena Deuve 2001	Neotropical	1	
Filicerozaena Deuve 2001	Neotropical	10	

Table 3 (continued)

Tribe, subtribe, genus	Distribution	Number of species	Life form and relationship to ants
Gibbozaena Deuve 2001	Neotropical	2	
Inflatozaena Deuve 2001	Neotropical	1	
Mimozaena Deuve 2001	Neotropical	1	
Proozaena Deuve 2001	Neotropical	5	
Serratozaena Deuve 2001	Neotropical	1	
Ozaenini: Ozaenina Hope 1838			
Ozaena Olivier 1812	Neotropical, *SW-Nearctic*	12	Larvae unknown; adults show structural traits which are often associated with myrmecophily, such as crassate antennae, antennomeres with sensory fields similar to Paussini, and loss of tactile setae
Platycerozaena Bänninger 1927	Neotropical	4	
Ozaenini: Physeina Jeannel 1946			
Physea Brullé 1834	Neotropical, *SW-Nearctic*	6	Adults and larvae of one species collected in *Atta* nests; adult body flattened and broadened, with tubercles and long elytral setae (trichomes?); mouthparts basically of ordinary caraboid habitus, but mandibles falcate; feed on larvae of staphylinids which are guests of *Atta*, larva hyperprognathous, slightly physogastric
Physeomorpha Ogueta 1963	Neotropical	1	Larva unknown, but due to close relationship to *Physea* and similar body shape of adults with crassate antennae and broadened body myrmecophilous life habit may be inferred
Protopaussini Gestro 1892 (8 extant and 1 fossil species)			
Protopaussus Gestro 1892	Oriental, *SE Palearctic*, Dominican Amber[a]	8, 1[a]	Adults with trichomes, mouthparts strongly diverging from ordinary caraboid habitus, adapted to fluid feeding, myrmecophilous, larvae unknown
Paussini Latreille 1807 (563 extant and 27 fossil species)			All adult Paussini have mouthparts strongly diverging from the ordinary caraboid groundplan, all are adapted to fluid feeding; myrmecophily of adults is further demonstrated by crassate antennae, antennomere 11 with sensory field, loss of tactile setae, adults show protective body shape, or are equipped with trichomes; most probably all taxa invade ant nests and feed on ants in the adult and larval stages, the adults of some taxa (like *Arthropterus*) perhaps not obligatory myrmecophiles or only for short periods
Paussini: subtribal assignment unclarified, possibly Carabidomemnina Wasmann 1928			
Eopaussus Wasmann 1926[a]	Baltic amber[a]	1[a]	Boat-shaped antennal club with trichomes, ants in the same piece of amber closely attached to the beetle, myrmecophilous
Pleurarthropterus Wasmann 1927[a]	Baltic amber[a]	1[a]	Possibly with trichomes, myrmecophilous
Acmarthropterus Wasmann, 1929[a]	Baltic amber[a]	1[a]	Hornlike structure at vertex, possibly myrmecophilous
Paussini: Carabidomemnina Wasmann 1928			
Balticarthropterus Nagel 1987[a]	Baltic amber[a], German Middle Eocene lacustrine deposits[a]	12[a]	Antennae crassate but no unequivocally myrmecophilous structures
Succinarthropterus Kolbe, 1926[a] (incl. *Arthropterillus* Wasmann, 1926)	Baltic amber[a]	3[a]	
Arthropterites Wasmann, 1925[a]	Baltic amber[a]	1[a]	
Protocerapterus Wasmann, 1926[a]	Baltic amber[a]	2[a]	No trichomes, body shape similar to the protective type of *Cerapterus*, possibly myrmecophilous
Cerapterites Wasmann, 1925[a]	Baltic amber[a]	3[a]	
Carabidomemnus Kolbe, 1924s.l.	Afrotropical	27	
Eohomopterus Wasmann, 1919	Neotropical, Dominican amber[a], Mexican amber[a]	2, 3[a]	Adults with crassate antennae, no trichomes, sometimes found together with ants; larvae unknown

Taxon	Distribution	No.	Notes
Paussini: Arthropterina Nagel 1987			
Megalopaussus Lea 1906	Australian	1	Adults once found in an ant nest but without clear myrmecophilous structures, except mouthparts and crassate antennae; larvae unknown
Arthropterus MacLeay 1838	Australian *(inclusive of New Guinea and Bismarck Archipelago)*	66	Adults sometimes of the protective body shape, mouthparts of fluid feeding type, rarely found together with ants or in ant nests; larva prognathous, with immoveable terminal disk, distinct myrmecophilous structures
Paussini: Heteropaussina Janssens 1953			
Heteropaussus Thomson 1860	Afrotropical	26	Adults with trichomes, larvae inadequately described and generic assignment uncertain
Paussini: Cerapterina Billberg 1820			
Cerapterus Swederus 1788	Afrotropical, Oriental, *SE Palearctic*	32	No trichomes but body shape of the protective type, mouthparts of fluid feeding type, myrmecophilous, larvae unknown
Mesarthropterus Wasmann, 1926	Afrotropical	1	
Paussini: Pentaplatarthrina Jeannel 1946			
Hexaplatarthrus Jeannel 1955	Madagascan	1	Adults without clear myrmecophilous structures, larvae unknown
Hyperpentarthrus Kolbe 1927	Afrotropical	1	Adults with trichomes, larva unknown
Pentaplatarthrus Westwood 1833	Afrotropical	7	Adults with trichomes, larvae inadequately described and generic assignment doubtful
Paussini: Homopterina Wasmann 1920			
Homopterus Westwood 1841	Neotropical	12, 1[a]	No trichomes but body shape of the protective type, myrmecophilous, larvae unknown
Paussini: Platyrhopalina Jeannel 1946			
Lebioderus Westwood 1838	Oriental	7	Adults with trichomes or other myrmecophilous structures, many records from ants' nests, larvae physogastric, with distinct myrmecophilous structures
Euplatyrhopalus Desneux, 1905	Oriental, *SE Palearctic*	6	
Stenorhopalus Wasmann 1918	Oriental, *SE Palearctic*	2	
Platyrhopalus Westwood 1838	Oriental, *SE Palearctic*	14	
Platyrhopalopsis Desneux 1905	Oriental, *SE Palearctic*	3	
Paussini : Ceratoderina Darlington 1950			
Ceratoderus Westwood 1841	Oriental, *SE+E- Palearctic*	7	
Melanospilus Westwood 1845	Oriental, *SE Palearctic*	3	
Paussomorphus Raffray 1885	Afrotropical	3	
Paussini : Paussina Latreille 1807			
Leleupaussus Luna de Carvalho, 1962	Afrotropical	1	
Paussus Linné, 1775 (sensu lato, cf. Nagel 2003)	Afrotropical, Oriental, SW- and SE Palearctic, Madagascan	329	
Granulopaussus Kolbe, 1938	Afrotropical	4	
Hylotorus Dalman 1823	Afrotropical	8	

The number of recent species is drawn from Lorenz (2005), with additions and amendments from Deuve (2004, 2005) and Nagel (2006). The distribution data refer to the classical zoogeographic regions. The main distribution is given in normal characters, adjacent ranges are in italics. The phylogenetic relationships are based on larval and adult characters (DiGiulio et al. 2003; DiGiulio and Moore 2004; Moore and DiGiulio 2006; Nagel 1987a, 1997). Trichomes and other structural traits are regarded as evidence for myrmecophily (see text for further explanation).

[a] Fossils

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