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Myrmecophily in beetles (Coleoptera): evolutionary patterns and biological mechanisms

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Abstract

Socially parasitic myrmecophily has evolved numerous times in arthropods, but myrmecophilous lineages are non-randomly distributed across phylogeny. Evolution of this way of life is heavily biased towards the Coleoptera, within this order towards rove beetles (Staphylinidae), and within rove beetles to two subfamilies. Here, I provide an overview of the diversity of myrmecophilous beetles and discuss advances in comprehending their biology, systematics, and evolution. I address possible factors underlying the skewed phylogenetic distribution of myrmecophily across the Coleoptera. Accounting for this trend requires knowledge of ancestral ecologies and phenotypic attributes in clades where taxa are predisposed to undergo the evolutionary transition from free-living to myrmecophilous. Clades that are primitively predatory, small in body size, and possess defensive strategies, either physical or chemical, that permit some degree of protection from policing worker ants, appear to be preadapted to evolve myrmecophily repeatedly. I propose that the mode of colony exploitation employed during the initial phase of evolution, combined with the potential evolvability of the body plan, has important consequences for subsequent evolutionary steps: These parameters influence if and how different taxa undergo specialisation to colony life and the mechanisms the most advanced myrmecophiles employ to achieve social integration. Myrmecophily is a paradigm of intricate symbiosis, which in certain clades of beetles evolves recurrently from an ancestral preadaptive ground state and follows a relatively predictable phenotypic trajectory. These clades are potentially powerful systems to explore the evolution and mechanistic bases of symbiotic relationships in animals.

Key words: Myrmecophily, social parasitism, symbiosis, beetles, ants, preadaptations, evolution, development, convergence, review.

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Introduction

Symbioses in the natural world embody some of the most extraordinary and captivating biological phenomena. This is surely because the interrelations between participant species are often idiosyncratic and peculiar; as intricate associations evolve, selection takes phenotypes down paths rarely travelled, and in the process generates the unusual, complex, and seemingly inexplicable. Nowhere is this basic maxim borne out so clearly as in the case of myrmecophily, herein defined as the partial or complete dependence on ant colonies by non-ant species (see Box 1). Among arthropods, an estimated 10,000 species are myrmecophilous to some degree (ELMES 1996), exploiting the various resources that ant colonies have to offer. The extent to which this lifestyle exposes taxa to novel pressures is revealed by comparing many obligate myrmecophiles to their generalised, free-living relatives. When so juxtaposed, the myrmecophiles' distortions and deformations emerge in stark relief – the products of intense selection driving radical changes in form. Historically, myrmecophiles have received attention from some prominent entomologists, but knowledge of this kind of symbiosis nevertheless remains fragmentary. One can typically only guess at the functions of many of the dramatic morphologies and accompanying behaviours that myrmecophiles display; the development, lifecycles, and ecologies of all but a few species are mysterious, and aside from superficial biochemical profiling, the molecular and neurological mechanisms that mediate myrmecophile-host interactions are almost fully unknown.

Yet, as bizarre and understudied as they so often are, patterns emerge by considering the collective diversity of myrmecophiles. Principles may be inferred regarding the factors promoting the initial evolution of this lifestyle, and predictions made about the phenotypic trajectory of myrmecophilous lineages as they evolve increasingly intimate relationships with their hosts. In this article, I explore what can be learned from examining the phylogenetic distribution of myrmecophilous taxa, since such species are not scattered randomly across the arthropod tree of life; rather, their evolution is strongly biased to certain groups, and in these groups especially, evolutionary replication enables hypotheses to be constructed about the origination of this lifestyle and its attendant biological mechanisms. The focus is necessarily on beetles, the arthropod order where myrmecophily is most prevalent, and where the range of inquilinous forms is most varied. I attempt to explain why this beetle bias exists, before outlining the taxonomic spectrum of ant-associated Coleoptera and examining recent

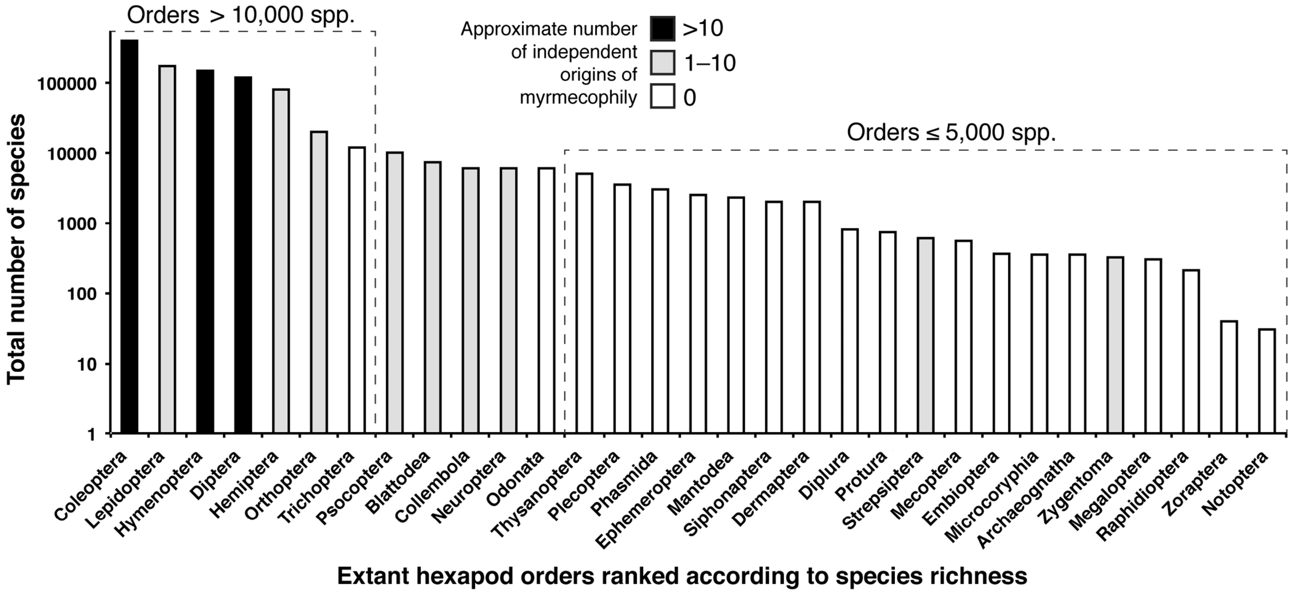

Fig. 1: Prevalence of myrmecophily across orders of Hexapoda. A log plot of ranked described species richness of the 31 extant hexapod orders. Bars are coloured according to the estimated number of independent evolutionary transitions from a free-living to a myrmecophilous state (as defined in Box 1; both obligate and facultative) within the order. White bars: no known examples of myrmecophily; grey bars: fewer than ten putative independent origins; black bars: more than ten putative independent origins. The number of origins of myrmecophily for each order is a rough estimate based primarily on the inventory of Hölldobler & Wilson (1990) and more recent taxon-specific works cited herein. Attempts were made to gauge the relatedness of the different myrmecophilous taxa found within each order or family. Cases of myrmecophagy, trophobiosis and some indirect relationships (e.g., nymphalid and papilionid associations with ant bird droppings) were excluded following the definition of myrmecophily in Box 1. Note that socially parasitic myrmecophily in Lycaenidae (Lepidoptera) evolves repeatedly from an ancestral mutualism with ants, rather than from a free-living state (Pierce & al. 2002), so was scored only once.

advances in inquiline biology and evolution. Within beetles, further discrepancies exist among higher-level taxa in the proportion of descendent lineages that are myrmecophilous. I discuss clade-level attributes that predispose certain groups to evolve myrmecophily, and propose a corollary, that characteristics of the ancestral stock from which myrmecophilous lineages emerge strongly influence the subsequent evolution of the ant-beetle relationship, promoting its evolution towards intimacy in some groups, but potentially limiting its elaboration in others. I identify putative preadaptations that may have been involved recurrently in independent lineages during the evolutionary transition to myrmecophily, and suggest that studying these traits in a comparative framework involving related, free-living species may shed important mechanistic light on the evolution of this mode of life.

Beetle-biased: the phylogenetic distribution of myrmecophily

Why evolve myrmecophily? Ant colonies are efficiently policed against intruders, ranking them among the most impenetrable and inhospitable of places for the majority of arthropods. But the presence of a largely immobile brood, harvested or cultivated food and discarded refuse means that nests represent resource-rich environments. Strategies to bypass or mimic ant nestmate recognition systems may be selectively advantageous, and bring the secondary benefit of exempting taxa that evolve them from extrinsic mortality in the form of predators or climatic extremes. Consequently, a large number of arthropods have evolved some capacity to target ant colonies, living as social parasites with varying degrees of intimacy with their hosts. The taxonomic diversity of myrmecophiles was compiled in catalogue form by Wasmann (1894a) and has never been updated, but a general compendium of global myrmecophile diversity was provided in two works by Kistner (1979, 1982), while Hölldobler & Wilson tabulated instances of this lifestyle across higher arthropod taxa in "The ants" (1990). All such inventories reveal the spectacular taxonomic breadth of arthropods that have been recorded living in some kind of association with ants. Such diversity is an empirical testament to the benefits of evolving myrmecophily. But what is especially interesting to do is to scan these lists and identify arthropod taxa that are missing – a far greater number – and speculate why.

Figure 1 shows the ranked species richness of extant hexapod orders labelled according to the approximate degree to which they contain definitively myrmecophilous lineages. The overall pattern is very clear: Orders tend not to include myrmecophiles if they are relatively small (17 of the 19 orders with 5,000 species or fewer lack myrmecophiles; only the families Nicoletiidae in Zygentoma and Myrmecolacidae in Strepsiptera target ants, and the latter may be more accurately regarded as endoparasites than social parasites). Orders with more than 5,000 species do not contain myrmecophiles if ecologically constrained by aquatic larval stages (Odonata and Trichoptera), and of the big orders (10,000 species or more), the three that are the most trophically conservative – Hemiptera, Orthoptera and Lepidoptera, comprised predominantly of phytophagous species – have disproportionately few instances of myrmecophily relative to their size (cases

Box 1: Defining myrmecophily, social integration and social parasitism.

Myrmecophily. Translated literally as "ant-loving", myrmecophily is a vague term that can mean different things to a coleopterist (social parasitism), a hemipterist (mutualism) and a hymenopterist (ant parasitoidism). To define myrmecophily for this article, the term is restricted to species whose livelihoods rely on some aspect of the social structure of colonies, without returning obvious benefits. This covers burdensome social parasites (excluding socially parasitic ants) and extends to scavenging nest dwellers, saprophagous refuse dump inhabitants, as well as some parasitoids. What distinguishes myrmecophily as an ecological strategy distinct from predation or parasitism is that myrmecophilous species capitalise on the social fabric of ant biology, for example, through the exploitation of colonies, or by cheating nestmate communication to achieve reward. Interactions with hosts may occur both inside and outside nests, but this definition rules out many myrmecophagous and parasitic organisms that simply prey on or target individual ants, unless it can be demonstrated that such species employ socially parasitic tactics. Since myrmecophily is the product of evolution, however, there are necessarily borderline examples, such as some obligately myrmecophagous carabids. These marginal cases are also discussed, since they may represent the limits of the spectrum of myrmecophily. Similarly, facultative myrmecophiles that appear not to live in strict association with colonies are considered if the relationship appears more than incidental. Mutualistic trophobionts, found in Lepidoptera and Hemiptera, are excluded (those belonging to the latter order were the subject of an excellent recent review, IVENS 2015). Ant mutalism appears to be absent from the Coleoptera, probably because beetles do not produce metabolic byproducts like honeydew that could form the basis for this lifestyle.

Another point of clarification concerns mites (Acarina). A huge number of mite species are associated with ants (KISTNER 1982, HÖLLDOBLER & WILSON 1990), rivalling or surpassing the number of myrmecophilous beetle species. Several mite taxa are highly specialised for colony life (RETTENMEYER & al. 2010); some, such as *Antennophorus*, siphon off liquid food during stomodeal trophallaxis between workers (JANET 1897), and are thus manifestly socially parasitic. However, these species are a minority, and most ant-associated mites appear simply to be phoretic, or to a lesser extent, ectoparasitic on individual ants, rather than actual social parasites. No group of terrestrial arthropods is immune to mites; if ants were non-social but just as numerous and speciose, they would still retain an overabundance of mites. Ants would not, however, form colonies, and so would not be targeted by colony-exploiting myrmecophiles. Hence, when looking at myrmecophily across the Arthropoda, it is the Coleoptera – not mites – where this lifestyle has evolved to the most significant degree.

Social integration. Myrmecophilous species utilise colonies in a multitude of ways. Taxa that have sacrificed a free-living existence to ecologically specialise on colonies often (but not always) display overt morphological or behavioural modifications, which vary according to the myrmecophilous strategy employed. One key axis of variation among myrmecophiles is the extent to which the organism is recognised and accepted by its hosts – its degree of social integration (KISTNER 1979). The majority of myrmecophiles are nest intruders that are either largely ignored by their hosts, or recognised and treated aggressively. Such species may possess defensive anatomical modifications that protect the body from potential worker hostility, and exhibit behavioural responses that permit rapid escape or shielding of fragile body regions (Box 2). In contrast, species that are socially integrated are treated without aggression by their accommodating hosts, becoming behaviourally assimilated into colony life with some degree of intimacy. This advanced and highly intricate manifestation of the myrmecophilous relationship is reflected in a suite of morphological and behavioural adaptations that mediate habituation to the social structure of the nest (Box 2). It should be noted that distinction between integrated and non-integrated species is not always clear or absolute; for example, during its lifecycle, a species may enter a nest and initially be treated with hostility, yet go on to achieve social integration through successful execution of a socially parasitic strategy, such as behavioural or chemical manipulation.

Social parasitism. Briefly, many myrmecologists employ the term "social parasitism" to refer to the parasitic dependence of one social species on another (e.g., BUSCHINGER 2009). In contrast, myrmecophile biologists routinely apply the term more widely to any species that targets ant nests and inflicts a cost, or exploits the social structure of the colony for its own gain. This definition treats the myrmecophile as a parasite and the ant colony as its "superorganismal" host. This second usage is employed here. Note also that following the literal definition used by KISTNER (1979), the term "symbiosis" and "symbionts" refer simply to species living closely together, and not necessarily engaging in a mutualistic relationship.

of trophobiosis, myrmecophagy and myrmecomorphy excluded). Most myrmecophiles are also holometabolous, so complete metamorphosis may be an additional promoting factor, by permitting distinct ecologies to evolve for each stage of an organism's life history. Indeed, many holometabolous myrmecophiles associate with ants only as larvae or as adults.

At this deep taxonomic level, then, the larger the order, and the less ecologically and trophically constrained it is, the greater the number of myrmecophilous lineages it contains. The conclusion is that, despite the empirically-supported practicability of myrmecophily as a way of life, evolving it is quite unlikely for most groups – even for some of vast size. The inventories of Wasmann, Kistner, and Hölldobler & Wilson may give the impression of myrmecophily as a taxonomic free-for-all, but in reality, it is profoundly phylogenetically biased. By far the majority of myrmecophilous lineages are clustered into three giant holo-

Box 2: Myrmecophilous morphology.

Important adaptive morphological features seen repeatedly in myrmecophilous Coleoptera include:

Epidermal exocrine glands. Chemical communication lies at the heart of myrmecophily and may be mediated by the de novo synthesis of compounds that modify host behaviour (e.g., by promoting host appeasement or panic, instead of aggression) or act to disguise the intruder (mimicry or other chemically adaptive strategies). Where known, such compounds may be volatile organic compounds, non-volatile molecules such as longer chain hydrocarbons, and possibly proteins (Hölldobler 1970, Blum & al. 1971, Steidle & Dettner 1993, Stoeffler & al. 2007). These chemical cues are secreted by glands with outlets on the cuticle. Secretory tissue may consist of single or clusters of gland cells in the epidermis with ducts opening onto the cuticle, or of "gland complexes", in which multiple gland cells fuel a reservoir inside the body cavity that has a large outlet onto the integument. Gland complexes may be positioned centrally as single unpaired structures, or paired symmetrically on either side of the body. In some species, glands are serially repeated in abdominal segments.

Trichomes. Clusters of gland cells, as well as gland complexes, are commonly associated with "trichomes": groups of setae that are often golden or yellow in colour (Fig. 2E, I, K, N, R). Trichomes may consist of long, erect brush-like bunches of setae that sprout prominently from the body, sometimes fashioned into elaborate shapes; in other cases they may form patches of short setae that cover or encircle glandular areas. Host workers have been observed licking trichomes of at least some trichome-bearing myrmecophiles (e.g., Donisthorpe 1927, Park 1932b, Reichensperger 1948, Hölldobler 1970, Akre & Hill 1973), fuelling the notion that trichomes generally function as wick-like delivery devices, conducting glandular exudates along their length.

Grasping notches. Worker ants commonly pick up myrmecophilous beetles and carry them around nests. Deep furrows and indentations of the integument are widespread in myrmecophiles (Fig. 2B, D, E, K, N, P, R, S), and in some species have been observed to function as handles for worker mandibles (Leschen 1991). Glandular tissue, as well as associated trichomes, may be embedded in or surround these notches.

Body shape modifications. Evolutionary specialisation to colony life has selected for changes in the entire shape of the body in some obligate myrmecophiles. Morphologically similar and functionally equivalent body shapes have arisen convergently in beetles (Seevers 1965, Kistner 1979). The most commonly observed body plan is "**limuloid**", a defensive, horseshoe crab- or teardrop-like form where the anterior body is strongly expanded to protect the head. Usually the pronotum is strongly enlarged, convex and explanate, covering the head (Fig. 2C, L, O, Q). In other cases, the head is laterally expanded over the eyes to form a hood (Fig. 2F, G). Limuloid species are typically not strongly socially integrated into host colonies, and are found in diverse families including Carabidae (Pseudomorphinae), Staphylinidae (Aleocharinae, Pselaphinae, Tachyporinae), Ptiliidae (Cephaloplectinae), Hydrophilidae, Leiodidae and Tenebrionidae. The second convergent shape is the ant-mimicking "**myrmecoid**" body plan (Fig. 2H). Here, the abdomen is petiolate, the antennae are geniculate and the legs are extremely elongate. Myrmecoid taxa occur only with true army ants (Dorylinae) and some other nomadic or group-foraging ants such as *Leptogenys* (see Hlaváč & Janda 1999) and *Carebara diversus* (see Kistner 1983). Where known, they appear to be highly integrated into host colonies.

Leg modifications. Aside from gross changes in body shape, analogous defensive modifications of the limbs are widespread among myrmecophilous Coleoptera that interact directly with ants. Many species, both socially integrated as well as not, possess short, thickened, legs. Compaction of the tarsus in particular, as well as flattening and lateral expansion of the tibiae (e.g., Figs. 2A, S) are seen widely, occurring in Carabidae (some Paussini), Staphylinidae (some Aleocharinae, Pselaphinae and Tachyporinae), Histeridae (Haeteriinae and Chlamydopsinae), Hydrophilidae, Curculionidae (Eremoxinini), Scarabaeidae (*Haroldius*, *Alloscellus* and some Eupariini) and others. Presumably for non-integrated species as well as integrated ones, interactions with ants, aggressive or otherwise, involve handling by ant mandibles and can lead to loss of appendages.

Antennal modifications. In addition to the legs, reinforcement of the antennae is also common. This usually involves flattening or thickening of the antennomeres, and compaction of the segments by reducing or concealing the weaker, connecting antennomere pedicels (e.g., Figs. 2F, J, K, M, P, S, 6, beetle at far right). Complete or partial fusion of the antennomeres making up the flagellum also occurs in some groups, most notably paussine carabids (Fig. 2A, B) and the Clavigeritae (Staphylinidae: Pselaphinae; Figs. 2K, 6, beetle at middle right). The antennal apex of Clavigeritae is truncate (Fig. 2K), with a setose cavity that has a glandular function and is licked by workers (Cammaerts 1992). Similar truncate antennal apices are also seen in myrmecophilous ptinine anobiids, salpingids, haeteriine histerids and myrmecophilous Endomychidae (*Trochideus*, *Pleganophorus*), but whether these are gland-associated in all such taxa is unknown.

metabolous, polyphagous orders: Coleoptera, Hymenoptera and Diptera. Instances outside of these orders are sporadic, albeit anticipated, evolutionary quirks – affirmation that given enough cladogenesis, one lineage may eventually take the leap.

Among the three principal orders, myrmecophily is further strongly biased to beetles. While Diptera and Hymenoptera house an array of classical endo- and ectoparasitoids, some of which specialise on ants (Feener & Brown 1997, Lachaud & Pérez-Lachaud 2012), the bulk of these species merely target individuals (usually workers or larvae) as hosts for oviposition. Dipterans and non-formicid hymenopterans that exploit colonies in socially parasitic ways are far less numerous than within the Coleoptera. This beetle bias has several probable causes. Naturally, as the biggest order with almost 400,000 described species, Coleoptera contains a larger pool of lineages with the potential for transitioning to myrmecophily. But beetles also have proportionally more evolutionary instances of myrmecophily than Diptera and Hymenoptera (WASMANN 1894a, KISTNER 1979, KISTNER 1982, HÖLLDOBLER & WILSON 1990), so the bias additionally stems from beetles being relatively more preadapted for this way of life. One component of this is that as both adults and larvae, the great majority of beetles occupy the same microhabitats as ants, coexisting in or on, and moving through, the same substrates. Like ants, beetles are often primarily crawlers rather than fliers, and groups that do employ flight as their predominant mode of locomotion (ariel searching) are nevertheless more adept at, and more behaviouraly inclined to, crawling or tunnelling through substrates than are most dipterans and hymenopterans. It follows that beetles may be more ecologically predisposed to the initial, facultative exploration of colonies, as well as the subsequent evolutionary transition of all developmental stages to life inside them.

Finally, the major evolutionary innovation of beetles – the transformation of the mesothoracic wings into hardened elytra – is a protective modification that safeguards the adult trunk and flight wings. Indeed, the whole integument is often very heavily sclerotised. The combination of elytra and thickly sclerotised cuticle no doubt serves beetles well as a defensive shield in ant encounters. In adult Diptera and Hymenoptera, the body and delicate flight wings lack such protection, and consequently in myrmecophilous species, colony life appears to be most commonly limited to the immature stages alone (HÖLLDOBLER & WILSON 1990). Wholesale lifecycle transitions in which both adults and juveniles have evolved to live within colonies seem rare, and restricted in Hymenoptera to scattered genera in the families Diapriidae and Braconidae (LACHAUD & PÉREZ-LACHAUD 2012) and within Diptera to genera of Phoridae and Sphaeroceridae (KISTNER 1982). In such cases, adults may evolve aptery, or lose or shed their wings on colony entry; moreover, this wingless, colony-based life may be limited only to females. Socially parasitic behaviours displayed by species that retain their wings as adults are likewise uncommon, and appear limited to opportunistic acts of kleptoparasitism, trophallaxis, or parasitism of ant-attended aphid herds, all of which typically take place outside of nests (MASCHWITZ & SCHÖNEGGE 1980, LIEPERT & DETTNER 1993, VÖLKL & al. 1996, SIVINSKI & al. 1999, WILD & BRAKE 2009). For the majority of ant-associated dipterans and hymenopterans where colony residence is limited to immature stages, the problem of gaining nest access for larval development must still be overcome. Dipteran females may opportunistically scamper into nests and oviposit (e.g., milichiids targeting *Atta*, see MOSER & NEFF 1971), eggs may be laid outside and transported inside (e.g., the syrphid *Microdon*, see ELMES & al. 1999) or dropped into nests from above by adults on the wing (e.g., some calliphorids and muscids, KISTNER 1982). Among parasitoids, at least in cases where oviposition has been observed, females may lay directly into workers outside nests, into the larvae or pupae the workers are carrying, or into colony-less, foundress queens (BRUES 1922, FEENER & BROWN 1997, LACHAUD & PÉREZ-LACHAUD 2012). In the Eucharitidae – the only major hymenopteran clade comprised exclusively of myrmecophilous parasitoids – phoretic larvae enter nests by attaching to workers (MURRAY & al. 2013, TORRÉNS 2013). Compared to all such strategies, the protection afforded by beetles' elytra would seem to hugely simplify the problem of nest intrusion.

In summary, three factors in combination are posited to underlie the beetle bias: the huge species richness of Coleoptera, their ecological predisposition to encountering and exploring ant colonies, and their possession of a major defensive preadaptation in the form of elytra. These elements have synergised to make beetles exceptionally prone to evolving myrmecophily. Yet, the upshot in evolutionary terms is far more profound than just an enhanced prevalence of this way of life across the order. Without exaggeration, the outcome is an incomparable explosion in phenotypic diversification (Fig. 2), as numerous independent phyletic lines have shifted to this symbiotic mode of existence. The myriad cases of myrmecophily in beetles are all so fascinating because each one marks an evolutionary shift in ecology that goes hand in hand with extraordinary phenotypic change – behavioural, chemical, morphological, developmental or ecological – as a lineage departs an ancestral free-living existence to engage in social parasitism. It is among the myrmecophiles that beetle morphology is pushed to its limits, and behaviour reaches new levels of intricacy. But as with arthropods as a whole, even among the beetles there is bias, for among the different groups of Coleoptera there are stark asymmetries in the incidence of myrmecophily evolving. To explain this skew requires examination of the spectrum of myrmecophilous beetle lineages, their phylogenetic relationships, and the phenotypic attributes of the higher taxa from which they emerge.

Biodiversity of myrmecophilous Coleoptera

The taxonomic diversity of myrmecophilous Coleoptera is impressive, and documenting its true extent remains a work very much in progress. In his catalogue of inquilinous arthropods, WASMANN (1894a) listed 1177 myrmecophilous insect species, 993 of which were beetles. It is certainly conservative to estimate that since Wasmann's time the number of such species has more than doubled. Also notable from Wasmann's catalogue is the number of family names that are no longer recognised: "Paussidae", "Gnostidae", "Clavigeridae", "Ectrephidae", "Thorictidae" – all of these were erected based on the bizarre and distinctive morphology of the myrmecophilous species they contain. Yet, following detailed anatomical study and improved understanding of systematically important characters in beetles, all have now been subsumed into larger families. This reflects another advance since Wasmann's time: that our understanding of the phylogenetic relationships of beetle myrmecophiles has improved markedly.

Table 1 shows the family-group spread of myrmecophilous beetles as we know it today. At least thirty-three, or approximately one fifth, of the beetle families have thus far been documented to include one or more taxa that exhibit a more than casual association with ant colonies. A

Tab. 1: Family level taxonomic inventory of myrmecophilous Coleoptera. Families with myrmecophiles are shown, with some relevant subtaxa listed. Groups in bold are comprised primarily or exclusively of myrmecophiles. Asterisks mark taxa that have not been found with ants, but which are thought to be myrmecophilous based on morphology. Staphylinidae is partitioned into Aleocharinae and Pselaphinae (with myrmecophile-containing tribes listed), and other staphylinid subfamilies. Representative publications for each group are shown. Although most literature listed is systematic, where possible, biological studies or works that provide summaries of the known biology (and which contain further relevant references) are listed. Some families listed in Navarrete-Heredia (2001) that have occasionally turned up in external refuse dumps of *Atta* nests are not included here, nor are some likely incidental captures listed in Hölldobler & Wilson's "The ants" (1990), Wasmann's (1894a) inventory, and two works by Lea on Australian inquilines (Lea 1910, 1912).

Family	**Subfamily / tribe / genus**	**Reference(s)**
Anobiidae	Ptininae	Lawrence & Reichardt (1969)
Anthicidae		Chandler (2010)
Brentidae	**Eremoxenini**	Le Masne & Torossian (1965), Maruyama & al. (2014)
Buprestidae	*Habroloma*	Bily & al. (2008)
Carabidae	**Paussinae**	Geiselhardt & al. (2007)
	Pseudomorphini	Erwin (1981)
	Graphipterini	Dinter & al. (2002)
Cerylonidae		Kistner (1982), Slipinski & Lawrence (2010a)
Chelonariidae		Janzen (1974), Spangler (1980)
Chrysomelidae	Clytrini	Jolivet & Petitpierre (1981), Erber (1988), Selman (1988)
Coccinellidae		Vantaux & al. (2012)
Cryptophagidae		Leschen (1999)
Curculionidae		Oberprieler & al. (2014)
Dermestidae	**Thorictini**	Kistner (1982), Lenoir & al. (2013)
Discolomatidae		Cline & Ślipiński (2010)
Elateridae	*Agraeus**	—
Endomychidae		Shockley & al. (2009)
Erotylidae		Lea (1910)
Hydrophilidae		Fikacek & al. (2013), Fikacek & al. (2015)
Histeridae	**Chlamydopsinae**	Caterino & Dégallier (2007)
	Haeteriinae	Akre (1968), Helava & al. (1985)
	Other subfamilies	Kovarik & Caterino (2005)
Jacobsoniidae	*Sarothrias**	Philips & al. (2002)
Lampyridae		Sivinski & al. (1998)
Latridiidae		Lapeva-Gjonova & Rücker (2011)
Leiodidae		Jeannel (1936), Peck (1976), Kistner (1982)
Lucanidae	*Holloceratognathus*	Holloway (1998)
Monotomidae	*Monotoma*	Bousquet & Laplante (1999)
Nitidulidae	*Amphotis*	Hölldobler & Wilson (1990), Lencina & al. (2011)
Ochodaeidae	*Ochodaeus*	Deloya & al. (1995)
Ptiliidae	**Cephaloplectinae**	Park (1933a), Wilson & al. (1954)
Salpingidae	**Dacoderinae**	Aalbu & al. (2005)
Scarabaeidae	Cetoniinae	Komatsu & al. (2014), Puker & al. (2014)
	Aphodiinae	Stebnicka (2007), Maruyama (2010)
	Scarabaeinae	Halffter & Matthews (1966), Larsen & al. (2006), Krell & Philips (2010)
Silvanidae		Thomas & Leschen (2010)
Tenebrionidae		Matthews & al. (2010)
Zopheridae	*Rhopalocerus*	Slipinski & Lawrence (2010b)
Staphylinidae		
(Aleocharinae)	**Aenictoteratini**	Kistner (1993), Maruyama & al. (2009)
	Aleocharini	Assing (1999), Maruyama & Hlaváč (2003), Maruyama & al. (2011)
	Athetini	Kistner (1982), Elven & al. (2012), Mathis & Eldredge (2014)
	Crematoxenini	Jacobson & Kistner (1992)
	Dorylogastrini	Kistner (1993)
	Dorylomimini	Kistner (1993)
	Dorylophilini	Kistner (1993)
	Ecitocharini	Kistner & Jacobson (1990)
	Ecitogastrini	Seevers (1965)
	Falagriini	Kistner (1983), Assing (2001)
	Lomechusini	Hölldobler & Wilson (1990), Hlaváč & al. (2011)
	Mesoporini	Seevers (1957)
	Mimanommatini	Kistner (1993)
	Mimecitini	Jacobson & Kistner (1991)
	Oxypodini	Hölldobler (1973), Quinet & Pasteels (1995), Zagaja & al. (2014)
	Paradoxenusini	Bruch (1937)
	Phyllodinardini	Wasmann (1916b)
	Pygostenini	Kistner (1979)
	Sahlbergiini	Kistner (1973), Kistner (1993)
	Sceptobiini	Danoff-Burg (1994), Danoff-Burg (1996)
	Trilobitideini	Kistner (2006)
(Pselaphinae)	**Arnyliini**	Maruyama & al. (2013)
	Amauropini	Barr (1974)
	Arhytodini	Bruch (1918), Chandler & Wolda (1986)
	Attapseniini	Bruch (1933), Park (1942)
	Batrisini	Donisthorpe (1927), Park (1947a), Maruyama & al. (2013)
	Brachyglutini	Chandler (2001), Maruyama & Sugaya (2004), Chandler & al. (2015)
	Bythinini	Pearce (1957)
	Bythinoplectini	Newton & al. (2000)
	Clavigerini	Donisthorpe (1927), Akre & Hill (1973), Parker & Grimaldi (2014)
	Colilodionini	Besuchet (1991), Löbl (1994), Parker & Grimaldi (2014)

(Pselaphinae, continued)	**Ctenistini**	NEWTON & al. (2000), CHANDLER (2001)
	Cyathigerini	LEA (1912), SUGAYA & al. (2004)
	Euplectini	*Capnites* JEANNEL (1954), incorrectly placed in Iniocyphini (J. Parker, unpubl.)
	Goniacerini	JEANNEL (1959)
	Jubini	PARK (1942)
	Metopiasini	PARK (1942)
	Pselaphini	CHANDLER (2001)
	Tiracerini	CHANDLER (2001), PARKER & GRIMALDI (2014)
	Tmesiphorini	PARK (1933b), CHANDLER (2001), MARUYAMA & al. (2013)
	Trichonychini	PEARCE (1957), YIN & al. (2011), NOMURA & LESCHEN (2015)
	Trogastrini	PARKER & MARUYAMA (2013)
	Tyrini	PARK (1964), NEWTON & al. (2000), CHANDLER (2001)
(other subfamilies)	Osoriinae	BURAKOWSKI & NEWTON (1992)
	Oxytelinae	SEEVERS (1965), HERMAN (1970), HERMAN (2003)
	Paederinae	SEEVERS (1965), KISTNER (1982)
	Tachyporinae	SEEVERS (1958), AKRE & TORGERSON (1969)
	Scydmaeninae	O'KEEFE (2000), JAŁOSZYŃSKI (2013)
	Staphylininae	SEEVERS (1965), KISTNER (1982)
	Steninae	ZERCHE (2009), PUTHZ (2010)

few of these taxa represent significant, exclusively myrmecophilous radiations with hundreds of species; others are families or subfamilies in which numerous independent lineages have convergently evolved this lifestyle; still others represent small, isolated instances of myrmecophily in families with few or no other myrmecophilous lineages. In what follows, I present a taxonomic breakdown of beetles that live with ants. This is not an exhaustive review, akin to that attempted by KISTNER (1979, 1982). Rather, it is a summary of different myrmecophilous groups and their biologies, deliberately designed to convey basic trends in the evolution of myrmecophily that exist within the Coleoptera. Its purpose is to prime the reader for a discussion of the acute bias evident in the phylogenetic distribution of myrmecophilous beetle lineages, as well as the striking convergence and parallel trait evolution that exists among these lineages. I have, however, used it as opportunity to synthesise important recent studies that are clarifying our understanding of the biology, systematics and evolution of beetle myrmecophiles. Where possible, I include some discussion of larval as well as adult biology. Several morphological terms describing adaptive characters for myrmecophily are used repeatedly, and these are explained in Box 2. The taxonomic scheme follows BOUCHARD & al. (2011).

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Order Coleoptera

Across the Coleoptera, myrmecophily is confined to the two largest suborders: Adephaga and Polyphaga. Instances in the remaining two suborders, Myxophaga and Archostemata, which together include eight families and only 140 or so species, are unknown.

Suborder Adephaga

Among the 11 families and ~46,000 species of adephagans, myrmecophily is known definitively in Carabidae alone.

Adephaga: Carabidae

Carabids (ground beetles) are a family of ~40,000 predominantly predatory species. While opportunistic ant predation and casual nest intrusion may be relatively common in carabids (HENGEVELD 1979, KISTNER 1982), instances of myrmecophily are infrequent (ERWIN 1979), especially given the size of the family. However, in the subfamily Paussinae (formerly regarded as a separate family), Carabidae contains one of the largest clades of obligate, morphologically specialised myrmecophiles.

Carabidae: Paussinae. Of the five tribes of Paussinae (~800 species), the ~600 described species of Paussini are currently ranked as the largest clade of exclusively myrmecophilous beetles, occurring in most global regions and utilising diverse ant hosts. They are charismatic beetles (two spectacular examples are shown in Figures 2A, 2B), with dramatic morphologies and numerous adaptive characters for myrmecophily (see Box 2): across the tribe, genera may exhibit gland-associated trichomes, fusions of antennal segments, modified mouthparts and even stridulatory organs that mimic host ant vibrational cues (DI GIULIO & al. 2014, DI GIULIO & al. 2015). Where known, the beetles appear highly socially integrated into host colonies (see Box 1), with adults feeding on the brood and workers (GEISELHARDT & al. 2007). Larvae are also thought to be obligately myrmecophilous nest inhabitants, with a cup-shaped abdominal tip that exudes substances that are attractive to worker ants, and reduced mouthparts for possible trophallaxis (DI GIULIO & MOORE 2004, DI GIULIO & al. 2011). Paussini likely represents one of the more ancient clades of myrmecophiles, with crown-group members occurring in Middle Eocene Baltic amber (~44 million years old) (WASMANN 1929). This antiquity has provided a long time for diversification, and may have contributed to the group's great size and zoogeographic range. However, a recent molecular dating analysis indicates that major components of the extant paussine fauna are unexpectedly young. The largest genus, *Paussus* (~400 species) was inferred to have originated only 23.3 million years ago, and has undergone a particularly rapid radiation in Madagascar, yielding 86 known species in the last 2.6 million years alone (MOORE & ROBERTSON 2014). This same molecular study revealed surprising convergent evolution in the shape of the antenna – an organ which in *Paussus* is transformed into a complex glandular structure, where the antennomeres are fused into a hollow disc or tube filled with secretory cell types (DI GIULIO & al. 2009). Independent acquisition of near-identical antennal morphologies in distinct *Paussus* lineages may stem from their utilisation of similar host ants (MOORE & ROBERTSON 2014), although how the exact antennal form influences the myrmecophile-host relationship is mysterious. Members of Paussini's presumed sister tribe, Protopaussini (containing the single genus *Protopaussus*), are also thought to be obligate myrmecophiles based on their morphology (NAGEL 1997), so it is probable that myrmecophily in Paussini+Protopaussini has a single evolutionary origin. Elsewhere in the subfamily Paussinae, tribes are largely composed of free-living taxa (GEISELHARDT & al. 2007), the main exception being beetles of the genus *Physea* (Ozaenini) which inhabit *Atta* nests, and possible facultative myrmecophily in some other ozaenine genera (MOORE 2008), as well as in the tribe Metriini (MOORE & DI GIULIO 2008).

Carabidae: other subfamilies. Aside from Paussinae (more specifically, Paussini), no other carabids show such an advanced form of myrmecophily, and socially parasitic relationships with ants are uncommon (ERWIN 1979, KISTNER 1982, KOTZE & al. 2011). Arguably, the next most notable group is the tribe Pseudomorphini (Fig. 2C), where adults and larvae of some genera have been found frequenting colonies, feeding on ant larvae (ERWIN 1981, 2013). Adults appear defensively adapted for myrmecophily with a compact, near-limuloid shape and shortened appendages that can be largely concealed underneath the explanate body margins (Fig. 2C). In an Australian pseudomorphine genus, *Sphallomorpha*, larvae construct burrows adjacent to *Iridomyrmex* colonies and prey on passing workers (MOORE 1974). The probable sister group of Pseudomorphini is the tribe Graphipterini (OBER & MADDISON 2008), in which adults are free-living and morphologically generalised, but larvae of at least the genus *Graphipterus* are myrmecophilous, inhabiting colonies of various ant species and feeding on the brood; analogous biology is also seen in the more distantly related *Anthia* (subgenus *Termophilum*) (see DINTER & al. 2002). In the Holarctic region, adults of a few carabid species are consistently collected from colonies, including some North American *Elaphrops* (see BALL & BOUSQUET 2000), the Western Palearctic *Pseudotrechus mutilatus* (see DE FERRER & al. 2008) and Japanese *Lachnoderma asperum* (see MARUYAMA & al. 2013), but their habits are unknown. Aside from these examples, the few other accounts of ant associations in Carabidae describe instances of myrmecophagy. For example, adults of species of *Helluomorphoides* locate *Neivamyrmex* raiding and emigration trails, picking off workers, brood and dropped food items, and displaying an impressive capacity to withstand attacks from the ants (PLSEK & al. 1969, TOPOFF 1969). Remnants of ants in gut contents of related genera of *Helluomorphoides*' subtribe (Helluonini: Omphrina) imply myrmecophagy may be the prevailing diet in these carabids (REICHARDT 1974). TALARICO & al. (2009) have discussed whether certain behaviours of *Siagona europea*, another obligate ant predator, signify an intermediate evolutionary stage between myrmecophagy and myrmecophily. Myrmecophily in Rhysodinae (OKE 1932) is doubtful (MAKAROV 2008).

Suborder Polyphaga

Across the 156 families and ~350,000 species of polyphagans, myrmecophily has evolved in a great many groups (Tab. 1), but instances of its evolution are strongly biased to Histeridae and Staphylinidae, and moreover, to certain subfamilies of the latter. Recurrent evolution of myrmecophily has also occurred in some other families, most notably Scarabaeidae and Tenebrionidae, albeit less frequently and with weaker intimacy than can be routinely observed in staphylinids and histerids.

Polyphaga: Histeridae

Histerids (clown beetles) are a family of moderate size (~4621 described species), most of which are presumed to be predatory, and many of which have somewhat cryptic ecologies, including subcortical species (living under bark), inhabitants of decaying organic substrates such as dung and carrion, and bird nest and mammal burrow dwellers (CATERINO & VOGLER 2002). Most histerids have a heavily sclerotised, broadly convex and robust body, with short retractable appendages; the head is also retractable and protected from above by the overlying pronotum. Myrmecophily is widespread in histerids (KOVARIK & CATERINO 2005), with the subfamilies Haeteriinae and Chlamydopsinae representing two large radiations of predominantly obligate myrmecophiles, many of which are morphologically remarkable.

Histeridae: Haeteriinae. Haeteriines (Fig. 2D) number 335 described species in more than 100 genera, although the true diversity is far larger (M. Caterino, pers. comm.). Monophyly of the group is highly likely, aside from a few aberrant genera of questionable placement (KOVARIK & CATERINO 2005), and the subfamily may rank alongside Paussini (Carabidae, discussed above) and Clavigeritae (Staphylinidae: Pselaphinae, discussed below) as one of the most speciose clades of beetle myrmecophiles. The group also includes scattered termitophilous species (TISHECHKIN 2005). As with paussines and clavigerites, many genera include one or just a few species – a symptom of the extreme morphological diversity of the subfamily that can obscure even close phylogenetic relationships. Haeteriines range from small species with relatively generalised morphologies, to larger-bodied and heavily armoured species with dramatic cuticular protruberances, particularly on the pronotum, most likely for withstanding grasping ant mandibles. Trichomes are present in various taxa, and some have very elongate legs to grasp or groom hosts (AKRE 1968, KISTNER 1982). Haeteriines are predominantly Neotropical, but extend into North America and three genera also occur in the Palaearctic. Individual haeteriine genera are adapted to their ant hosts in diverse ways: some are attacked or largely ignored by their hosts, while others are highly integrated guests, which may be fed trophallactically by workers (WHEELER 1908, HENDERSON & JEANNE

Fig. 2: Diversity of myrmecophilous and putatively myrmecophilous beetles. Photograph credits in parentheses. (A, B) Carabidae: Paussini: *Platyrhopalopsis picteti* (A; R. Dudko), *Euplatyrhopalus tadauchii* (B; M. Maruyama); (C) Carabidae: Pseudomorphini: *Guyanemorpha spectabilis* (K. Darrow); (D) Histeridae: Haeteriinae: *Bastactister* sp. (A. Tishechkin); (E) Histeridae: Chlamydopsinae: *Chlamydopsis dispersa* (A. Tishechkin); (F - I) Staphylinidae: Aleocharinae: *Aenictoxenides mirabilis* (F; M. Maruyama), *Trilobitideus* sp. (G; M. Maruyama), *Aenictosymbia cornuta* (H, H' lateral and dorsal views, respectively; M. Maruyama), *Lomechusoides strumosus* (I; M. Smirnov); (J) Staphylinidae: Scydmaeninae: *Plaumanniola sanctaecatharinae* (P. Jałoszyński / Zootaxa); (K - N) Staphylinidae: Pselaphinae: *Theocerus* sp. (K; J. Parker), *Jubogaster towai* (L; J. Parker & M. Maruyama / Zootaxa), *Songius hlavaci* (M; Z. Yin), *Epicaris* sp. (N; P. Krásenský); (O) Hydrophilidae: *Chimaerocyon shimadai* (M. Fikáček / Zootaxa); (P) Anobiidae: Ptininae: *Fabrasia wheeleri* (K.T. Eldredge); (Q) Buprestidae: *Habroloma myrmecophila* (M. Fikáček); (R) Elateridae: *Agraeus* sp. (H. Schillhammer); (S) Brentidae: Eremoxenini: *Pycnotarsobrentus inuiae* (M. Maruyama).


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1990). A recent biochemical study of one of the European genera, *Sternocoelis*, provided evidence that the beetles can actively synthesise cuticular hydrocarbon blends to match the odour profiles of their *Aphaenogaster* host colonies (LENOIR & al. 2012). The greatest number of haeteriine species are army ant inquilines (HELAVA & al. 1985, TISHECHKIN 2005), with almost 30 genera associated with *Eciton* alone. Adults appear to be highly host-specific (TISHECHKIN 2005), and are attracted to trails of their hosts and repelled by trails of non-host species (AKRE & RETTENMEYER 1968). The beetles have been observed feeding on the ants' brood and harvested food, and to run with or phoretically attach to workers during emigrations (AKRE 1968). DNA sequencing of histerid larvae sifted from under *Eciton* bivouacs and refuse dumps successfully identified haeteriines (CATERINO & TISHECHKIN 2006), implying that the entire lifecycles of at least some of these army ant guests take place in or around, host colonies.

Histeridae: Chlamydopsinae. With 177 species, chlamydopsines (Fig. 2E) form the second significant radiation of histerid myrmecophiles, with a single species recorded in association with termites (CATERINO & DÉGALLIER 2007). The group is confined principally to the tropics of the Australasian, Indomalayan and Oceanian regions, but extends northwards into subtropical Japan. Most species appear to be morphologically specialised obligate colony guests, possessing trichomes that envelop deep clefts or depressions on the elytral humeri, or more rarely on the pronotum. Unfortunately, the biology of chlamydopsines is exceptionally poorly known, although the beetles have been observed feeding on ant larvae and being carried by their hosts, which may use the elytral clefts as grasping notches (OKE 1923). Although the majority of species have been collected using flight intercept traps and thus lack host association data (TISHECHKIN 2009), collections made directly from colonies reveal that as a group, chlamydopsines utilise diverse host ants, although ponerines appear to be the most commonly used ant subfamily (CATERINO & DÉGALLIER 2007). Chlamydopsine larvae await discovery.

Histeridae: other subfamilies. In addition to the spectacular haeteriines and chlamydopsines, myrmecophily has arisen independently numerous times elsewhere in Histeridae (KOVARIK & CATERINO 2005), with eight out of eleven subfamilies containing multiple lineages of inquilinous species (CATERINO & DÉGALLIER 2007). Collectively, these other instances emphasise the preponderance of this lifestyle across the family, although estimating the approximate number of origins of myrmecophily is hindered by a lack of phylogenetic information. To give the reader a sense of the prevalence of this lifestyle, almost 30% of the 57 North American histerid genera listed in KOVARIK & CATERINO (2000) include at least one species that has been found with ants, and these species span six subfamilies. With exceptions, outside of the Haeteriinae and Chlamydopsinae, most inquilinous species are not obviously specialised for myrmecophily beyond their possession of the normal protective body form that is typical of most histerids; and in at least some cases, field observations indicate correspondingly less intimate relationships with hosts. For example, NAVARRETE-HEREDIA (2001) listed 61 species belonging to six histerid subfamilies as having been found with attine leaf cutter ants; the majority were recorded from refuse piles, where the beetles likely prey on developing Diptera and Coleoptera (KOVARIK & CATERINO 2005). Nevertheless, there is clearly extensive variation in the nature of the myrmecophilous relationship, with other taxa behaving as colony parasites that target the brood. Even within genera there may be vast discrepancies: the 177 species of the New World genus *Operclipygus* (Histerinae: Exosternini) exhibit diverse ecologies; some are free-living, while others frequent peripheral refuse sites of *Atta* and *Acromyrmex* colonies; still others associate with *Aphaenogaster* and are carried by, and ride on top of, their hosts, suggesting some degree of social integration (CATERINO & TISHECHKIN 2013a). In another large New World genus, *Baconia* (also Exosternini), one of the 116 described species is putatively myrmecophilous, having evolved trichomes on the abdominal pygidium (CATERINO & TISHECHKIN 2013b). There is thus evidence for a family-wide predisposition to evolving myrmecophily in Histeridae. Perhaps the majority of histerid genera may be capable of making the evolutionary shift to this lifestyle quite readily, should ecological opportunity permit.

Polyphaga: Staphylinidae

Staphylinids (rove beetles) are currently the largest family of beetles (and indeed of all animals), with 61,575 species organised into 32 subfamilies (THAYER 2005, GREBENNIKOV & NEWTON 2009). In the majority of staphylinids, the elytra are short, exposing most of the dorsal abdomen, which is usually relatively elongate and flexible. It is within the staphylinids that by far the greatest number of myrmecophilous lineages is found. These occur predominantly in the two largest subfamilies, Aleocharinae and Pselaphinae, with an additional, somewhat weaker evolutionary predisposition to myrmecophily occurring in Scydmaeninae.

Staphylinidae: Aleocharinae. The 16,191 species and 1,296 genera of Aleocharinae are globally distributed, and together form the largest rove beetle subfamily. Aside from a subset of strictly mycophagous, saprophagous and scattered palynophagous taxa, aleocharines are believed to be predatory on microarthropods (THAYER 2005) or omnivorous (KLIMASZEWSKI & al. 2013). In general, the beetles are small in size (usually between 2 - 6 mm) and morphologically conservative, with most species possessing an elongate, flexible body plan with short elytra, akin to the majority of rove beetles. Despite their basic homogeneity in body form, the subfamily has invaded ant colonies many times during its evolution, producing an unparalleled diversity of myrmecophilous lifestyles, and these are sometimes concomitant with radical changes in external anatomy (Figs. 2F - I). The biology of inquilinous Aleocharinae ranges from facultative associations to obligate relationships that encompass brood predation, kleptoparasitism, phoresis and highly socially integrated symbioses. The latter involve some of the most dramatic inquilinous morphologies and elaborate, host-deceptive behaviours seen among beetle myrmecophiles. An evolutionary predisposition to myrmecophily seems to be inherent in Aleocharinae, although the lifestyle is more common in certain tribes and notably absent from others. Twenty-three of the 62 tribes of Aleocharinae include myrmecophiles, and several are comprised predominantly or exclusively of such species (Tab. 1). Many of the wholly inquilinous higher taxa have been erected based on the obscure morphology of a single genus or small collection of genera, so in reality, most (perhaps all) of these groups probably emerge from within other, larger and principally free-living tribes. Indeed, numerous additional instances of myrmecophily pervade the bigger tribes, including many species with generalised morphologies that largely resemble their free-living close relatives. In the North American fauna, 20 of the 183 genera spanning six out of 21 tribes include species that are associated with ants (SEEVERS 1978, NEWTON & al. 2000). Aleocharinae also includes multiple termitophilous taxa, not discussed here, some of which belong to tribes that include myrmecophiles.

Among the aleocharines are species that arguably represent the best-studied myrmecophilous beetles. Indeed, the rampant, recurring evolution of myrmecophily in Aleocharinae means that the subfamily as a whole serves as a paradigm for understanding the evolution of biological mechanisms mediating social insect symbioses. Seminal works by Bert Hölldobler revealed the instrumental role of aleocharine glandular chemistry in governing interactions with ants. Most aleocharines possess a "tergal gland" complex between tergites VI and VII on the abdomen, with a large chemical reservoir that secretes defensive irritants such as quinones (JORDAN 1913, STEIDLE & DETTNER 1993). However, in the Palaearctic *Lomechusa* (= *Atemeles*), a highly integrated guest of *Formica* and *Myrmica* that is accepted and fed trophallactically by its hosts in both the adult and larval stages (HÖLLDOBLER 1967, 1969, 1970; Fig. 2I shows the closely related *Lomechusoides*), additional, evolutionarily novel glands are present on the abdomen. One kind, at the abdominal tip, synthesises unidentified proteinaceous compounds that elicit appeasement of aggressive host ants; another type, serially repeated on anterior abdominal segments and associated with trichomes, produces secretions that stimulate the workers to adopt the beetles into colonies (HÖLLDOBLER 1970) (Figs. 4B, C). By this means, the beetles are permitted access to brood galleries where they feed on ant larvae and lay eggs, their own offspring behaving as impostors that are reared by workers (HÖLLDOBLER 1967). Putative appeasement behaviour mediated by abdominal glandular secretions occurs in species of the more weakly integrated *Pella*, a related genus of the same tribe (Lomechusini), which inhabits more peripheral nest chambers and feeds mostly on dead ants (HÖLLDOBLER & al. 1981). A similar appeasement strategy and associated abdominal glandular complex may also exist in the more distantly related *Dinarda* (Oxypodini) (see HÖLLDOBLER 1973).

The de novo synthesis of pheromonal cues thus appears to be a significant part of the socially parasitic strategy employed by many aleocharines. Confirming earlier speculation (KISTNER & BLUM 1971), recent studies have shown that the tergal gland itself can play a role in mediating myrmecophily in species that have "reprogrammed" the chemistry of the gland, replacing or supplementing the quinones with novel volatile compounds that modify host ant behaviour. In some *Pella* species, sulcatone is emitted from the tergal gland, which functions as a "panic alarm" pheromone that overrides aggression from the beetle's host, *Lasius fuliginosus*, acting to disperse workers and allowing the beetles to escape (STOEFFLER & al. 2007, STOEFFLER & al. 2011). In certain species of *Zyras* (also Lomechusini), the gland produces terpenes that may mimic the volatile cues produced by *L. fuliginosus*-tended aphids (STOEFFLER & al. 2013). Hence, employment of diverse compounds secreted by the tergal gland, or various novel glands, is seen repeatedly among aleocharines, and appears to be a widely used means to attenuate host aggression. Several studies have provided evidence that aleocharines chemically mimic their hosts' cuticular hydrocarbon profiles (AKINO 2002, MARUYAMA & al. 2009, LENOIR & al. 2012). However, there are exceptions (STOEFFLER & al. 2011), suggesting that hydrocarbon mimicry may not be universal, or in some cases a consequence of nest occupancy rather than a primary integrating strategy.

In addition to studies of their chemical communication, myrmecophilous aleocharines are equally well known for their relationships with army ants. More so than any other beetle taxon, aleocharines include the greatest diversity of "dorylophiles", these associations having arisen independently numerous times in taxa from both the Old and New World tropics (SEEVERS 1965). Many such species are closely associated with their hosts, accompanying them on emigrations and raids, and possessing specialised morphologies, most notably various defensive "limuloid" forms (Fig. 2F, G), or ant-mimicking "myrmecoid" body plans (Fig. 2H) (Box 2). Myrmecoid taxa in particular are truly remarkable, with many such species strikingly resembling their host's shape, down to minute details of body sculpturation. Myrmecoid morphology appears to go hand in hand with a suite of behaviours that indicates a high degree of social integration in host colonies. The beetles frequently interact with their hosts, actively grooming workers, presumably to procure the colony's cuticular hydrocarbon profile (AKRE & RETTENMEYER 1966, AKRE & TORGERSON 1968); they feed alongside their hosts on captured prey items, and some species are carried by workers as if they are colony brood (KISTNER & JACOBSON 1975, MARUYAMA & al. 2009). The beetles soon die if kept away from colonies (AKRE & RETTENMEYER 1966). Consistent with the theme of aleocharine chemical manipulation of host behaviour, different myrmecoid taxa have evolved novel glands in new positions on the abdomen, and these are suspected to play a role in the assimilation of these beetles into the army ant society (KISTNER & JACOBSON 1990, KISTNER 1993, MARUYAMA & al. 2011).

The combination of morphological changes and behaviours seen in myrmecoid aleocharines constitutes an adaptive syndrome that adjusts these beetles to life with their nomadic hosts. However, myrmecoid syndrome presents two distinct evolutionary conundrums. First, it remains unclear why these beetles mimic their hosts at all, when the latter are visually blind to the beetle's body form. It has been suggested that the myrmecoid shape may not function in host deception, but rather achieves Batesian mimicry, protecting the beetles during colony raids and emigrations from vertebrate predators that avoid targeting the ants (HÖLLDOBLER 1971, KISTNER & JACOBSON 1990). Indeed, in some genera, such as the *Eciton*-associated *Ecitophya* (Ecitocharini), even the body colouration closely matches that of the workers, making the beetles challenging to spot amongst their aggressive hosts. This hypothesis cannot be universal, however, given that some myrmecoid taxa, such as the *Labidus*-associated Mimecitini, differ strongly in body colour from their hosts, which moreover are hypogaeic, making body colour possibly irrelevant. If the alternative possibility is true – that ant-like shape evolved for deceiving the host, and functions in social integration ("Wasmannian mimicry", RETTENMEYER 1970), then it may accomplish tactile mimicry as opposed to a visual resemblance to the ants (KISTNER 1979, KISTNER 1993). Perhaps both explanations are true: host deception being the primary selective agent driving body shape mimicry, with colouration being a secondary adaptation against predators in species utilising epigaeic hosts that raid or emigrate during daylight.

Second, controversy surrounds whether myrmecoid syndrome has a single principal origin, or multiple independent origins. In a major work on army ant associated rove beetles, SEEVERS (1965) proposed a single major origin of myrmecoid syndrome in aleocharines, forming the large pan-tropical tribe Dorylomimini. Aside from some minor myrmecoid-like forms elsewhere in aleocharines and other rove beetle subfamilies, Seevers' Dorylomimini incorporated all 33 Old and New World aleocharine genera known at that time that exhibit an anatomically specialised myrmecoid body form (SEEVERS 1965, KISTNER 1979). This single, primary origin of myrmecoid syndrome parallels the now well-supported monophyly of army ants (BRADY 2003, BRADY & al. 2014), and suggests that these beetles may be an ancient clade that radiated globally in the tropics as their hosts diversified into modern army ant genera. However, in a series of revisions, Kistner split Seevers' Dorylomimini into eight tribes, three in the New World: Ecitocharini (KISTNER & JACOBSON 1990), Mimecitini (= Leptanillophilini) (JACOBSON & KISTNER 1991) and Crematoxenini (JACOBSON & KISTNER 1992), and five in the Old World: Dorylomimini, Dorylogastrini, Sahlbergiini, Mimanommatini and Aenictoteratini (KISTNER 1993). Kistner emphasised key morphological differences between these tribes that imply a possible polyphyletic origin of myrmecoid syndrome within Aleocharinae. This scenario implies rampant – and stunning – morphological and behavioural convergence between aleocharine lineages that have independently evolved associations with army ants. Laborious collecting of myrmecoid aleocharines throughout the world's tropics has now enabled these alternative scenarios to be tested using molecular data (M. Maruyama, K.T. Eldredge & J. Parker, unpubl.). This has revealed an unprecedented number of independent origins of myrmecoid syndrome, only partially congruent with Kistner's revisions, with each clade typically highly host-specific to a single army ant genus. The extent of morphological convergence between unrelated clades in different tropical regions is extraordinary – a striking example of parallel trait evolution in animals.

Staphylinidae: Pselaphinae. Pselaphines constitute a clade of 9,854 species in 1,247 genera. The body size is always small (typically 1 - 3 mm in length) and their form differs from most rove beetles in that the exposed abdominal segments are relatively inflexible due to a reduction of the intersegmental membranes. The whole integument is usually quite thick, and in the majority of species, the abdomen is short, broad and convex, making the overall body plan compact and consolidated (Figs. 2K - N). Pselaphinae occur globally outside of the polar regions, attaining their highest taxonomic diversity as well as massive ecological abundance in tropical forest leaf litter (NEWTON & CHANDLER 1989, OLSON 1994, SAKCHOOWONG & al. 2007, SAKCHOOWONG & al. 2008). All species are believed to be predatory, with the majority preying on microarthropods such as mites and collembolans (PARK 1932a, CHANDLER 1990, SCHOMANN & al. 2008). As in Aleocharinae, myrmecophily is rife in Pselaphinae: among the 39 tribes, fully 22 include taxa that display evidence of myrmecophily (Tab. 1). Thirty-two of the 163 Australian pselaphine genera have been collected from ant colonies (CHANDLER 2001), while in North America the total is 24 out of 100 genera (NEWTON & al. 2000 and subsequent observations). It is evident from the phylogenetic distribution of inquilinous lineages that this lifestyle has arisen independently an inordinate number of times (PARK 1942; J. Parker, unpubl.). Aside from numerous exclusively myrmecophilous tribes and genera, it is not unusual to find some species within predominantly free-living genera living obligately or facultatively with ants. For example, among the 29 North American *Brachygluta* – a primarily waterside litter-inhabiting genus – two newly described species appear to be myrmecophiles (CHANDLER & al. 2015); likewise, a sizeable but phylogenetically dispersed subset of species in the large Holarctic genus *Batrisodes* are routinely collected with ants (PARK 1942, 1947a, PEARCE 1957), while among species of the largely Neotropical litter-dwelling genus *Hamotus*, several are myrmecophilous, including the only pselaphine guest of army ants (*H. ecitophilus*). The list of such examples is very long, their frequency revealing a near-subfamily-wide evolutionary predisposition to myrmecophily.

Despite their minute size, Pselaphinae is a morphologically explosive subfamily and this is especially so for the inquilinous groups. These can be difficult to place systematically. For example, the recently discovered *Jubogaster* (Fig. 2L), a Peruvian guest of *Pheidole xanthogaster* and one of the physically largest species ever discovered (5.1 mm), defied tribal placement until molecular data showed it to be a morphologically derived member of the predominantly free-living tribe Trogastrini (PARKER & MARUYAMA 2013). Pselaphine morphology is pushed to its extreme in the supertribe Clavigeritae, an exclusively myrmecophilous group that was originally treated as a separate family. Clavigerites constitute a major radiation of obligate myrmecophiles, perhaps surpassing paussine carabids and haeteriine histerids, with 369 extant species and severalfold this number undescribed. The beetles rank among the most highly socially integrated myrmecophiles, with external morphology heavily modified for colony parasitism (Figs. 2K, 5A, 6, beetle at middle right). Trichomes at the base of the abdomen or tips of the elytra are associated with large "Wasmann glands" that exude putative host appeasement compounds (CAMMAERTS 1974, HILL & al. 1976) (Figs. 2K, 5A, B, 6), with this part of the body fashioned into a grasping notch for workers to pick up and carry the beetles (LESCHEN 1991). The mouthparts are recessed inside the oral cavity to mediate trophallaxis with hosts; the maxillary palpi – often extraordinarily large and elaborate in pselaphines – are reduced to a single rudimentary segment, and the beetle's blunt mandibles are suitable only for scraping and piercing ant eggs and larvae. To strengthen the body, the appendages are shortened, the three largest tergites of the abdomen (IV - VI) are fused into a single shield-like "tergal plate", and the antennomeres are likewise fused (different species have between 3 and 6 antennomeres, whereas most other pselaphines have the ancestral complement of 11). The North American *Adranes* and Palaearctic *Claviger* are both eyeless and flightless. One especially curious genus, *Semiclaviger*, is almost limuloid in form, an unusual body shape for the subfamily (HLAVÁČ & al. 2013). Detailed biological data exist for some temperate species (DONISTHORPE 1927, PARK 1932b, 1942, 1947b, AKRE & HILL 1973, LESCHEN 1991, CAMMAERTS 1992, 1995, 1996, 1999, AKINO 2002). Juvenile stages of Clavigeritae have never been discovered, although a photograph of a putative larva was presented by WASMANN (1918a).

As with paussine carabids, discussed above, the evolutionary success of Clavigeritae may be partly explained by the group's age. A recent paper described a fossil clavigerite, *Protoclaviger trichodens*, in Early Eocene Cambay amber that represents the earliest known definitive myrmecophile (PARKER & GRIMALDI 2014) (Fig. 5D). *Protoclaviger* is a stem group, with transitional morphology that captures the evolution of extreme myrmecophilous specialisation midway: trichomes are present, but the dorsal abdomen retains the primitive segmentation of other pselaphines and the trichomes are serially repeated on the first three visible tergites (IV - VI) (Fig. 5D); the antennomeres are fused together but only partially so (8 antennomeres are present, instead of 3 - 6), and the maxillary palpi are reduced in size and made of only a single segment but extend further outside of the oral cavity than in modern species. Although prototypical in form, *Protoclaviger* evidently represents a sophisticated incarnation of myrmecophily, with the morphological hallmarks that mediate social integration. Cambay amber records one of the oldest paleoenvironments with a significant ecological presence of ants (RUST & al. 2010), although still at a fraction of their present day abundance (GRIMALDI & AGOSTI 2000, LAPOLLA & DLUSSKY 2013). *Protoclaviger* is evidence that socially parasitic exploitation of colonies was well underway by the first appearance of crown group members of modern ant subfamilies. Molecular dating suggests that Clavigeritae in fact originated in the late Cretaceous, and underwent a radiation correlated with (and probably catalysed by) the ecological rise of modern ants during the Cenozoic (PARKER & GRIMALDI 2014).

Outside of the extraordinary Clavigeritae, most myrmecophilous pselaphines do not show such clear evidence of social integration; most can be observed walking in nest galleries, for the most part unnoticed by hosts, feeding on ant eggs, larvae, and other colony invertebrates (DONISTHORPE 1927, PARK 1932a, 1964). Many such species appear unspecialised, with morphologies similar to their free-living relatives. Others are clearly adapted to colony life: They may possess a smooth, sometimes oily and glistening integument, thicker and more robust appendages, and antennomeres that are more compact and reduced in length (e.g., Fig. 2M). Repeatedly across the subfamily, however, several groups seem to have independently evolved more intimate host relationships, and these instances appear to obey a remarkable, recurrent phenotypic trend, whereby the morphology converges on the same suite of adaptive characters exhibited by the Clavigeritae. For example, in the largely myrmecophilous tribe Ctenistini, the African genus *Epicaris* (collected with *Brachyponera sennaarensis*) possesses trichomes on the elytral margins flanking the basal abdomen (Fig. 2N, JEANNEL 1959), just like many Clavigeritae. One recently described *Epicaris* species from Socotra even has miniaturised maxillary palpi (HLAVÁČ & BAŇAR 2014), suggesting a shift to feeding on the immobile brood or possible trophallaxis, akin to Clavigeritae. Elsewhere in Ctenistini, a *Messor*-associated species of *Desimia* (subgenus *Xenodesimia*; *X. rugosiventris*) has analogously converged on this same morphology, with elytral trichomes and small palpi (JEANNEL 1959). In *Attapsenius* (Attapseniini), an obligate guest of *Atta sexdens* fungus galleries, trichomes are again seen at the base of the abdomen (Fig. 6, bottom right), and once more the maxillary palpi are miniscule; in this genus the antennal segments are also very compact, perhaps functioning like the fused antennomeres of Clavigeritae (PARK 1942). Basal abdominal trichomes are also seen in several other genera that currently lack host associations: *Batrisiotes*, *Baceysus* and *Gadgarra* of Batrisini (see CHANDLER 2001, LOBL & KURBATOV 2001), and the trichonychine genus *Millaa* (see CHANDLER 2001). What these cases collectively reveal is an evolutionary trend in pselaphines comparable to the recurrent evolution of the myrmecoid body form in army ant associated aleocharines, mentioned above. As increasingly intimate associations with ants evolve, pselaphine lineages follow a predictable phenotypic trajectory, ultimately recapitulating the morphological innovations of Clavigeritae.

Staphylinidae: Scydmaeninae. Scydmaenines (~5,210 species) differ from the majority of rove beetles by their possession of long elytra that usually cover the abdomen, and a small, compact body form that approximates the size and shape of most pselaphines. Up until a few years ago the group was given family status, until a detailed morphological study placed them as a subfamily within Staphylinidae (see GREBENNIKOV & NEWTON 2009), a relationship supported by a recent molecular phylogenetic study (MCKENNA & al. 2014). Scydmaenines are predominantly leaf litter and soil inhabitants, and like pselaphines, their abundance and diversity explode in tropical forest litter (OLSON 1994, SAKCHOOWONG & al. 2008). Most are thought to be specialised mite predators (reviewed in JAŁOSZYŃSKI 2012), targeting armoured mites (Oribatida) with modified mouthparts able to cut through the thick integument (JAŁOSZYŃSKI & BEUTEL 2012, JAŁOSZYŃSKI & OLSZANOWSKI 2013), although some have a preference for softer-bodied arthropods (JAŁOSZYŃSKI 2012). The myrmecophilous habits of scydmaenines are poorly studied, but O'KEEFE (2000) provided a review of the recorded ant associations in this subfamily and listed 117 species in 20 genera that had been collected from colonies. Importantly, however, many of these species are also commonly found outside of nests, indicating that these associations are probably facultative. Consistent with this idea, some of these species can be maintained in captivity without any ants (JAŁOSZYŃSKI 2012), and given the specialised feeding habits of some scydmaenines, it may be that the beetles enter colonies to feed on mites and other microarthropods rather than the brood (O'KEEFE 2000). It is also notable that the few apparently obligate myrmecophiles in this subfamily show no obvious morphological adaptations for this lifestyle, instead closely resembling their free-living relatives (JAŁOSZYŃSKI 2013). In fact, the only genera with morphologies that strongly imply myrmecophily have yet to be demonstrated as inquilinous. *Trur-*

lia and *Trichokrater*, two closely allied Indomalayan genera in the tribe Cepheniini, have setose, trichome-like glandular openings on the pronotum (JAŁOSZYŃSKI 2011), but the biology of both genera is unknown. Arguably the most heavily modified and myrmecophile-like scydmaenine is the Neotropical genus *Plaumanniola* (Fig. 2J), which has a body capable of protective conglobation (ball-forming), and robust, compact antennae like a great many inquilines. Here again, however, the status of this genus as a myrmecophile is questionable, with only a single specimen having been collected with ants (LAWRENCE & REICHARDT 1966, JAŁOSZYŃSKI 2013). Hence, although myrmecophily in scydmaenines may be widespread, obligate associations with host ants appear to be relatively uncommon, and enigmatic taxa with morphological specialisations await to be confirmed as definitive myrmecophiles.

Staphylinidae: other subfamilies: Myrmecophily has evolved definitively in just six of the other 29 staphylinid subfamilies (Tab. 1), and at a much reduced frequency compared to aleocharines, pselaphines and scydmaenines. A handful of instances occur in the large and primarily predaceous subfamilies Staphylininae and Paederinae, sister groups with "typical" flexible rove beetle morphology that together number some 15,369 species. The remainder are found scattered in Tachyporinae (1,553 species), Steninae (2,804 species) and two non-predatory families, Osoriinae (2,351 species) and Oxytelinae (2,099 species). Some of these taxa are morphologically remarkable, and potentially highly integrated into host colonies. For example, myrmecoid army ant guests exist in both Staphylininae and Paederinae: in the single Neotropical genus *Ecitophytes* in Staphylininae (an *Eciton* guest), and – with somewhat less convincing mimicry – in species of the *Ecitonides*- and *Mimophites*-generic groups of Paederinae (all members found with *Labidus*) (see SEEVERS 1965). These represent the only known myrmecoid beetles outside of Aleocharinae. Related to *Ecitophytes* in Staphylininae are the less morphologically derived *Xenobius* (collected with *Nomamyrmex*), *Proxenobius* (with *Eciton*) and *Phileciton* (with *Labidus*) (see CHANI-POSSE 2013, 2014), but Staphylininae contains few other myrmecophiles with obvious anatomical modifications. East Asian *Philetaerius* somewhat resemble the sheen and colour of their *Lasius* (*Dendrolasius*) hosts (MARUYAMA & al. 2000). Several groups nevertheless appear obligately dependent on ants, including a variety of large-bodied Neotropical genera of the subtribe Xanthopygina known to preferentially hunt in the refuse dumps of leaf cutter ants (NAVARRETE-HEREDIA 2001, CHATZIMANOLIS 2014). One possibly myrmecophagous species in the genus *Glenus* (near *biplagiatus*) has been observed entering *Atta* nests, killing workers which it accumulates in a pile outside of the colony (L. Gilbert & S. Chatzimanolis, pers. comm.). A few morphologically generalised staphylinines are also known to associate with Neotropical army ants (SEEVERS 1965), notably *Termitoquedius*, which walks in *Eciton* emigration columns and mimics the ants' body colouration. Isolated myrmecophilous species also exist in the large and otherwise free-living genera *Quedius*, *Platydracus*, *Xantholinus*, and *Leptacinus* (see WASMANN 1887, 1894b, NAVARRETE-HEREDIA 2001, MARUYAMA & al. 2013).

Similarly, in Paederinae, aside from the myrmecoid taxa mentioned above, few other specialised inquilines are found. *Ecitosaurus* and *Ecitobium* are limuloid symbionts of *Labidus* colonies (SEEVERS 1965), while *Myrmecosaurus* is a heavily armoured Neotropical *Solenopsis* guest that undergoes its whole lifecycle inside the colony (WASMANN 1918b); one Argentinian species, *M. ferrugineus*, is adventive in the southern United States with its invasive host ants, *S. invicta* and *S. richteri* (see FRANK 1977). The East Asian *Ophryomedon crenatus* (see WASMANN 1916a) is morphologically similar. WASMANN & AACHEN (1925) believed the paederine *Attaxenus horridus* to be a highly integrated mimic of the major worker of its attine host, *Acromyrmex lobicornis*. The few other known myrmecophilous paederines are less remarkable, possessing generalised morphologies like free-living relatives. Several species of *Dacnochilus* (see JIMÉNEZ-SÁNCHEZ & GALIÁN 2013) and *Astenus* (such as the subgenus *Eurysunius*, ASSING 2003) are associated with ants, but their biology is unknown. The behaviour of *Megastilicus formicarius*, a common guest of *Formica* in the US, has been studied in some detail, and the beetle is clearly non-integrated, and persecuted by its hosts (PARK 1935). Beyond these examples, myrmecophily in both Staphylininae and Paederinae is scarce, with many recorded collections of beetles from nests (e.g., KISTNER 1982) being isolated events and most likely not indicative of myrmecophily.

In Tachyporinae, the body plan of most of the 39 genera is approximately limuloid, but surprisingly few taxa have capitalised on this and transitioned to myrmecophily. The most notable genus is *Vatesus*, a big-bodied, fast moving, non-integrated guest of various Neotropical army ant genera (SEEVERS 1958). *Vatesus* possesses an exaggerated limuloid morphology with a hugely expanded pronotum that guards the modified head and appendages from worker attacks (KISTNER 1979). One species, the *Eciton*-associated *V. clypeatus*, is among the few army ant associated myrmecophiles where the lifecycle is known in any detail. Larvae of this species were identified by raising them to adulthood (AKRE & TORGERSON 1969), and are putative brood predators, hatching during statary phase to emigrate with the host colony until metamorphosis, at which point they probably leave the colony to pupate in soil (AKRE & TORGERSON 1969). Aside from *Vatesus*, the small European genera *Lamprinus* (1 species) and *Lamprinodes* (3 species) are obligately associated with ants (FRANC 1992), while collections of the large, free-living genera *Sepedophilus*, *Tachyporus* and *Tachinus* from colonies (e.g., PAIVINEN & al. 2002) are probably incidental. In Steninae, myrmecophily is again rare: five or six of the 2,600 species of *Stenus* have been collected with ants, with the European *Stenus aterrimus* obligately associated with *Formica* wood ants. This species was recently split into a complex where each species was proposed as host-specific, utilising different *Formica* species (ZERCHE 2009); however, these species have since been synonymised (PUTHZ 2010).

Osoriinae and Oxytelinae are groups of comparable morphology and diet: the body plan is often heavily sclerotised and robust, and the species in both subfamilies are saprophagous or mycophagous. Among the 113 genera of Osoriinae, one European species of the predominantly free-living genus *Thoracophorus*, *T. corticinus*, is associated with *Lasius brunneus*, feeding on fungal hyphae growing on the walls of colony galleries (BURAKOWSKI & NEW-

TON 1992). Several North American *Clavilispinus* are frequently found with *Camponotus* and *Formica* (see SCHWARZ 1894), but their biology is unknown and these associations may not be obligate. A small number of rarely collected tropical genera are clearly specialised myrmecophiles with heavily armoured bodies. These are *Synaenictus*, an eyeless *Aenictus* guest from Kenya (PATRIZI 1947); *Myrmelibia*, collected with *Iridomyrmex* in Australia (NEWTON 1990); and *Pselaphomimus* and four closely allied genera from the Neotropical region, some of which have elaborate, sculptured heads with putative grasping notches bearing small, trichome-like brushes (BRUCH 1942, BURAKOWSKI & NEWTON 1992). In Oxytelinae, a number of genera were erected that were composed solely of myrmecophilous species (HERMAN 1970), but most of these were subsequently synonymised with *Oxytelus* and probably represent specialised forms of this large genus (MAKRANCZY 2006). Two other genera remain valid: *Ecitoclimax* in the Neotropics (SEEVERS 1965) and *Jerozenia* in the Afrotropics (HERMAN 2003), both of which are associated with army ants. Nothing is known about the biology of any of these beetles aside from their host associations, but all have defensive morphologies with cuticular thickenings and tubercles. One genus in Miocene Dominican amber possesses similar morphology to *Jerozenia*, suggesting similar ecological habits (ENGEL & CHATZIMANOLIS 2009).

Polyphaga: Scarabaeidae

Scarabaeids (scarab beetles, including chafers and most dung beetles) are a family of ~28,000 species in which myrmecophily has arisen several times, and is most notably manifested in the subfamilies Cetoniinae and Aphodiinae. Scarabs are predominantly saprophagous, coprophagous or phytophagous beetles, and this is reflected in the bulk of the known myrmecophilous species utilising colony refuse, with examples of more closely integrated species being far rarer. Compared to the three main staphylinid subfamilies discussed above and histerids, the prevalence of myrmecophily in scarabs is weaker, with fewer putative independent origins of this lifestyle.

Scarabaeidae: Cetoniinae: Cetoniines (flower chafers) are a clade of ~4,000 species in which the adults of most species are phytophagous and feed on flowers or fruit, while larvae tend to be saprophagous or xylophagous. Species within several genera of the tribe Cetoniini are known to occupy ant colony debris piles as adults and / or larvae, although these peripheral nest associations appear to be mostly facultative, or do not involve significant, direct interactions with hosts (DONISTHORPE 1927, KISTNER 1982, NAVARRETE-HEREDIA 2001, OROZCO 2012, PUKER & al. 2014). However, in the tribe Cremastocheilini, obligate, socially parasitic myrmecophily is well known (KISTNER 1982, PUKER & al. 2014), and cases of termitophily have also been reported (WASMANN 1918c). The biology of myrmecophilous cremastocheilines has been best worked out for the North American *Cremastocheilus* (~45 species). Here, adults enter nests to prey on ant larvae and pupae (CAZIER & MORTENSON 1965), and are shielded from attacks by their heavy integument, shortened tarsi, and an expanded mentum that conceals the mouthparts; the beetles also secrete defensive fluid (ALPERT & RITCHER 1975). Small trichomes on the pronotum imply involvement of appeasement-type compounds, but the role of these structures is unclear (KISTNER 1982), and they are not present in other ant-associated cremastocheiline genera. In contrast to adults, larvae of *Cremastocheilus* develop at the nest periphery, and can be reared in captivity simply on rich soil without ants, so they may not be dependent on the colony itself (ALPERT & RITCHER 1975). A counterpart to this lifecycle has recently been reported for another cremastocheiline, the South East Asian *Campsiura nigripennis*. In this species, larvae have been found to develop in elephant dung, whereas adults frequent arboreal nests of *Oecophylla smaragdina*. Here they probably feed on larvae and pupae, and are physically protected from rampant host attacks by morphological modifications akin to those of *Cremastocheilus* (see KOMATSU & al. 2014).

Scarabaeidae: Aphodiinae. Within this subfamily of ~3,200 species, a few members of the speciose and morphologically generalised genus *Aphodius* have been recorded from the external debris of *Atta* colonies (NAVARRETE-HEREDIA 2001). However, the bulk of myrmecophilous aphodiines are concentrated within the tribe Eupariini (~600 species), where multiple genera, some apparently more specialised in form, have been taken in association with ants. The biology of one obligately myrmecophilous eupariine, *Martineziana dutertrei* (= *Myrmecaphodius excavaticollis*), has been intensively studied because of the invasive nature of its hosts, *Solenopsis richteri* and *S. invicta*, in North America. The beetles are physically well protected from their aggressive hosts, and procure the workers' cuticular hydrocarbons during attacks, resulting in a matching odour profile – the first documented example of acquired chemical mimicry (VANDER MEER & WOJCIK 1982). Consistent with this mode of colony integration, some myrmecophilous eupariines possess what appear to be defensive morphologies, with integumental thickenings and protuberances, as well as shortened tarsi (MARUYAMA 2010); one distinctive *Atta*-associated genus, *Cartwrightia* – albeit contentiously placed in Eupariini (see STEBNICKA 2007) – possesses dense pubescence at the elytral tips that may constitute functional trichomes. In keeping with the predominantly saprophagous or coprophagous feeding habits of aphodiines (STEBNICKA 2001), most myrmecophilous Eupariini inhabit colony debris piles and chambers, usually of attine leaf cutter ants (STEBNICKA 2007), with some of these species additionally able to access the fungus gardens (NAVARRETE-HEREDIA 2001). Such species are likely saprophagous, but the observation that *Martineziana dutertrei* feeds on the *Solenopsis* brood led KISTNER (1982) to speculate that other eupariines may likewise be predatory. This notion seems unlikely given that myrmecophilous eupariines retain the same non-biting mouthparts adapted for "soft saprophagy" present in all non-myrmecophilous members of the tribe (STEBNICKA 2007), and instead implies that the predatory habits of *M. dutertrei* are an anomaly.

Scarabaeidae: other subfamilies. Outside of Cetoniinae and Aphodiinae, the subfamily Scarabaeinae ("true" dung beetles, numbering ~5,000 species) holds the bulk of the myrmecophilous scarabs (HALFFTER & MATTHEWS 1966). Published accounts of myrmecophily in this subfamily, at least in the New World, appear mostly connected to their utilisation of attine colony debris, probably as a substrate for brood rearing (HALFFTER & MATTHEWS 1966, VAZ-DE-MELLO & al. 1998, NAVARRETE-HEREDIA 2001, PHILIPS & BELL 2008, ALARCÓN & al. 2009, GENIER 2010). Indeed, the observation that many scaraebaeine species cannot be collected using pitfall traps baited with mammal dung has led to speculation that ant nest debris may be a commonly used alternative (LARSEN & al. 2006). A major departure from this ecology is seen in some Neotropical species of *Canthon*, such as *C. virens* and *C. dives*, which may be considered myrmecophagous: female beetles decapitate *Atta* foundresses and use them as brood balls for their larvae (HERTEL & COLLI 1998, SILVEIRA & al. 2006, FORTI & al. 2012, CANTIL & al. 2014). In the Old World, knowledge of scarabaeine myrmecophily is especially impoverished, but two genera are known that live with predatory ants. The first, *Haroldius*, collected with *Diacamma*, *Pheidole* and *Ponera* (see SILVESTRI 1924, HALFFTER & MATTHEWS 1966, PHILIPS & SCHOLTZ 2000), includes a group of African species with what appear to be small trichomes on the hind margin of the pronotum (KRELL & PHILIPS 2010), implying that these species may be somewhat integrated into host colonies. The second genus, *Alloscelus*, has been repeatedly collected from *Dorylus* columns and bivouacs, unmolested by its hosts (KRELL 1999), but again, its biology is otherwise unknown. Both *Haroldius* and *Alloscelus* are compact and globular with shortened legs, suggesting a protective morphology (HALFFTER & MATTHEWS 1966). Elsewhere in the Scarabaeidae, there are isolated records of ant associations for species in Dynastinae, Rutelinae and Melolonthinae (KISTNER 1982, MACKAY 1983, NAVARRETE-HEREDIA 2001), some of which, at least in the latter two subfamilies, may represent incidental collections of these beetles in or around nests.

Polyphaga: Tenebrionidae

Tenebrionids (darkling beetles; ~20,000 species) are a predominantly saprophagous and mycetophagous family, broadly similar to Scarabaeidae in terms of both diet and prevalence of myrmecophily. The lifestyle has arisen several times, in a few cases producing morphologically specialised taxa, but as pointed out by KISTNER (1982), the recurrence of myrmecophily in Tenebrionidae is relatively modest given the size of the family. Scattered instances are known from 13 of the 97 tenebrionid tribes (MATTHEWS & al. 2010).

Tenebrionidae: Pimeliinae. Most tenebrionid myrmecophiles belong to the large subfamily Pimeliinae, which contains approximately half of all tenebrionid species. Of the 39 pimeliine tribes, two are comprised mostly or exclusively of myrmecophiles. The Cossyphodini are a small, primarily Old World tribe with one Neotropical genus. The beetles possess a protective, flattened, disc-shaped body with wide expansions of the head, pronotum and elytra, and are probably non-integrated scavengers on the debris in and around nests (STEINER 1980, SCHAWALLER & al. 2011). One genus, *Cossyphodites*, has what appear to be trichomes at the abdominal tip, implying a potentially more intimate relationship with hosts (BRAUNS 1901). Members of the second predominantly myrmecophilous tribe, Stenosini, are also defensively modified with thick, compact antennae and cuticular protuberances of the head to protect the eyes and mouthparts. Some species among the ~35 genera have reduced or absent eyes. The biology of the Palearctic *Dichillus* was reviewed by KISTNER (1982), and with more recent observations on the Nearctic *Araeoschizus* and Neotropical *Discopleurus* (AALBU & ANDREWS 1996, HENDRICKS & HENDRICKS 1999) indicates that myrmecophilous stenosines subsist on harvested plant material or nest detritus, and are not closely integrated in colonies. The beetles are commonly found at the nest periphery or outside, and if recognised by workers, are carried away or killed (KISTNER 1982, HENDRICKS & HENDRICKS 1999). Outside of Cossyphodini and Stenosini, myrmecophily has evolved in a handful of other pimeliine genera within the tribes Adelostomini (see SCHAWALLER 2007) and Cnemeplatiini (see MATTHEWS & al. 2010). Of these, the eyeless North American cnemeplatiine *Alaudes* is notable in possessing ornate pronotal trichomes, and has the bases of the elytra and prothorax fashioned into a possible grasping notch (BLAISDELL 1919). Myrmecophily has also been inferred based on inquiline-like morphology in the Kuhitangiini (the genus *Kuhitangia* from Turkmenistan), but has not been observed (MEDVEDEV 1962).

Tenebrionidae: other subfamilies. Elsewhere in Tenebrionidae, myrmecophilous associations have been reported or inferred for species in approximately a dozen genera scattered across the subfamilies Alleculinae (3 genera), Lagriinae (2 genera), Tenebrioninae (2 genera, including at least one species belonging to the genus *Tribolium*) and Diaperinae (5 genera) (KISTNER 1982, MATTHEWS & al. 2010). The biology of these myrmecophiles is practically unknown, but all are presumed to be scavengers on nest debris, and a number of other tenebrionid species have been recorded engaging in seemingly facultative associations with colonies. For example, NAVARRETE-HEREDIA (2001) listed 17 tenebrionid species in 10 genera that had been recorded in association with *Atta* and *Acromyrmex*, most having been taken from the external debris piles of *Atta mexicana*. MATTHEWS & al. (2010) accumulated multiple additional examples of otherwise free-living tenebrionids recovered from colonies of various ant species, all presumably exploiting nest refuse or harvested food in some way.

Polyphaga: other families

Although the list of families containing myrmecophiles is relatively long (Tab. 1), the reality is that myrmecophily in the majority of beetle families where it occurs is manifested as an isolated evolutionary event, or a small collection of infrequent events; nowhere is it expressed to the dramatic extents seen in the major inquilinous groups discussed above. Instead, the rest of the Coleoptera is littered with a plethora of less speciose, or less myrmecophily-prone, clades or isolated genera (all within the Polyphaga). While it is impossible to cover these myriad minor taxa here, Table 1 lists some relevant literature for occurrences of myrmecophily in these other families, and the reader is also encouraged to consult KISTNER (1982), as well as regional treatments for beetles or inquilines specifically for Australia (LEA 1910, 1912, LAWRENCE & ŚLIPIŃSKI 2013), Japan (MARUYAMA & al. 2013), North America (ARNETT & THOMAS 2000, ARNETT & al. 2002) and the United Kingdom (DONISTHORPE 1927). The three Coleoptera volumes of the Handbook of Zoology series are also valuable, including summaries of the known biology of all beetle families (BEUTEL & LESCHEN 2005, LESCHEN & al. 2010, LESCHEN & BEUTEL 2014).

To briefly summarise, many of the most familiar beetle families contain at least one surprising lineage that inhabits ant colonies. The nature of colony exploitation by these groups varies significantly, with species ranging from scavengers and refuse dwellers, to tolerated or highly integrated guests. In most cases, clear parallels can be drawn with the myrmecophilous lifestyles seen in the major inquilinous groups discussed above, even down to functionally equivalent and seemingly convergent morphological adaptations. For example, a select few species may rank among the most advanced myrmecophiles, with anatomical modifications akin to those of paussines and clavigerites that mediate social interaction with hosts. In Brentidae (straight-snouted weevils), members of one tribe, Eremoxenini, are obligate and highly specialised myrmecophiles with gland-associated cuticular notches bearing trichomes, along with flattened or compact antennae (Fig. 2S). At least some species are highly socially integrated, engaging in trophallaxis with their hosts (LE MASNE & TOROSSIAN 1965). Analogous characters indicating advanced social integration are also seen in ant-associated genera that are morphological and ecological outliers in their families: genera scattered among Anobiidae (subfamily Ptininae; Fig. 2P), Salpingidae (subfamily Dacoderinae) and Dermestidae (*Thorictus*). *Agraeus*, a genus of Elateridae (click beetles), bears the same morphological hallmarks of myrmecophily (Fig. 2R), but has never been collected with ants (P.J. Johnson, pers. comm.).

Other myrmecophilous taxa are specialised for colony life through defensive modifications that are analogues of the limuloid body form. Within Hydrophilidae (water scavenger beetles), two recently described myrmecophilous genera from South East Asia, *Chimaerocyon* (Fig. 2O) and *Sphaerocetum*, possess a smooth integument and a protective, quasi-limuloid body form, along with shortened tarsi which likely protect against ant aggression (FIKÁČEK & al. 2013, FIKÁČEK & al. 2015). Functionally equivalent limuloid forms are also seen in Cephaloplectinae, a subfamily of Ptiliidae (featherwing beetles), where the miniscule body size permits phoresis on host ants, on whose cuticles the beetles graze (PARK 1933a, WILSON & al. 1954). Within the leiodid genus *Ptomaphagus*, limuloid morphology appears once more in the subgenus *Echinocoleus*, a guest of *Pogonomyrmex* colonies in the US with a widened "turtle-like" body and expanded pronotum (PECK 1976, PECK & GNASPINI 1997). In still other cases where the biology is known, species appear more ecologically than morphologically specialised on colonies, often having little interaction with the ants themselves. Chrysomelidae (leaf beetles) of the tribe Clytrini are phytophagous as adults, but some species have myrmecophilous larvae that encase themselves in soil and excrement, and scavenge on debris inside colonies, unmolested by workers (DONISTHORPE 1902, ERBER 1988, SELMAN 1988).

In addition to these clear-cut cases of myrmecophily, an unknown but no doubt very large number of beetle species have been recorded from colonies where the reason for nest occupancy is mysterious. Many such species have been recorded just once or on a limited number of occasions (Tab. VII in KISTNER 1982 lists a large number of beetle families that have unverified or ambiguous associations with social insect colonies, including those of ants). What the ecologies of these species are, or whether indeed their relationship with ants is real, await further study. Despite these nebulous cases, what is abundantly clear is that a good proportion of beetle families have at some stage in their evolution transitioned definitively to myrmecophily. Exceptional recent discoveries, such as *Habroloma myrmecophila* (Fig. 2Q), the first myrmecophilous member of Buprestidae (jewel beetles) (BÍLÝ & al. 2008), suggest that even at the family level, the list of myrmecophilous beetle taxa may continue expanding for some time.

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Evolutionary patterns in beetle myrmecophily

Evident from the above review is that an extensive body of literature exists on beetle myrmecophily. Although knowledge of the life histories and evolution of most species is clearly still patchy at best, distilling the above summary nevertheless reveals two major and very clear emergent trends, which capture the evolution of myrmecophily in beetles and require explanation:

Pattern 1: phylogenetic skew. As was the case with myrmecophily's distribution across the Hexapoda (Fig. 1), it is evident that evolutionary origins of this way of life in the Coleoptera are strongly biased to a small number of higher taxa. It is only within the Staphylinidae, Histeridae and (to a lesser extent) Scarabaeidae and Tenebrionidae that myrmecophily has repeatedly evolved to a notable extent, each group having yielded numerous phylogenetically independent origins of the lifestyle (origins identified as myrmecophilous subfamilies, tribes or genera emerging from otherwise non-myrmecophilous higher taxa, or myrmecophilous species descending from largely free-living genera). Furthermore, within Staphylinidae, myrmecophilous lineages are mostly within the subfamilies Aleocharinae and Pselaphinae alone; they are also relatively numerous in Scydmaeninae but these associations appear usually weaker or facultative, while the other 29 rove beetle subfamilies contain few or no cases of myrmecophily. Outside of these four main families, myrmecophily is far more thinly spread across the Coleoptera, evolving at best sporadically in some beetle families, and in most families not evolving at all (to our present knowledge).

This phylogenetic skew is depicted in Figure 3, where the species richness of each higher taxon of Coleoptera is shown, and labelled according to the approximate number of independent origins of myrmecophily it contains. Importantly, unlike the case of the Hexapoda (Fig. 1), there is a much weaker influence of taxon size on the likelihood of myrmecophily evolving. To demonstrate, consider that aleocharines, pselaphines and histerids contain only ~15,000, ~10,000 and ~4,000 species respectively, but each group includes dozens of phylogenetically independent myrmecophilous lineages (likely exceeding 100). In glaring contrast, several other higher taxa dwarf these three groups, but contain barely any myrmecophiles whatsoever. Within the ~63,000 species of the superfamily Chrysomeloidea, there are perhaps only two or three lineages that definitively associate with ants (members of Clytrini, some Cryptocephalini and Eumolpinae, all of which are found within the 35,000 species of Chrysomelidae, while no myrmecophiles are known among the ~20,000 species of Cerambycidae, although some are myrmecomorphic). Among the ~62,000 species of the superfamily Curculionoidea, only

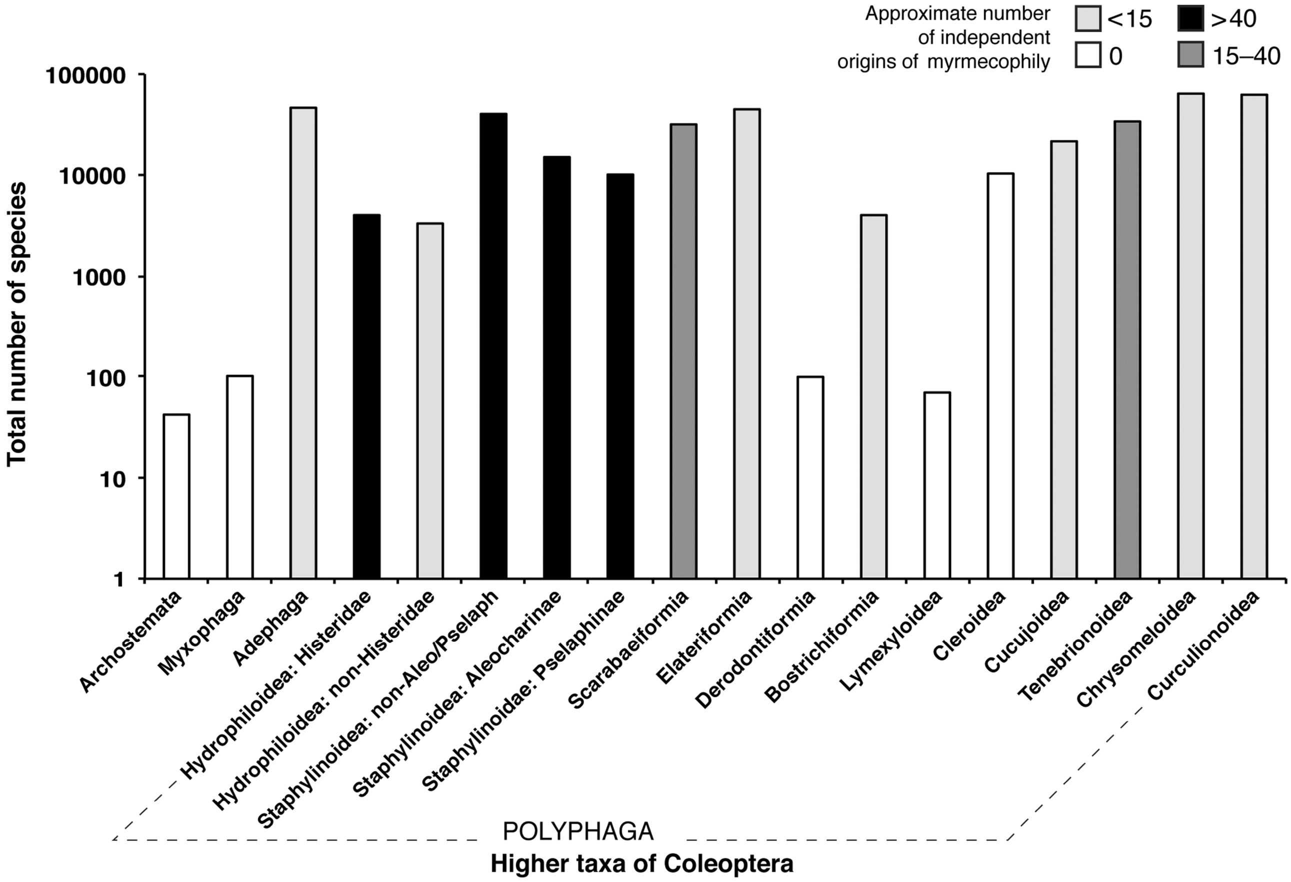

Fig. 3: Prevalence of myrmecophily among higher taxa of Coleoptera. A log plot of described species richness of beetle suborders arranged taxonomically from left to right, with Polyphaga divided into constituent series; the two biggest series, Staphyliniformia and Cucujiformia, are split into superfamilies, with Staphylinoidea further split into Aleocharinae, Pselaphinae, and remaining Staphylinoidea. Bars are coloured according to the estimated number of independent evolutionary transitions within the group from a free-living to a myrmecophilous state (both obligate and facultative). White bars: no definitive examples of myrmecophily; light grey bars: fewer than 15 putative independent origins; dark grey bars: 15 - 40 putative independent origins; black bars: more than 40 putative independent origins. The number of origins of myrmecophily for each order is an approximation based on the literature surveyed for this article and an attempt to gauge the relatedness of the different myrmecophilous taxa within each higher taxon. Examples of myrmecophagy were excluded, following the definition in Box 1.

the eremoxine brentids (Fig. 2S) and five or so genera of Curculionidae with mysterious biologies are myrmecophilous (and some of these only putatively so). In the whole suborder Adephaga (~46,000 species), there are again only a tiny number of instances: Paussini+Protopaussini (a single origin), Pseudomorphini + Graphipterini (probably also a single origin) and scarce other genera have evolved to exploit colonies, and only in the Paussini has the relationship progressed to the advanced phenotypic degree seen repeatedly in histerids, aleocharines and pselaphines. Likewise, only a few definitive evolutionary origins of myrmecophily have been discovered among the 43,000 species of Elateriformia (only one species among the 15,000 species of Buprestidae, one or possibly two genera among the 10,000 species of Elateridae, once or twice in the ~2,200 species of Lampyridae and an unconfirmed example for larval Chelonariidae). In the ~34,000 species of Tenebrionoidea, the vast majority of myrmecophiles exist among the 20,000 or so Tenebrionidae, with a tiny remainder occurring among the remaining 27 families (limited to Anthicidae, Salpingidae and Zopheridae). Finally, within Staphylinidae, I estimate that well over 90% of the independent origins of myrmecophily are found in the ~50% of the family comprised of the three subfamilies Aleocharinae, Pselaphinae and Scydmaeninae.

If these three staphylinid subfamilies were to vanish along with histerids, scarabs and tenebrionids, we would be left a Coleoptera with a much diminished background frequency of myrmecophily evolution – a frequency still probably higher than the other Hexapod orders, but not excessively so. The skew becomes even more acute if we consider the narrower definition of myrmecophiles as overtly socially parasitic organisms, and exclude those species that utilise nest refuse or have equivalently peripheral associations with colonies. Such a definition removes the bulk of ant-associated scarabaeids and tenebrionids; it is only in the cremastocheiline scarabs and *Martineziana* (Aphodiinae) that brood-targeting social parasitism has been demonstrated unambiguously (although it may be suspected in some other genera).

It is essential to add here that this extreme skew is not an artefact of clade age; no beetle group has had a "longer time to evolve" myrmecophily relative to others. Compared to the beetle higher taxa in Figure 3, ants are a relatively young group evolutionarily. Inferences from the ant fossil record, combined with molecular dating estimates, suggest that ants evolved not long before the mid-Cretaceous, which is the age of the earliest-known definitive ant fossils (GRIMALDI & AGOSTI 2000, WILSON & HÖLLDOBLER 2005, BRADY & al. 2006, LAPOLLA & DLUSSKY 2013, MOREAU & BELL 2013). Moreover, fossil abundance data argue that it was not until much later, during the early Cenozoic and Eocene in particular, that ants started to dominate ecologically (GRIMALDI & AGOSTI 2000, WILSON & HÖLLDOBLER 2005, LAPOLLA & DLUSSKY 2013, BARDEN & GRIMALDI 2014). All of the beetle taxa in Figure 3 are either as old as, or older than, the Early to mid-Cretaceous age of ants (GRIMALDI & ENGEL 2005, HUNT & al. 2007, MCKENNA & al. 2015). And all of them strongly predate the Cenozoic – a time when opportunities for evolving myrmecophily may have been enhanced by ants' ecological ascendancy. The conclusion must be that the strong bias in the frequency of evolving myrmecophily to just a small number of taxa stems from these groups possessing either unique novel traits, or unique combinations of traits, not seen elsewhere.

Pattern 2: parallel trait evolution. Across the diversity of myrmecophilous Coleoptera, the same kinds of putative adaptations, detailed in Box 2, seem to have arisen repeatedly. For example, numerous phylogenetically dispersed lineages of weakly- or non-integrated taxa show analogous defensive morphologies: a convex, limuloid or broadly explanate body shape, with shortened appendages that may be withdrawn into or under the body. Likewise, in species scattered across disparate families that have evolved much more intimate relationships with host ants, seemingly equivalent traits are again seen: glands with associated trichomes and grasping notches are recurring structures among these species, often combined with mouthpart modifications reflecting shifts in feeding strategies. Regardless of their degree of social integration, myrmecophiles in general tend to exhibit thickening and consolidation of the appendages: compaction or fusion of antennomeres and legs with broad, flattened femora and tibiae and shortened tarsi, presumably to withstand biting or handling by ant mandibles. Evidently, different beetle taxa have been subjected to a common set of selection pressures inside host colonies and responded in similar ways, culminating in morphologically and, presumably, functionally convergent traits.

What is even more notable, however, is the parallel evolutionary trend seen within clades that have repeatedly spawned myrmecophilous taxa. In these groups, a recurring evolutionary scenario has played out: from a free-living ancestral phylogenetic stock, multiple lineages have emerged that have followed a very similar evolutionary trajectory during the shift to myrmecophily, resulting in their independent acquisition of analogous lifestyles and phenotypic traits – "ecomorphs" in the sense of WILLIAMS (1972). The outcome is an evolutionary tendency for these families or subfamilies to engage in a particular mode of ecological relationship with ants, and exhibit certain morphological specialisations (or in some clades, an allusive lack of such specialisations). This parallel trend is manifested ecologically in the prevailing mode of colony utilisation in scarabaeids and tenebrionids, where multiple lineages have converged to utilise nest debris. It is seen in the scydmaenines, where the repeated tendency seems to be to engage in associations with ants that are facultative or devoid of overt morphological specialisations. And it is most striking in the groups that have recurrently evolved highly socially integrated biologies, the two clearest examples being myrmecophiles belonging to Aleocharinae and Pselaphinae. In Aleocharinae, parallel trait evolution is seen in the evolution of new glands in similar positions on the abdomen in different myrmecophilous taxa; it is seen in derived modifications in tergal gland chemistry (even though the chemicals themselves may differ, the general strategy of reprogramming the chemistry of the tergal gland is the same); and it is seen once more in army ant associated species in the recurrent evolution of the dramatic myrmecoid body plan. In Pselaphinae, parallel evolution is witnessed in the evolution of trichomes in the same body region – down to the exact abdominal segment – in multiple lineages, as well as the reduction of the mouthparts into structures for trophallaxis or feeding on immobile food items.

The repeated evolution of similar traits suggests that within these groups, natural selection has taken a relatively conserved morphological and ecological "ground plan" and fashioned it along paths of least resistance, several times over. In Scarabaeidae, Scydmaeninae and Tenebrionidae, evolution appears to be constrained, such that phenotypic change is predominantly behavioural and ecological, with morphological changes being uncommon. The opposite is true in Aleocharinae and Pselaphinae: these clades are not simply predisposed to evolve myrmecophily, but to evolve it in its most advanced, socially parasitic manifestation through a routine set of anatomical modifications, the ground plan acting as a constraining template for developmental remodelling. It has been argued that the term "parallel evolution" should be abandoned, since it implies parallel changes at the genomic level, when, in reality, convergent phenotypes are commonly produced by mutations in different loci irrespective of the relatedness of the lineages in question (ARENDT & REZNICK 2008). However, the term "parallel trait evolution" has some clear utility to describe the trend seen in these clades of myrmecophilous beetles. Because the ancestral, free-living and derived, myrmecophilous phenotypes correspond so similarly in each independent case, it seems reasonable to infer that lineages have been shaped by similar selective forces, and – at the phenotypic level at least – followed parallel evolutionary trajectories. Parallel trait evolution is thus a useful description for this phenomenon, even if the underlying genomic changes are not necessarily the same each time.

Explaining the patterns: preadaptations

The hypothesis advanced here is that both trends observed in myrmecophilous Coleoptera – phylogenetic bias and parallel trait evolution – stem from preadaptations present in certain taxa and not others. The concept of the preadaptation, a trait that evolves in one environment but serendipitously confers adaptive value in a novel environment, was employed earlier to explain the preponderance of myrmecophiles in Coleoptera relative to other hexapod orders. Here, I develop this idea further and identify two different types of preadaptation – primary and secondary – each relevant specifically to one of the two trends discussed above.

Primary preadaptations are invoked to explain why some beetle taxa evolve myrmecophily repeatedly, far more frequently than other groups. Primary preadaptations are defined as plesiomorphic traits that all species of an ancestrally free-living higher taxon possess, which increase the likelihood of those species encountering and utilizing colony resources, at least at some facultative level, and hence engaging in myrmecophilous associations with ants. As I argue in detail below, the most important primary preadaptations for myrmecophily in beetles are the ancestral diet and habitat type of a clade, the extent of its defensive morphology, and its typical body size range. "Preadapted" in this case means possession of a suite of traits that collectively promote the facultative exploration and utilisation of ant colonies – presumably a common initial step towards evolving obligate myrmecophily. The preadapted state may usually be one that confers sufficient behavioural or ecological plasticity to permit facultative colony exploration. Alternatively, the preadapted state may correspond to a genetic constitution that readily gives rise to colony exploration following minimal additional genetic change.

Secondary preadaptations are plesiomorphic phenotypic or genetic features that all members of a clade possess that predispose those species to evolve a certain mode of ecological specialisation, as the myrmecophilous relationship, once established, advances evolutionarily. I discuss below how much of the remarkable morphological innovation seen in myrmecophiles appears not to be rooted in the de novo evolution of bona fide "phenotypic novelties"; instead, many key functional traits likely arose via the re-fashioning of structures already present in free-living ancestors, or the spatial redeployment of preexisting developmental genetic cassettes during ontogeny. These antecedent features are secondary preadaptations: an ensuing tier of attributes that come into play during the subsequent phase of evolutionary adaptation, channelling phenotypic change in certain directions. In species where myrmecophily has newly evolved – most often through the predisposing action of primary preadaptations – secondary preadaptations become relevant, acting to enhance the likelihood that ecological specialisation to colonies will occur, but simultaneously biasing phenotypic evolution to a limited number of routes. Secondary preadaptations are invoked to explain why some clades that repeatedly evolve myrmecophily spawn taxa that undergo parallel trait evolution. Taxa such as aleocharines and pselaphines exhibit some of the most advanced manifestations of myrmecophily, but the overtly similar changes in morphology observed repeatedly across lineages within these groups imply that during evolutionary specialisation, exploration of the potential morphological and ecological "phenotype space" has been constrained to certain avenues. Preadapted in this second case means phenotypically (and thus genetically) "poised" to evolve certain kinds of new, functional characters that confer a selective advantage in the context of myrmecophily, through the modification or multiplication of preexisting traits. Unlike primary preadaptations, the exact structures that correspond to secondary preadaptations may be much more taxon-specific, varying clade-by-clade.

In short, primary preadaptations bias myrmecophily to evolving most frequently in specific taxonomic groups, whereas secondary preadaptations bias subsequent phenotypic evolution to specific organismal traits. The combined macroevolutionary outcome of primary and secondary preadaptations is to skew the phylogenetic distribution of myrmecophily to a few beetle clades (Pattern 1), in which the same traits – most obviously morphological ones, but potentially behavioural and biochemical traits also – are subject to evolutionary modification in independent myrmecophilous lineages, leading to parallel trait evolution (Pattern 2). It should be noted that although primary and secondary preadaptations have been developed here specifically for characterising the evolution of myrmecophily, these twin concepts are more broadly applicable. During the evolution of any novel life history, primary and secondary preadaptations may conceivably be involved – the first effecting an initial shift in ecology, the second raising the likelihood that the shift will be followed by specialisation, and turn into an obligate aspect of a species' biology.

Below, I present a synthesis to explain how preadaptations have shaped the evolution of myrmecophily in beetles. With the caveat that much of the biology and evolution of myrmecophiles remains poorly understood, the hypothesis advanced here is that, together, primary and secondary preadaptations have profoundly influenced beetle myrmecophily, fostering the evolution of this lifestyle in certain higher taxa, and biasing the trajectory of adaptive evolution to specific avenues of phenotypic change. Preadaptations have provided the foundations for much of the diversity seen among beetle myrmecophiles. I propose that by focusing on the development, evolution and functional roles of these characters – both in myrmecophiles and in their free-living relatives – much can be learned about the evolution and biological mechanisms of myrmecophily.

Primary preadaptations: promoting colony exploitation

In essence, accounting for the biased phylogenetic distribution of myrmecophily in beetles comes down to explaining why this lifestyle evolves with great frequency in six "myrmecophily-prone" clades, and with far less frequency in all other beetle taxa. The myrmecophily-prone clades are the rove beetle subfamilies Aleocharinae, Pselaphinae and Scydmaeninae (hereafter "APS staphylinids"), and the families Histeridae, Scarabaeidae and Tenebrionidae (the latter two families having a reduced prevalence of myrmecophily compared to the four former groups).

Why the pervasiveness of myrmecophily in these taxa? DONISTHORPE (1909) considered the evolutionary steps leading to myrmecophily, and theorised:

> "Of course the ancestral form of any species of truly Myrmecophilous Coleoptera is lost, and unknown to-day, but it appears to me that by studying the habits of those species which are occasionally and not always found with ants, but more generally elsewhere, we may learn how the ancestral forms of regularly myrmecophilous beetles first acquired their present habit of life."

In species that "are occasionally and not always found with ants", Donisthorpe was referring to facultative myrmecophiles. He went on to discuss a number of British beetles that commonly frequent nests, but which are also routinely collected away from them. Most of the species that Donisthorpe mentioned belong to the six myrmecophily-prone clades; presumably, these species, which are predominantly free-living but nevertheless have the capacity to enter and exploit ant colonies, embody the initial stage in the evolution of myrmecophily in the groups to which they belong.

Here, I build on this notion that myrmecophily most frequently evolves from an initial facultative association with ants, and propose that the likelihood of a free-living beetle lineage transitioning to myrmecophily rests largely on three primary preadaptations that encourage the facultative exploitation of colonies. I suggest that these primary preadaptations function synergistically, such that in beetle clades where the majority of species possess them, the probability of evolving myrmecophily is substantially enhanced. I argue that the aforementioned myrmecophily-prone clades are the only beetle groups that satisfy all of these preadaptive criteria. The groundplans of these groups mean that negligible phenotypic evolution is required for the beetles to adjust to a life spent, partially and opportunistically, in colonies – the primary step to evolving obligate myrmecophily.

1. Diet and microhabitat. Diet is a strong determinant of the habitats in which species can live, and with the exception of Scarabaeidae and Tenebrionidae, beetle higher taxa that have repeatedly evolved myrmecophily with greatest frequency are predatory. The APS staphylinid clades and Histeridae are all groups in which the vast majority of species are believed to feed primarily on other invertebrates. That such groups would readily transition to myrmecophily makes intuitive sense given both the food available inside ant colonies and the microhabitats that free-living members of these predaceous beetle groups tend to occupy. Species in these four groups are typically free roaming hunters living in the same substrates – soil, litter, under bark or decaying wood – in which ants commonly form colonies. The likelihood of encountering nests is therefore very high, and these beetles are behaviourally driven, morphologically equipped and physiologically adapted to feed on and digest many of the living resources present inside – the brood, other microarthropods such as mites and collembolans, or the workers themselves. On these intertwined, diet-related fronts, then, these four clades of predatory beetles are predisposed to profit from facultative nest exploitation, and thus preadapted for myrmecophily.

In stark comparison, examples of myrmecophilous taxa emerging from predominantly phytophagous clades are exceptionally rare, especially given the huge species richness of phytophagous beetles. The superfamilies Chrysomeloidea and Curculionoidea, collectively the "Phytophaga" – a giant, plant-feeding clade that accounts for almost a third of the entire Coleoptera – contain only two unambiguously myrmecophilous higher taxa (eremoxinine brentids and clytrine chrysomelids) and fewer than ten other genera that have been recorded with ants (JOLIVET & PETITPIERRE 1981, KISTNER 1982, SELMAN 1988, OBERPRIELER & al. 2014), the status of most of these as genuine myrmecophiles remaining unconfirmed. Myrmecophily in Buprestidae, the largest phytophagous family outside of the Phytophaga, is likewise rare, with just a single known species (BÍLÝ & al. 2008). Unlike the four predatory groups, phytophagous species tend to reside on or inside their foodplants. Their contact with ants is limited to foraging or trophobiont-tending workers; aside from species that feed on myrmecophytes or co-occur with arboreal ants (against which they may be well adapted to defend themselves, SELMAN 1988), encountering colonies is unlikely. Moreover, regardless of whether they are generalist herbivores or specialised on certain plants, phytophagous beetles are morphologically equipped to chew, and physiologically adapted to digest, plant material. There is little of appropriate nourishment inside colonies, and no impetus to explore them.

For predatory beetle groups, the evolutionary shift to myrmecophily does not demand radical changes in diet or habitat, whereas the same cannot be said for phytophagous groups. Taxa that are saprophagous or mycophagous, most notably the scarabs and tenebrionids, but also endomychids, cryptophagids, osoriine and oxyteline staphylinids and various scavenger groups such as ptinine anobiids, and leiodids, collectively show a somewhat higher incidence of myrmecophily compared to phytophagous groups. This is again likely explained in part by the lack of a major dietary or habitat shift in myrmecophilous species compared to their free-living ancestors. Similarity in diet has been implicated previously in the evolution of social insect inquilinism in mycophagous Cryptophagidae, where the decaying nest debris and refuse piles used by myrmecophilous species are little different from the habitats used by free-living relatives (LESCHEN 1999). Observed fungal grazing by the myrmecophilous osoriine *Thoracophorus corticinus* (see BURAKOWSKI & NEWTON 1992) and nest debris found in gut contents of cossyphodine tenebrionids (STEINER 1980) both support the notion that ant colonies can have resources suitable for at least some mycophagous and saprophagous groups. Like the four myrmecophily-prone predatory taxa, the majority of saprophagous and mycophagous beetles also live in litter, subcortical microhabitats or various decaying substrates harbouring an abundance of ant nests, increasing the likelihood of facultative colony exploration. The frequency of myrmecophily in saprophagous and mycophagous groups is nevertheless much lower compared to the four predatory groups mentioned. This difference may reflect the fact that, for the most part, the galleries of ant colonies do not house such concentrated bounties of resources for these species in the way that they do for predatory beetles. Colony refuse piles are the exception, and it is no surprise that many saprophagous groups have capitalised on this rich resource, most successfully the scarabaeids. Most scarab myrmecophiles utilise nest refuse as a substrate for oviposition, much like the substrates used by their non-myrmecophilous relatives. Indeed, volatile cues from the decaying organic matter output by colonies may even overlap chemically with odours emanating from decomposing plant material, carrion and dung, acting as an olfactory attractant for adults in search of oviposition sites. Hence, the recurring evolution of colony exploitation in scarabs again seems to be facilitated by diet.

Importantly, what all of these examples show is that the plesiomorphic diet of a clade not only governs the probability of lineages transitioning to myrmecophily, but additionally, that ancestral feeding habits also strongly dictate the prevailing mode of colony utilisation among these taxa. Inasmuch as the ancestral trophic ecologies of the groups to which they belong are, to a large extent, maintained, myrmecophilous beetles exhibit a degree of "phylogenetic niche conservatism" (LOSOS 2008), despite converting to life in ant colonies. Especially during the early phase of the evolution of myrmecophily, these inherited diets and modes of feeding likely govern how beetles interact with colonies and the kinds of resources they seek out. This initial mode of interaction may have important ramifications for subsequent evolutionary steps, in determining if and how taxa specialise on colonies. The majority of morphologically specialised or socially integrated myrmecophiles descend from predatory groups – aleocharines, pselaphines and histerids in particular. A predatory diet is often reflected in targeting of the brood, which demands that beetles enter the more heavily policed, central nest areas. It is this exposure to novel pressures that has selected for elaborate defensive or host-deceptive phenotype modifications seen in many myrmecophiles from these groups. Moreover, successful targeting of brood galleries has itself opened up new frontiers of ecological opportunity, leading to the most intimate manifestations of myrmecophily involving behavioural manipulation and trophallactic exchange. Such routes of specialisation are much less likely to be embarked upon by non-predatory taxa, which have no historically, genetically entrenched urge to target the brood or other protein-rich food sources inside nests. In this way, predation is not simply the diet most predisposing to the evolution of myrmecophily, but the most conducive to myrmecophily's progression into an intimate, socially parasitic symbiosis.

The relationship between a clade's plesiomorphic diet and its predilection to evolving myrmecophily is not so simple, however. If predaceous habits are a predisposing factor to myrmecophily in APS staphylinids and Histeridae, then why do the several remaining groups of terrestrial predatory beetles contain comparatively few origins of myrmecophily? The most notable counterexample is the hugely speciose and largely predatory Carabidae, a family in which myrmecophilous lineages are notably scarce. The dearth of myrmecophiles among the 15,369 species of Staphylininae and Paederinae, two big predatory sister subfamilies of Staphylinidae, is almost as curious. All three of these diverse taxa inhabit soil and litter microhabitats, and would thus be expected to coexist in ant-rich habitats, further enhancing their likelihood of frequently evolving myrmecophily. Several other beetle families are composed at least in large part of predatory species and are of sufficient size to gauge the relative incidence of myrmecophily: Coccinellidae (ladybirds; 5,000 species), Lampyridae (fireflies; 2,200 species), Cleridae (chequered beetles: 3,600 species) and Melyridae (soft-winged flower beetles; 6,000 species). All contain few or no known myrmecophiles. Adults of the latter two families tend to be arboreal or visit flowers, so their ecologies may exempt them from commonly encountering colonies. In contrast, coccinellids, by way of their specialised predation on aphids and scale insects, routinely interact with ants and have evolved various defensive strategies to deal with trophobiont-tending workers (VANTAUX & al. 2012). Myrmecophily (as defined in Box 1) is, however, rare in coccinelids, but not unknown (ORIVEL & al. 2004, VANTAUX & al. 2010). The family is thus a predatory group with few myrmecophiles, but which nevertheless supports the general rule that a clade's plesiomorphic diet constrains the nature of the beetle-ant relationship. For all of these predatory beetle taxa, however, the low prevalence of myrmecophily stems additionally from the fact that diet and habitat type alone are insufficient to predispose lineages to myrmecophily; all of these taxa lack one or more additional primary preadaptations, discussed below, which APS staphylinids and histerids possess.

2. Defensive morphology. The evolutionary transition to myrmecophily presumably begins most frequently with facultative nest exploration by free-living species. Beetle higher taxa that have recurrently evolved myrmecophily exhibit clade-wide morphological attributes that, in myrmecophilous species, have been co-opted to function in withstanding or evading worker aggression. Such defensive structures appear to be ancestral within these clades: They, or close progenitors of them, are present in the majority of species, including free-living ones, and so their evolutionary origin must predate myrmecophily. Moreover, their ancestral function may not necessarily have been in defence. Hence, the second primary preadaptation of myrmecophily-prone beetle clades is their plesiomorphic possession of morphologies that predispose them to survive better inside colonies than the majority of other beetle groups. These preadaptive defensive traits can be identified by observing how free-living or non-specialised facultatively myrmecophilous species cope when encountering ants. One of the clearest examples of a defensive preadaptation for myrmecophily occurs in aleocharines, in the form of the tergal gland. *Drusilla canaliculata* (= *Astilbus canaliculatus*), a largely free-living aleocharine that scavenges on dead ants, serves to demonstrate the utility of this gland in promoting myrmecophily. This species probably embodies an incipient stage in the evolution of myrmecophily in Lomechusini, a speciose tribe with multiple inquilinous lineages. *Drusilla*'s tergal gland contains the same, primitive, quinone-based chemistry common to the majority of aleocharines (BRAND & al. 1973, STEIDLE & DETTNER 1993). When attacked by *Lasius* workers, *Drusilla* twists its abdomen, aiming the gland at the ants and smearing its contents over them (DONISTHORPE 1909, PASTEELS 1968a). This action repels the ants, enabling the beetle to escape, and is a typical aleocharine defensive strategy when encountering any aggressor – formicid or otherwise (Fig. 4A shows the lomechusine *Pella* targeting its abdomen at its host).

The tergal gland thus facilitates the initial evolutionary step towards myrmecophily by equipping aleocharines like *Drusilla* with a targetable chemical deterrent. The gland likely contributes to why many other morphologically generalised members of large, abundant and predominantly free-living tribes, such as Athetini, can commonly be collected from various ant colonies (KISTNER 1982). Indeed, all aleocharine tribes that include myrmecophilous taxa primitively possess the tergal gland, while, tellingly, the gland is absent from the basal tribes Gymnusini and Deinopsini (see STEIDLE & DETTNER 1993), two groups that lack any myrmecophilous species. The tergal gland is retained in perhaps all non-integrated obligate myrmecophiles, with at least some of these species modulating gland compounds to optimise the chemistry for their respective host species (KISTNER & BLUM 1971, STOEFFLER & al. 2007, STOEFFLER & al. 2011, STOEFFLER & al. 2013). Some highly socially integrated taxa, such as *Lomechusa*, also retain the gland, presumably as a "backup" mecha-

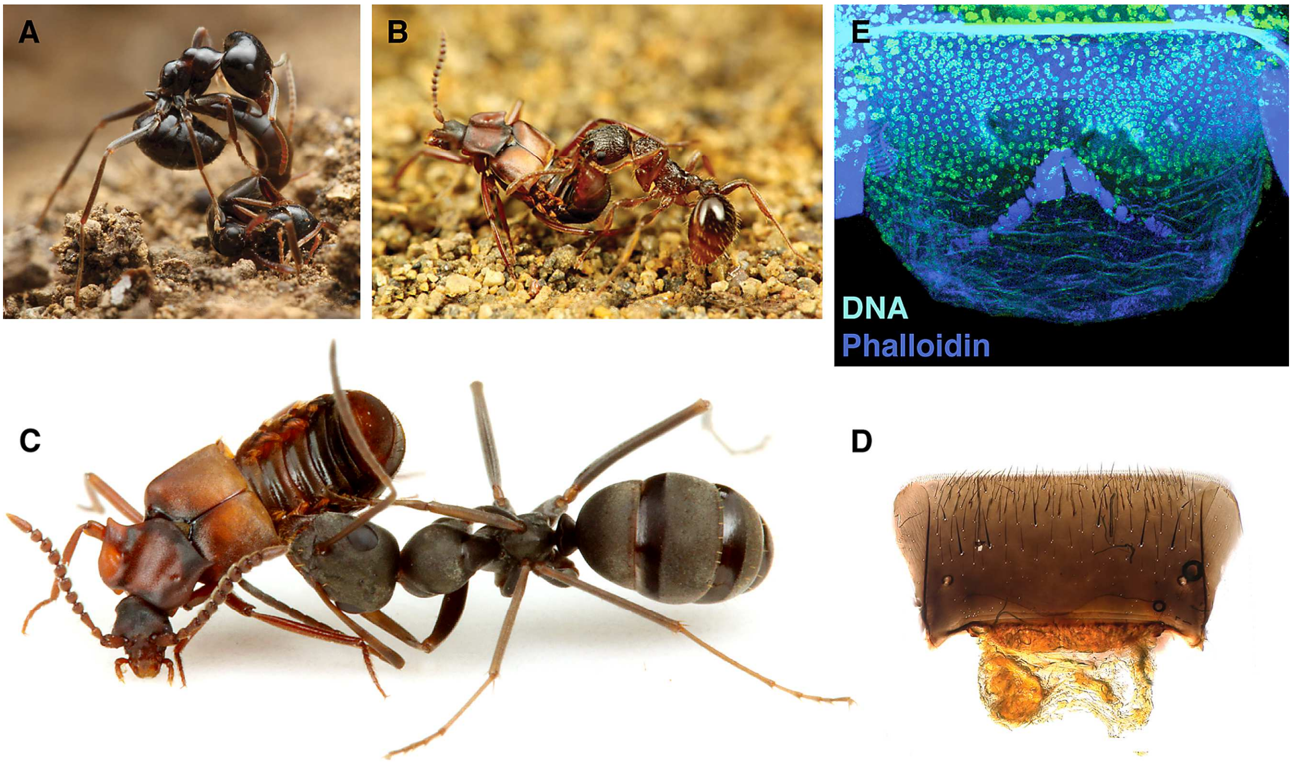

Fig. 4: Abdominal exocrine glands in Aleocharinae and their suspected involvement in myrmecophily. (A) *Pella* smearing its defensive tergal gland secretion on a *Dendrolasius* worker. (B) A *Myrmica kotokui* worker licking the appeasement gland at the tip of *Lomechusa sinuata*'s abdomen (C) *Formica lemani* worker licking the trichome-bearing adoption glands of *Lomechusa sinuata*. (D) Dissected tergal gland of the free-living species *Dalotia coriaria* (Athetini) showing the large reservoir containing yellow-coloured quinones dissolved in undecane solvent. (E) Confocal projection of *Dalotia*'s tergal gland with nuclei labelled in green and phalloidin-stained muscle in blue. Ectodermal D2 gland cells surround the reservoir, which is a chitinous sac formed from a cuticular invagination. Photo credits for A - C: T. Shimada / Antroom.

nism in rare cases of detection by hosts, or for defence during host colony switches or nest migrations (Hölldobler & al. 1981). However, the gland has undergone a secondary loss, or extreme reduction, in some other obligate and socially integrated groups, such as the Neotropical myrmecoid tribes Ecitocharini and Mimecitini (see Kistner & Jacobson 1990, Jacobson & Kistner 1991), and the Pygostenini (see Shower & Kistner 1977), a speciose Old World tribe associated with *Dorylus* and *Aenictus* army ants. Many highly specialised termitophilous taxa have similarly reduced the size of, or lost, the tergal gland (Pasteels 1968a, 1969, Kistner 1982). The conclusion must be that although this structure catalyses the initial transition to myrmecophily, subsequent evolution of novel strategies of social integration can render it obsolete, leading to diminished investment in tergal gland development.

In contrast to the chemically-preadapted aleocharines, the remaining myrmecophily-prone clades possess putatively preadaptive morphologies that confer physical protection inside nests. In Pselaphinae, the thick cuticle and reduced intersegmental membranes rigidify the body, which is further reinforced by foveae: pit-like invaginations of the cuticle that extend inside the body cavity to form apodemes and struts that function as internal buttressing, effectively forming an endoskeleton (Ohishi 1986, Chandler 2001). I have observed facultative or non-integrated pselaphines from a variety of genera, and the beetles are exceptionally good at withstanding aggression from their hosts. When attacked, the shortened abdomen and compact, convex shape of most pselaphines enable the beetles to retract their appendages and curl into a ball (conglobation). Tiny pselaphines may be picked up and compressed in the mandibles of a worker ant many times their size, only to be dropped apparently unharmed. The short intersegmental membranes of the abdominal segments ably block a worker's sting from penetrating the integument. Although pselaphines are seldom associated directly with army ants – presumably they are too small and slow moving to keep pace with their colonies – I have sifted rainforest leaf litter through which army ants were swarming and recovered numerous pselaphines. The beetles are clearly able to tolerate the ants' presence, unlike the majority of forest floor arthropods that are reportedly flushed out (Schneirla 1971). Park (1947a) observed the facultative myrmecophile *Batrisodes lineaticollis* (= *B. globosus*) emerging unharmed from attacks by *Lasius* and *Formica* workers, and Donisthorpe (1927) reported similar findings for British congeners. I suspect that most facultative or non-integrated myrmecophilous pselaphines are attacked by their hosts with some frequency, their reinforced bodies providing them with the means to survive these encounters. These physical interactions with host ants may themselves be adaptive, serving to transfer the hosts' cuticular hydrocarbons onto the beetles ("acquired chemical mimicry" sensu VON BEEREN & al. 2012), although this needs experimental verification.

As is the case with Aleocharinae, not all groups of Pselaphinae are prone to myrmecophily, and groups that are less compact and unable to conglobate, such as the basalmost and very staphylinid-like supertribe, Faronitae, contain few or no myrmecophiles. Notably, pselaphine lineages that have become more intimately associated with ants, including the Clavigeritae and inquilinous genera and individual species of Batrisini and Tyrini, consistently display an evolutionary loss of many fovea across the body (CHANDLER 2001, ZHAO & al. 2010, PARKER & MARUYAMA 2013, YIN & LI 2013). The regressive evolution of this aspect of their preadaptive defensive morphology appears to be a "use it or lose it" trend analogous to the reduction or loss of the tergal gland in myrmecophilous aleocharines. It should also be noted that some pselaphines possess an abdominal defensive gland, comparable to that of aleocharines (THAYER 1987, NEWTON & THAYER 1995). However, the gland is located ventrally and not particularly targetable due to the inflexible nature of the abdomen, and the gland reservoir is small. It seems unlikely that this structure serves as a defensive preadaptation for myrmecophily. Its evolution predates the Pselaphinae, and it can be found in many related subfamilies that include no myrmecophiles (including one of significant size, Omaliinae, with ~1,500 species). Moreover, the gland is inferred to have been evolutionarily lost in the common ancestor of some groups that went on to repeatedly evolve myrmecophily with great frequency, such as the tribes Ctenistini, Tyrini and Tmesiphorini (J. Parker, unpubl.).

Importantly, it is unclear whether the novel, reinforced morphology of pselaphines originally evolved solely as a defensive adaptation. Certainly defence is a possibility: pselaphines are slow moving compared to most other staphylinids, stalking rather than chasing their prey (SCHOMANN & al. 2008) and thus unable to easily flee; their strengthened, conglobating frame may have consequently evolved under selection to endure attacks from larger-bodied predators. But it is equally plausible that reinforcing the body in this way may have evolved initially for withstanding physical compaction while moving through deeper soil, or denser substrates than the majority of other staphylinids. The same may be true of the physically protective morphology of at least some of the remaining myrmecophily-prone clades. Scydmaenines are close in size and shape to pselaphines, their long elytra and compact shape likely defending them from ants in a comparable way. Free-living scydmaenines are typically collected from the same microhabitats as pselaphines, and this overlap in ecology raises the possibility that their morphology may have also evolved for reasons related to habitat use rather than defence. In a similar fashion, the (albeit much weaker) predisposition to myrmecophily in the staphylinid subfamilies Osoriinae and Oxytelinae may be partly attributable to the flattened, robust body form of most free-living species. Again, this plesiomorphic body plan may be an adaptation to life under bark or in humus, serving only secondarily as effective protection from ants.

Without question, the plesiomorphic groundplan of histerids is physically protective, and naturally predisposing for myrmecophily. Free-living species possess a smooth, shiny and extremely thick integument, a weakly to strongly convex body shape, a head that can be withdrawn underneath the broad, overlying pronotum, and short, retractable appendages. This tank-like morphology is eminently suited for nest intrusion. Indeed, aside from the addition of further cuticular protuberances and thickenings in some groups such as the haeteriines and chlamydopsines, this basic morphology is not further elaborated in the majority of myrmecophilous species. Again, aspects of this protective morphology, such as the smooth cuticle, flattened shape and short limbs may have first evolved for an interstitial or subcortical way of life. Similarly, scarabaeids may benefit from strengthened morphology during ant encounters. In general, the bulk of scarab myrmecophiles do not associate as closely with ants as do APS staphylinids and histerids, but the plesiomorphic scarab morphology, at least in the groups where myrmecophily is most prevalent – the cetoniines, aphodiines and scarabaeines – is also quite compact and relatively heavily armoured. Putatively free-living scarabs have been observed unharmed when overrun by swarming colonies of *Labidus* and *Dorylus* army ants (EMLEN 1996, KRELL 1999). The authors of both of these reports raise the possibility of physical defence, but also hypothesise that a chemical deterrent could play a role. Physical defence almost certainly plays a major role in the evolution of myrmecophily in Tenebrionidae. Most tenebrionid myrmecophiles belong to the robust-bodied Pimeliinae, a basal subfamily that are normally extremely heavily sclerotised and convex, and which lack any of the defensive glands seen in the "higher" tenebrionid subfamilies (MATTHEWS & al. 2010).

To summarise, the plesiomorphic body forms of myrmecophily-prone APS staphylinids, histerids, scarabs and tenebrionids need not undergo substantial modification to function as effective protection inside ant colonies. Free-living members of these groups are anatomically primed for myrmecophily through either chemical defence or physically protective cuticles and body shapes. Overtly defensive morphologies are not so evident in some of the other speciose and predatory beetle groups, mentioned previously, that contain few or no myrmecophiles. Melyridae, Cleridae and Lampyridae are comparatively soft-bodied beetles, and while some species may be toxic or distasteful to predators, they do not have an effective chemical defence against ants comparable to the aleocharine-type targetable defensive gland. Inadequate defence may also underlie the absence of myrmecophily in some beetle families with predatory larvae, such as cantharids (soldier beetles) and elaterids, since such species must still enter or exit nests as unprotected adults. Myrmecophilous clytrine chrysomelids perfectly demonstrate the perils of this predicament: their scavenging larvae pupate inside protective cases made from soil and fecal matter, only for the eclosing adults to experience extensive attacks and mortality when attempting to exit host colonies (DONISTHORPE 1902, ERBER 1988).

What remains to be explained is the shortage of myrmecophiles in the three largest such outstanding predatory groups: Carabidae, Staphylininae and Paederinae. The majority of species in these groups do not have overtly physically protective morphologies. However, many species from at least the first two groups possess abdominal defensive glands (WILL & al. 2001, FRANCKE & DETTNER

2005, Thayer 2005). The pygidial glands of carabids are well studied, and these either spray or ooze a diversity of compounds that vary depending on the species in question, but commonly include formic acid and quinones that should be effective ant deterrents (Will & al. 2001, Giglio & al. 2011). Likewise, many Staphylininae have small, paired tergal glands that evert onto tergites VIII and IX, releasing iridoid-containing secretions (Huth & Dettner 1990, Dettner 1993, Kanehisa & al. 1994, Weibel & al. 2001). These act as topical irritants, and can repel ants (Jefson & al. 1983). Both carabids and staphylinines would therefore seem to satisfy both of the primary preadaptive criteria discussed so far: a carnivorous diet, and a potential protective strategy from ants. In contrast, while at least some Paederinae possess an abdominal glandular complex positioned ventrally, close to the base of the abdomen (Kellner & Dettner 1992), its chemistry and function are unknown; if it serves a defensive role, its location on the body presumably means the gland is much less targetable than that of other chemically-defended groups. Moreover, glands with possible defensive roles remain undiscovered in the majority of paederine genera despite detailed anatomical study (L. Herman, pers. comm.), implying that the subfamily may mostly lack exocrine gland-based defence mechanisms. Combined with their flexible body plan and corresponding lack of physical protection, paederines may not be sufficiently well defended for nest intrusion.

If defensive shortcomings contribute to the relative scarcity of paederine myrmecophiles, the dearth of carabid and staphylinine myrmecophiles is still mysterious, but may also be explained in part by a basic inadequacy in their mode of chemical defense. Studies on carabid beetles have shown that spraying of pygidial gland contents soon exhausts the beetle's reserves: *Galerita lecontei* can deploy its formic acid spray only 6.5 times before exhaustion, and the gland takes 37 days to fully refill (Rossini & al. 1997). "Spray to exhaustion" measurements from other carabid species have produced similar figures (Will & al. 2010). While deployment of carabid pygidial glands is clearly effective in sporadic encounters with ants, spraying is an inefficient use of the gland's reserves, discharging large volumes over a wide arena. Carabids that ooze as opposed to spray their gland contents may be more conservative in their chemical deployment, but lack the abdominal flexibility needed to target their secretions. Persistent association of beetles with colonies demands a more sustainable and accurate mode of chemical deployment. The flexibility of the aleocharine abdomen enables the beetle to dab or smear its secretion, which conserves the contents of the reservoir (Brand & al. 1973). Smearing also enables precise application of the secretion onto the aggressor (Fig. 4A). Staphylinines, which, like aleocharines, also smear the secretions of their paired tergal glands, possess only small gland reservoirs that may soon become exhausted (Jefson & al. 1983, Huth & Dettner 1990). In contrast, reservoir volume varies widely among aleocharines, but reaches its maximum extent in the Athetini and Lomechusini (= Zyrasini) (see Steidle & Dettner 1993), two tribes that form a vast clade (Elven & al. 2010, Elven & al. 2012), harboring the greatest proportion of myrmecophilous lineages within the subfamily (M. Maruyama, K.T. Eldredge & J. Parker, unpubl.).

What these differences emphasize is that although carabids, staphylinines and aleocharines are chemically defended, only the latter group appears to be preadapted for nest intrusion by way of a very frugal and targetable mode of chemical release, backed up by large chemical reserves. Carabidae and Staphylininae are not so well equipped for long-term persistence inside ant colonies, and compounding their defensive limitations, many members of these two predatory groups face an additional hurdle to evolving myrmecophily discussed directly below: their relatively large body size, and potential for ecological exclusion from ant-dominated habitats.

3. Body size and ecological coexistence. In terms of body size, beetle myrmecophiles tend not to exceed the length of their hosts' workers, and are often smaller. Across the size distribution of all myrmecophilous beetles, I estimate that approximately 3 mm is the mean body length and ~6 mm probably close to the 95th percentile. Phoretic species such as some cephaloplectine ptiliids may be many times smaller than their hosts. The biggest size discrepancy known to me between a non-phoretic myrmecophile and its host exists between *Camponotus gigas* (~20 mm) and the pselaphine *Batrisopsis myrmecophila* (2.4 mm) (Raffray 1894). At the opposite end of the spectrum, several haeteriine histerid genera are relatively large or long-legged, as are some myrmecoid aleocharines, but all such species associate with correspondingly big-bodied army ants. In Pselaphinae, the Clavigeritae rarely exceed 2.5 mm and are always smaller than their hosts; one Madagascan genus, *Miroclaviger*, reaches 4 mm but associates with *Camponotus* species at least double this size (Jeannel 1954). The general rule of not exceeding worker size holds basically true for the four predatory, myrmecophily-prone clades, where the estimated body size range is 2 - 6 mm for myrmecophilous aleocharines, 1 - 3 mm for pselaphines, 1 - 2 mm for scydmaenines and 2 - 6 mm for histerids. Species that break this rule appear to be infrequent: A few *Pella* species are slightly longer than their hosts (Maruyama 2006), while the pselaphine *Jubogaster towai* is severalfold larger than major workers of its *Pheidole xanthogaster* host (Parker & Maruyama 2013). In contrast to these predatory clades, numerous scarab myrmecophiles clearly surpass the maximum worker size, including the Cremastocheilini, many scarabaeines, and most dramatically, the big dynastine *Coelosis biloba*, which undergoes larval development inside *Atta* fungal gardens (Navarrete-Heredia 2001, Gasca Alvarez & al. 2008).

Animal size correlates with many life history parameters (Calder 1996), and one can imagine various adaptive explanations for why most myrmecophilous beetles are small. A diminutive size may help myrmecophiles avoid detection inside nests. If detected, being small might safeguard against becoming subdued by groups of aggressive workers. For socially integrated species, approximating the size of a worker or immature could be advantageous for manipulating tactile nestmate recognition cues (size thus performing a role in Wasmannian mimicry). There are further constraints on body size that select for which organisms enter nests. A physical size limit may be set by the dimensions of nest galleries. Moreover, while food resources in even the smallest nests may be significant for small-bodied taxa, the payoff from nest intrusion may be less worthwhile for species above a certain size. For obligate myrmecophiles that are poor dispersers, host colonies may be perceived as islands (KURIS & al. 1980), limiting their foraging range size – often a strong correlate of body size in animal taxa, including invertebrates (MCNAB 1963, ROLAND & TAYLOR 1997, BURNESS & al. 2001, GREENLEAF & al. 2007).

Perhaps all of these explanations, and still others, have played a role in restricting the size distribution of myrmecophiles. But what is relevant is that, empirically, there seems to be a body size range that is most appropriate for myrmecophily. And in addition to diet and defence, the third important characteristic that the predatory, myrmecophily-prone beetle taxa have in common is that they fall within this size range. With few exceptions, APS staphylinids and histerids tend to be in the same size class as ants, or are smaller. If body size is indeed important, as it appears to be, then it follows that the plesiomorphic size range of these taxa is already optimal, and hence preadaptive, for myrmecophily. The two remaining myrmecophily-prone groups – the scarabs and tenebrionids – are much more variable in size, and often large-bodied, but many myrmecophiles from both groups tend to associate only peripherally with colonies through their use of refuse piles, and may thus be exempt from the size constraint. Aside from the cremastocheilines already mentioned, scarabs that venture deeply into colonies, such as the Eupariini (Aphodiinae) and *Haroldius* (Scarabaeinae), tend to be much smaller beetles. Likewise, obligately myrmecophilous tenebrionids including the Cossyphodini, Stenosini and *Alaudes* are small for the family, only a few millimetres long.

Crucially, other would-be myrmecophilous groups, the two most notable being the predatory carabids and staphylinines, span into far larger size classes. The rare myrmecophiles to have emerged from these higher taxa include major outliers in the host-myrmecophile body size relationship. Both of the notable myrmecophilous clades of Carabidae – Paussini and Pseudomorphini – are unusual examples of large beetles that are specialised for colony life, with some paussines perhaps being the only highly socially integrated beetles that are obviously larger than their hosts. In Staphylininae, *Termitoquedius* is larger than its *Eciton* hosts; so too are the *Dendrolasius*-associated *Philataerius*, and *Formica*- and *Lasius*-associated species of *Quedius* and *Xantholinus*. *Atta*-associated genera of Xanthopygina include some of the largest rove beetles known, and *Platydracus fulvomaculatus* (with *Atta mexicana*) is the largest staphylinid in the western hemisphere (A. Newton, pers. comm.). *Leptacinus formicetorum*, smaller than its host *Formica* workers, stands out among staphylinine myrmecophiles for obeying the prevailing myrmecophile size rule. The overall tendency is for myrmecophiles in these two groups to exceed, or at minimum equal, their hosts' body sizes.

I suggest that, in addition to potential inadequacies in their respective defensive strategies, a further factor reinforcing the surprising scarcity of myrmecophiles within Carabidae and Staphylininae is that broad swathes of these groups consist of species that are simply too big. Falling outside of the size range most adaptive for myrmecophily, large, free-living beetles may be excluded from engaging in the facultative exploration of colonies posited here to be a common first step towards evolving this way of life. Moreover, the inhibitory effect of being relatively large-bodied may be further reinforced by interspecific competition with ants. The general relationship between ants and carabids is, in some important habitats at least, one of ecological exclusion. Several authors have noted the negative relationship between ant and carabid abundance, with carabids typically very rare in ant-saturated lowland tropical forest litter (DARLINGTON 1971, WILSON 1990). Likewise in temperate forests, the density of *Formica* wood ants in particular has been shown to negatively impact carabid populations, and is an important determinant of carabid spatial distribution (NIEMELA & al. 1992, HAWES & al. 2002, REZNIKOVA & DOROSHEVA 2004). While APS staphylinids feed on microarthropods that ants tend to overlook (such as mites and collembolans), the consumption of larger invertebrates by bigger-bodied carabids presumably draws these beetles into interspecific competition with ants (WILSON 1990). Furthermore, ants may directly prey on or attack carabids above a certain size (DARLINGTON 1971, REZNIKOVA & DOROSHEVA 2004, HAWES & al. 2013), the larger body impairing the beetle's capacity to hide or defend itself effectively against hordes of workers. This size-dependent interaction with ants has been demonstrated empirically in temperate forests, where small carabids such as *Notiophilus* and *Calathus* can thrive in zones of high *Formica* density, while larger-bodied *Abax*, *Cychrus* and *Pterostichus* are frequently attacked and excluded from these areas (NIEMELA & al. 1992, HAWES & al. 2002).

The typically low abundance of carabids in ant-dominated habitats presumably represents the "ghost of competition past" (CONNELL 1980), and exposes a general inability of carabids to coexist with ants. Evolutionarily, the upshot is a reduction in habitat overlap between the two taxa that must surely have diminished the opportunity for carabids transitioning to myrmecophily. What has been observed for carabids may well hold true for Staphylininae – a group that includes many comparably sized, ground- or litter-inhabiting predatory beetles, but contrasts very strongly with the APS staphylinids. These smaller beetles flourish on the lowland rainforest floor and are clearly able to coexist with ants at extremely high densities, to the extent that they reach their global peaks in both numerical abundance and taxonomic diversity in this ant-dominated habitat. Their imperviousness to the ecological pressure of ants means that APS staphylinids frequently encounter colonies and are preadapted by diet, defence and size to enter them, enhancing the frequency with which these clades have undergone the transition to myrmecophily.

If ecological exclusion by ants does indeed restrict the distribution of carabids and (as a consequence) their predisposition to myrmecophily, an intriguing conundrum remains: although carabids are generally rare compared to other beetle groups in rainforest litter, tropical carabid diversity is still high due to the significant richness of the canopy fauna. Approaching two thirds of carabids in tropical forests are arboreal (OBER 2003), the group having successfully colonised this habitat despite the huge abundance of canopy ants (DAVIDSON & PATRELL-KIM 1996). Why arboreal carabids are not excluded from the canopy is hard to explain, but I suggest a possible reason may be found in analyses of stable nitrogen isotope ratios (δ15N) – a readout of trophic level – from ants collected from different forest strata (BLÜTHGEN & al. 2003, DAVIDSON & al. 2003). Such studies have revealed that canopy ants, unlike their litter counterparts, tend not to be predatory; instead, arboreal species derive significant N from herbivory and honeydew farmed from trophobionts (BLÜTHGEN & al. 2003, DAVIDSON & al. 2003). This trophic difference between litter and canopy ants may liberate arboreal carabids from competition and predation, permitting the two taxa to coexist. Living alongside canopy ants might therefore be expected to increase the prevalence of myrmecophily among arboreal carabids, but the general inaccessibility of the canopy means little is known of the biology of the carabids that live up there. In the Neotropics, the morphology of some members of the large arboreal genus *Agra* is suggestive of myrmecophily (ERWIN 1982, ERWIN 2000), and the ant-mimicking cicindeline *Ctenostoma spinosum* has been collected from inside *Cecropia*-nesting *Pachycondyla* colonies (JOLIVET 2002). A prediction might be that careful surveying of colonies of tree-nesting ants will reveal a number of myrmecophilous canopy carabids.

Synergistic primary preadaptations and the phylogenetic bias in myrmecophily

Diet, defence and size: the argument presented above is that these three primary preadaptations collectively account for the biased distribution of myrmecophily across the Coleoptera. The only beetle groups that perfectly satisfy all three criteria are the very taxa that have recurrently evolved myrmecophily with greatest frequency: the APS staphylinids and histerids. The plesiomorphic condition within each of these clades is to be predatory, well defended either physically or chemically, and small in size. Consequently, these groups have proliferated in many of the habitats that ants dominate, and, moreover, the majority of their free-living members are perfectly preadapted for facultative nest exploration, proposed here to be a common entry point on the pathway of ecological specialisation towards myrmecophily. Such groups – in particular the pselaphines and aleocharines – have also invaded termite colonies multiple times during their evolution, and this again probably stems from these beetles' predatory diets, small sizes and defensive capabilities.

In contrast, all other beetle groups have evolved myrmecophily at a notably lower frequency. Some have evolved it only sporadically, while most have never evolved it at all. This striking asymmetry arises because diet, defence and size act synergistically: although a large number of beetle families satisfy one of these preadaptive criteria, this alone does not markedly enhance the probability of myrmecophily evolving. But when two or (especially) all three preadaptive criteria are satisfied, the likelihood of transitioning to myrmecophily is substantially raised. For example, as discussed above, the non-predatory plesiomorphic diet of scarabaeids and tenebrionids probably explains the significantly reduced frequency of myrmecophilous lineages within these families relative to the predatory APS staphylinids and histerids. The same explanation applies to the relatively low prevalence of myrmecophily among the saprophagous osoriine and oxyteline staphylinids.

Most striking in their shortage of myrmecophilous lineages are the carabids and staphylinine rove beetles: Despite being predatory, these groups may not be adequately preadaptated for colony exploration, with potential shortcomings in their gland-based chemical protection that are further compounded by the large body sizes of many species. Similarly, paederine rove beetles are predatory and many are small in size, but members of this subfamily may simply not be outfitted defensively for entering colonies. The low incidence of myrmecophily in these and practically all other beetle groups testifies to the crucial role of the three primary preadaptations. Without them, the hurdles of gaining colony access and surviving once inside are set too high; ill-equipped for nest intrusion, the costs are too great for myrmecophily to routinely evolve. Yet, when the three primary preadaptive criteria are met, as in APS staphylinids and histerids, colony intrusion is straightforward. The preadaptations have provided free-living species in these groups with a license to experiment with facultative myrmecophily, and evolution of obligate myrmecophily has ensued repeatedly. The result is the extreme skew in the phylogenetic distribution of myrmecophily seen across the Coleoptera.

Secondary preadaptations: promoting specialisation

In each of the myrmecophily-prone clades, evolution shows a recurring pattern, with beetles typically adapting to colonies in a few prevailing ways. In groups that repeatedly evolve intimate, socially integrated relationships with ants – principally Aleocharinae, Pselaphinae and Histeridae – parallel trait evolution is seen that points to the existence of preadaptations that bias specialisation to certain pathways of phenotypic elaboration. This phenomenon is most obvious in the Aleocharinae, where recurring modes of specialisation are reflected in the evolution of analogous anatomical modifications in independent lineages: the multiple myrmecoid groups associated with army ants, the repeated appearance of apparently new gland types in new positions on the abdomen, and the evolutionary reprogramming of tergal gland biochemistry towards compounds that elicit behavioural effects on hosts. SEEVERS (1978, p. 3) recognised this adaptability of aleocharines, and homed in on one potential explanation:

> "The Aleocharinae have been especially successful in adapting to conditions of the societies of ants and termites. It is safe to say that this subfamily has provided more independently evolved inquilinous groups than any family of insects. Much of the success of the group for this mode of life may be attributed to the "genetic pliability" of the aleocharine abdomen. Not covered by elytra and being highly flexible, the abdomen has become physogastric (more or less inflated and membranous) for life in termite societies, myrmecoid (petiolate) for life in army-ant societies, and provided with trichomes for life with higher ants."

The repeated remodelling of the aleocharine body plan into shapes adaptive for myrmecophily is made permissable largely by way of the exposed and highly flexible abdomen. Having such a "genetically pliable" abdomen exemplifies the notion of a secondary preadaptation – a trait that both catalyses and canalises the subsequent process of specialisation after the ecological association with ants has evolved. Following the intial transition to life in ant colonies, the aleocharine body plan is still generalised, but the exposed flexible abdomen subsequently becomes a routine target for selection. Great innovation has arisen through remodelling the abdomen, and it is the potential evolvability of this part of the body that has enabled adaptations to arise that have driven the myrmecophilous relationship to new levels of intimacy. Yet, because the abdomen is so mutable and offers such a ready route for further innovation, it also acts to predispose the process of ecomorphological specialisation to a set of commonly exploited phenotypic avenues, leading to parallel anatomical changes in independent lineages.

Myrmecoid aleocharines associated with army ants provide the clearest demonstration of preadaptive abdominal morphology. The myrmecoid body plan has evolved independently in aleocharine clades associated with every known genus of doryline, "true" army ant, as well as in aleocharines associated with several other nomadic or processionary ant species (M. Maruyama, K.T. Eldredge & J. Parker, unpubl.). Such repeated evolution indicates that the myrmecoid body shape is highly adaptive. Evidently, during the process of specialisation, army ant associated aleocharines have been under strong selection pressure to take on an overtly ant-like form. Consequently, through some simple developmental changes to the exposed, flexible abdomen, the myrmecoid form has repeatedly been achieved. Narrowing of the abdominal base forms a petiole, with the precise segments modified to construct the waist differing among myrmecoid groups (SEEVERS 1965). The more apical abdominal segments commonly undergo expansion to form a bulbous gaster, and the flexibility of the abdomen permits it to articulate, so that it can be held in positions that further reinforce the myrmecoid shape. When deconstructed like this, these abdominal modifications seem so facile to achieve developmentally (and evolutionarily) that it is easy to see how the myrmecoid body shape has arisen independently in aleocharine clades associated with every army ant genus. Yet, this pathway of morphological innovation is shut off to most other beetles, where long elytra cover an abdomen comprised of less flexible segments. This difference is key in explaining why the myrmecoid form has evolved so many times in parallel in aleocharines, but so rarely elsewhere in the Coleoptera. In their flexible abdomens, aleocharines are offered an accessible route to ecomorphological specialisation that is improbable in other beetle groups where the morphology is too far removed. Consequently, aleocharines have adapted to vacant niches that can be deeply embedded within the social fabric of army ant colonies, but which tend not to be occupied by other beetle taxa simply because successful niche occupancy demands an ant-like form. Other staphylinid subfamilies with comparable morphology to aleocharines are theoretically capable of undergoing these same changes in form – the exceptional staphylinine *Ecitophytes* has done exactly that – but, as discussed above, no other rove beetle subfamily possesses the requisite primary preadaptations to routinely associate with army ants in the first place. Hence, ant-like morphology, and the associated suite of behaviours that together constitute myrmecoid syndrome, are confined principally to the Aleocharinae, and are seldom seen elsewhere.

Beyond permitting adaptive changes in overall body shape, the exposed, flexible abdomen has also been central to aleocharine chemical diversification – a fundamental parameter in the group's specialisation on social insects. The reason for this is twofold. First, as in other staphylinid subfamilies, the short elytra leave the abdomen physically unprotected, and this has necessitated the evolution of the defensive tergal gland that is present in the majority of free-living species (DETTNER 1993) (Figs. 4A, D, E). The tergal gland was discussed above as a primary preadaptation, which confers protection against worker aggression during the hypothesised initial, facultative evolutionary phase of myrmecophily (DONISTHORPE 1909, BRAND & al. 1973). Typically, quinones are the primary active components in tergal gland secretions, but the blend of chemicals can vary substantially across species (STEIDLE & DETTNER 1993), and in at least some myrmecophiles, the exudate has been fine-tuned to contain host-manipulating compounds (STOEFFLER & al. 2007, STOEFFLER & al. 2011, STOEFFLER & al. 2013). Through this capacity for chemical evolvability, the tergal gland has become an anatomical feature routinely targeted by selection to fit aleocharines to their ecological circumstances. The gland is thus both a primary preadaptation that enables facultative colony exploitation by free-living species, and a secondary preadaptation, which, via modification of its biosynthetic pathways, optimises aleocharines to a colony life during the subsequent phase of ecological specialisation.

The second way in which the aleocharine abdomen has facilitated chemical diversification is in enabling the development and evolution of new gland types (Figs. 4B, C). Among the specialised aleocharine myrmecophiles that have been studied in some detail, the majority appear to possess, in addition to the tergal gland, independently-evolved novel abdominal glands situated on various other segments. Novel gland-bearing taxa include a variety of army ant associated myrmecoid genera belonging to Ecitocharini (see KISTNER & JACOBSON 1990), Crematoxenini (see JACOBSON & KISTNER 1992) Lomechusini (see MARUYAMA & al. 2011), Dorylomimini, Dorylogastrini and Aenictoteratini (see KISTNER 1993, MARUYAMA & al. 2011); the appeasement-type glands identified in *Pella*, *Lomechusa* and (putatively) *Dinarda* (see HÖLLDOBLER 1970, 1973, HÖLLDOBLER & al. 1981) appear to be novel expansions of glandular tissue at the abdominal tip that are absent in free-living species (Fig. 4B); *Myrmigaster* (Lomechusini) possesses a large median gland complex on sternite VI (ASHE & KISTNER 2005), while *Lomechusa* and related genera (*Lomechusoides, Xenodusa*) additionally possess trichomes linked to novel, paired glands that are serially repeated on the basal tergites (Fig. 4C). The *Tapinoma*-associated *Myrmoecia* (Lomechusini) has what appear to be large trichome-associated median gland complexes on tergites IV and V (KISTNER 1982) – the segments anterior to those housing the tergal gland (Fig. 6, beetle on far left). Small trichome-like structures have also arisen in a few myrmecoid genera such as *Dorylobactrus* and *Dorylostethus* (both Dorylomimini), as well as *Lornechusula* (Lomechusini). Paralleling the situation in myrmecophiles, many termitophilous aleocharines have also developed new glands in various positions on the abdomen (PASTEELS 1968b, 1969, KISTNER 1979).

The secretions and functions of these novel glands are for the most part uncharacterised, but their independent evolution in a diversity of inquilines implies a general importance in the chemical adjustment of aleocharines to colony life. The aleocharine abdomen is conducive to the evolution of glands because this area of the body is not masked by elytra, and is flexible. Glands open out directly onto the cuticle, without any obstacle to the delivery of their exudates. Due to the elasticity of the abdomen, these glands are also targetable, especially those situated close to the abdominal apex (Figs. 4A, B). This abdominal arrangement led first to the evolution of the tergal gland, and has meant that the development of additional glands has been similarly selectively advantageous in myrmecophiles. Consequently, the abdomen has become an important interface mediating interactions between ant and beetle, with trichomes developing in some species to further aid the transport of gland secretions. Possessing such preadaptive abdominal morphology for gland development may have been bolstered by a further, genetic factor: in their possession of the tergal gland, most free-living aleocharines are already endowed with the developmental circuitry to construct glands on their abdomens (Figs. 4D, E). The appearance of novel gland types in new abdominal positions may conceivably have been achieved by the developmental redeployment of components of this preexisting genetic cassette. Hence, the ancestral presence of genetic circuitry for specifying exocrine gland cells on abdominal segments may be viewed as a distinct secondary preadaptation in its own right – one that has been repeatedly coopted during the transition to myrmecophily, as ecological specialisation on colonies has ensued.

What aleocharines exemplify is a general principle, that traits already in place in free-living ancestors can provide ready routes for myrmecophilous specialisation. In this specific case, the evolvability of the exposed flexible aleocharine abdomen, and its capacity for biochemical plasticity through novel gland development and biosynthetic reprogramming, are important secondary preadaptations that have led to the evolution of closer, obligate associations with ants. In Pselaphinae and Histeridae, secondary preadaptations likewise seem to have taken a leading role in helping to shape the phenotypes of the most specialised myrmecophiles. In Pselaphinae in particular, the exposed abdomen again appears to have been utilised for this purpose. Among species that possess trichomes, these structures tend to emerge at approximately the same body location, on the first visible abdominal tergite (IV). The trichomes may be situated laterally on the paratergites flanking tergite IV (Figs. 5A, B), on the edges of the elytra that overhang tergite IV (Fig. 2N), or positioned within tergite IV itself (Fig. 2K). Such structures have (putatively)

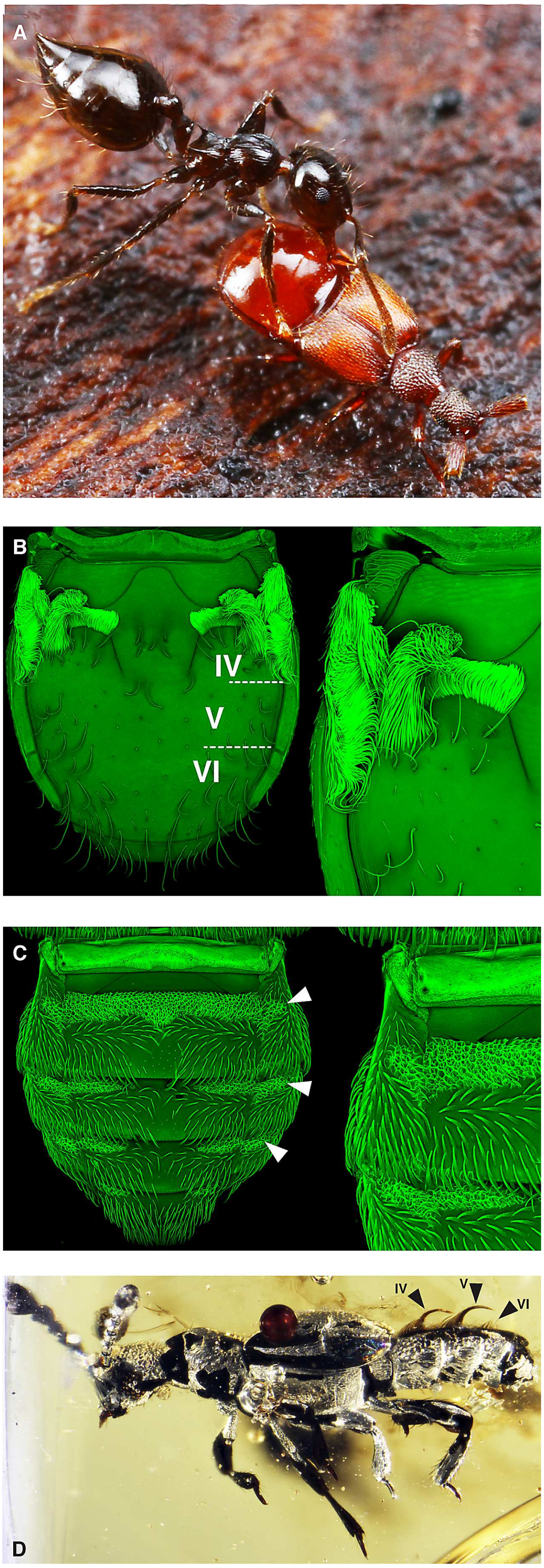

Fig. 5: Clavigeritae trichomes. (A) A *Crematogaster* worker licks the trichomes of *Fustiger* (Peru; photo credit: T. Komatsu). (B) Confocal reconstruction of the abdomen of the clavigerite *Diartiger fossulatus*, showing fusion of tergites IV - VI, with trichome situated in tergite / paratergite IV. Dashed lines indicate segmental boundaries as revealed by paratergite margins. (C) Confocal reconstruction of the abdomen of *Rhytus* (Arhytodini) showing squamous pubescence (arrowheads) at tergite boundaries. (D) *Protoclaviger trichodens*, an Early Eocene stem group clavigerite, with trichomes (arrowheads) emerging from paratergites IV, V and VI.

arisen eight times at minimum, most notably once in the ancestor of the speciose Clavigeritae, where the trichomes are known to traffic substances from the Wasmann glands that mediate interactions with hosts (CAMMAERTS 1974, HILL & al. 1976). The independent acquisition of similarly-situated trichomes in Clavigeritae and scattered other pselaphines suggests preadaptive anatomy in this part of the basal abdomen. In all eight cases, this same region has been targeted for specialisation, generating analogous morphology with presumably similar functional roles in myrmecophily.

One plausible explanation for this parallel trend is that ancestral precursor glands, embedded at the base of the abdomen, have been coopted for the production of compounds involved in myrmecophily. It is this inferred secondary preadaptation that would then have predisposed this part of the body to the subsequent evolution of trichomes in multiple taxa. If this explanation were indeed the case, then the Wasmann glands of Clavigeritae are not "true" novelties but enlarged, exaggerated glands that must have homologues across the Pselaphinae. An important insight into the evolutionary development of clavigerite trichomes may be provided by the transitional fossil *Protoclaviger*, a stem-group of Clavigeritae. Unlike all modern Clavigeritae, *Protoclaviger*'s abdomen is segmented dorsally, without the derived fusion of tergites into the tergal plate found in extant species (PARKER & GRIMALDI 2014). Each of the still-distinct tergites bears trichomes: large, hook-like ones emerge from paratergites IV and V, and an additional small trichome emerges from paratergite VI (Fig. 5D). The segmental repetition of the trichomes implies that the glands that fuel the trichomes with exudate may themselves be present in each of the corresponding abdominal segments. In the majority of insects, abdominal segments house oenocytes: large glandular lipid-processing cells that synthesise cuticular hydrocarbons and pheromones (MAKKI & al. 2014). When living clavigerites are observed, the trichomes often appear to be covered in a waxy substance (PARK 1942, AKRE & HILL 1973), and at least some of the enlarged gland cells that sit underneath the trichomes contain lipid-rich deposits (HILL & al. 1976). Such lipid-based secretions, and the possible segmental repetition of the cells that produce them in ancestral Clavigeritae, are consistent with an oenocytic identity of the Wasmann gland cells. This conclusion fits with HILL & al.'s (1976) hypothesis that, based on a detailed histological study of the clavigerite *Adranes taylori*, the expanded glandular system that fuels the trichomes arose from "hypertrophy of dermal glands … which are present in the general epidermis of many insects".

A scenario may be envisioned in which a myrmecophilous ancestor of Clavigeritae – symbolised by the character states seen in *Protoclaviger* – modified its oenocytes to synthesise lipid-based host appeasement compounds. The increased production of hydrophobic substances from these cells necessitated the evolution of serially repeated trichomes on tergites IV - VI, which helped to accelerate and direct the spread of the oenocytic exudate. Subsequently, the derived remodelling of the abdomen in modern Clavigeritae restricted this oenocytic modification to tergite IV alone, seen in modern species as the Wasmann glands and the trichomes that emerge from this segment. To extend this scenario even further back, the inferred sister group of Clavigeritae is a clade comprised in part of the tribe Arhytodini (see PARKER & GRIMALDI 2014), a group with poorly known biology but which are thought by some authors to be myrmecophilous (BRUCH 1918, CHANDLER & WOLDA 1986, PARKER & GRIMALDI 2014). Several arhytodine genera have sponge-like "squamous" pubescence on the margins of tergites, as well as on other parts of the body (Fig. 5C). Squamous pubescence probably serves to conduct secretions from nearby glands, and unlike modern Clavigeritae, *Protoclaviger* has what appear to be traces of this kind of pubescence on its abdomen (PARKER & GRIMALDI 2014). The arhytodine abdomen may thus embody a still earlier precursor of the clavigerite abdominal modifications than is seen in *Protoclaviger*.

The hypothesis that clavigerite appeasement glands have an oenocytic origin is, of course, untested at present. However, it provides a realistic basis for explaining the recurrent evolution of basal abdominal trichomes in pselaphines. Oenocytes are presumably present in all Pselaphinae, and could have been repeatedly coopted in myrmecophiles. However, no equivalent "intermediate" sister taxa with serially repeated trichomes akin to *Protoclaviger* are known for the other seven trichome-bearing myrmecophilous taxa, and the exact evolutionary scenario described here for Clavigeritae may not have played out similarly in these other lineages. It is worth noting that outside of Pselaphinae, the trichome-bearing "adoption" glands of *Lomechusa* and related genera (Aleocharinae: Lomechusini: Lomechusina) are serially repeated on tergites III, IV and V (Fig. 2I) (HÖLLDOBLER 1970), which again may point to an oenocytic origin.

In addition to the existence of preadaptive (presumably glandular) ancestral anatomy, there is a second feature of pselaphines that has likely contributed to the emergence of abdominal trichomes multiple times. Unlike in Aleocharinae, the exposed abdomen of most Pselaphinae is more compact, robust and inflexible. The thicker cuticle means the body as a whole is far more capable of withstanding mechanical force – a feature discussed above as a primary preadaptation serving a defensive purpose, and possibly encouraging physical interactions with hosts that lead to cuticular hydrocarbon transfer. However, the thick cuticle may have also been preadaptive for the evolution of closely integrated symbioses in some groups, where ants have been observed to pick the beetles up and carry them. In the vast majority of pselaphines, a transverse antebasal sulcus is present on tergite IV (CHANDLER 2001), and in the trichome-bearing taxa, this has been fashioned into a deep basin flanked by the paratergites. In Clavigeritae, and probably the other taxa that possess this morphological feature, the antebasal sulcus functions as a grasping notch (LESCHEN 1991), allowing the ants to lock their mandibles around the beetle. The strong supporting cuticle has effectively permitted the antebasal sulcus and trichome-associated glands to combine into a focal point that host ants habitually target, licking the trichomes and handling the beetle. The heavy pselaphine integument has thus permitted the evolution of physical interactions between host ant and beetle that may be less likely in other beetle taxa with less robust morphology. Indeed, in the few Aleocharinae known to be carried by their hosts, such as *Lomechusa* and allies, and some myrmecoid genera, the body is uncharacteristically robust and heavily sclerotised for the subfamily. This represents a derived modification of the integument that socially integrated pselaphines have not needed to undergo, although weaker areas of cuticle, such as the intersegmental membranes and antennal pedicels, have experienced reductions or fusions.

In Histeridae, a comparable phenomenon to the parallel evolution of trichomes seen in Pselaphinae may exist. Glandular openings decorating the exoskeleton are widespread in histerids, and may be broadly homologiseable across large swathes of higher taxa, if not the family as a whole (CATERINO & TISHECHKIN 2013a). One set of glands on the pronotum may provide the basis for the development of trichomes, which have evolved in this region several times in the family: on multiple independent occasions in Hetaeriinae (A. Tishechkin, pers. comm.), at least twice in the Chlamydopsinae (*Gomyopsis* and *Chlamydopsis caledoniae*, see DÉGALLIER 1984, CATERINO 2006) and once more in the onthophiline *Peploglyptus* (see CATERINO 2004). In the *Eciton hamatum*-associated hetaeriine *Pulvinister nevermanni* pores open out onto the pronotum (KISTNER 1982), the part of the body that is most often licked by host ants. Histological examination of the *Eciton quadriglume*-associated haeteriine *Chrysetaerius iheringi* revealed many gland cells in this pronotal area (SEYFRIED 1928), and it is tempting to think that they represent adaptive expansions of a more ancestral secretory system.

Collectively, the secondary preadaptations identified in Aleocharinae, Pselaphinae and Histeridae are posited to have contributed to much of the complex anatomical innovation observed among myrmecophiles belonging to these taxa. Given that these three groups account for the majority of specialised myrmecophiles within the Coleoptera, it follows that secondary preadaptations have taken a central role in the adaptive phenotypic diversification of beetle myrmecophiles. Although morphological characters provide the most obvious examples of secondary preadaptations, it is conceivable, indeed likely, that other kinds of traits present in free-living ancestors – behavioural, physiological and life history attributes – could also have provided the raw foundations for subsequent evolutionary modification in specialised taxa. One such example, suggested to me by Alfred Newton (Field Museum, Chicago), concerns the habitual use of patchily distributed resources by free-living members of some of the myrmecophily-prone beetle clades. Many histerids, scarabs and aleocharines utilise carrion, dung, fungi or other spatially scattered and ephemeral resources, which are located by smell during flight. Free-living species in these groups are adapted for targeting widely dispersed resources, with olfactory systems that are highly sensitive to volatile signals at extremely low ambient concentrations. Such species may therefore be preadapted for locating spatially isolated ant colonies, with simple fine-tuning of olfactory receptor repertoires to detect colony odours occuring in species that have evolved myrmecophily (A. Newton, pers. comm.).

Secondary preadaptations reveal their existence most clearly in clades that repeatedly evolve myrmecophily and exhibit parallel trait evolution: the recurring origin of similar traits implies some predisposing character present in the clade's ancestral groundplan. However, an important additional consideration is that secondary preadaptations may feasibly exist in any clade that has a descendent lineage that has undergone specialisation to colony life. In this regard, secondary and primary preadaptations differ: a clade that lacks the requisite primary preadaptations to regularly transition to myrmecophily may have yielded only a single myrmecophilous lineage; yet during the evolution of that lineage, an ancestral trait may have served as a progenitor structure for specialisation. Outside of the main myrmecophily-prone beetle clades, secondary preadaptations may have provided the template for specialisation in other, more isolated myrmecophilous lineages. For example, in Paussinae (Carabidae), the genus *Pachyteles* (Ozaenini) is not myrmecophilous; free-living larvae have a disc-like abdominal apex which has glandular activity and is used as a lure to capture prey. However, in laboratory experiments, the larval disc has been shown to be attractive to workers of various ant species (DI GIULIO & TAGLIANTI 2001). In the related and wholly myrmecophilous tribe Paussini, the larval terminal disk is present but has undergone a fusion of constituent parts that prevents it from being used to capture prey. Instead, the disk's glandular secretions appear to be involved in host appeasement (DI GIULIO & al. 2011).

The paussine larval disc provides yet another case of an ancestral structure being coopted during the evolution of socially-integrated myrmecophily. However, this time the example is confined to just one or a limited number of lineages (perhaps underlying rare cases of myrmecophily in some other ozaenine genera, DI GIULIO & al. 2011). It remains to be seen if secondary preadaptations have been more generally involved in other groups where specialised myrmecophily has not evolved to the same recurring extent seen in Aleocharinae, Pselaphinae and Histeridae. In addition to Paussini, perhaps the specialised morphologies seen in other isolated myrmecophilous taxa, such as eremoxine brentids and ptinine anobiids, were also built on preexisting secondary preadaptations.

Preadaptations and contrasting routes to specialisation

When viewed through the lens of preadaptations, myrmecophiles – though often enigmatic and amongst the most morphologically derived arthropods – are not so obscure as to be indecipherable. The biased evolution of myrmecophily in a few myrmecophily-prone clades can be interpreted as a consequence of these groups possessing the appropriate primary preadaptations to engage in successful, facultative nest exploitation. Furthermore, a substantial amount of the apparent morphological innovation seen in myrmecophile-rich clades such as Aleocharinae, Pselaphinae and Histeridae can be decomposed into relatively straightforward modifications or re-use of preexisting secondary preadaptations.

Based on the primary and secondary preadaptations identified in this work, hypotheses for the recurring patterns seen during the evolution of myrmecophily in the two groups most familiar to me – Aleocharinae and Pselaphinae – are summarised in Figure 6. While the phenotypic groundplans of free-living species predispose both subfamilies to target colonies, their contrasting anatomies have caused them to employ different evasive strategies during the initial facultative stage of myrmecophily. Aleocharines employ tergal gland-based chemical defense (combining it with rapid escape), whereas pselaphines exploit

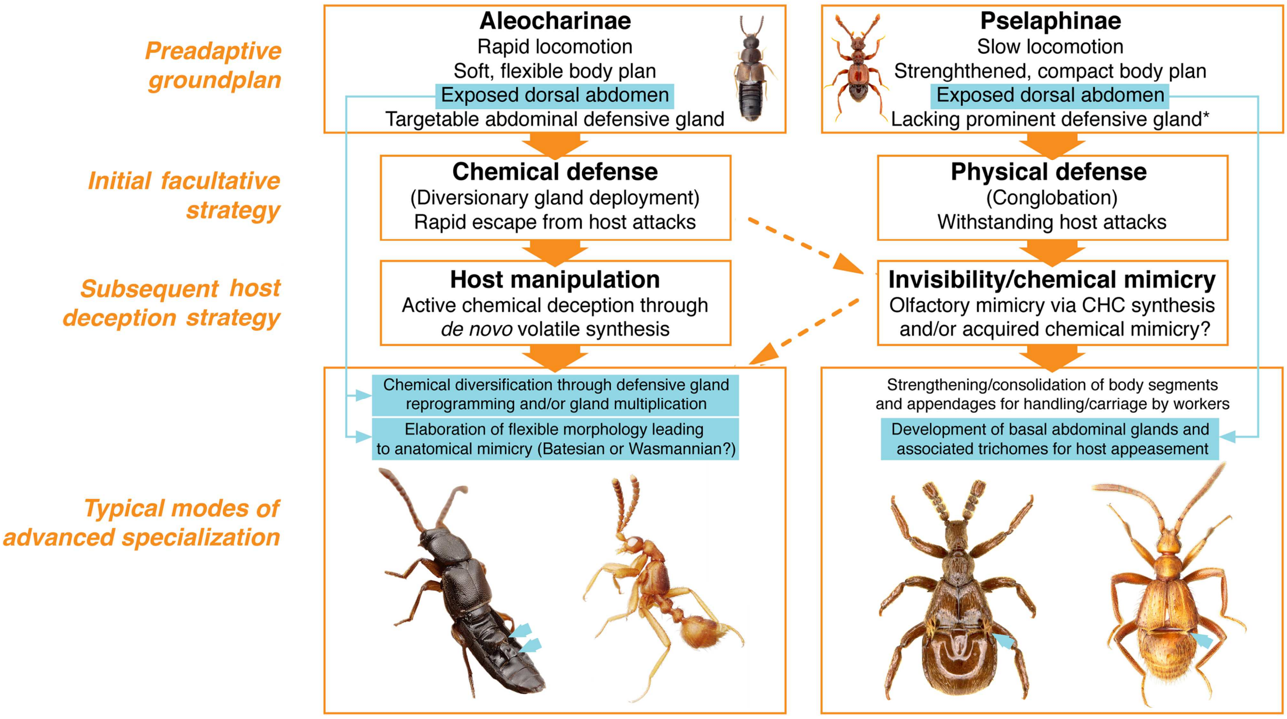

Fig. 6: Hypotheses for the repeated evolution of myrmecophily in Aleocharinae and Pselaphinae based on putative primary and secondary preadaptations. Preadaptive plesiomorphic groundplans of each taxon are shown. The mechanisms by which the primary preadaptations of these taxa promote facultative colony exploration are indicated in the "initial facultative strategy" box. Secondary preadaptations and their resultant functionally adaptative traits are highlighted in blue; the hypothetical "typical" routes of evolutionary specialisation for each taxon are shown, with secondary preadaptations becoming relevant during the advanced stages, as taxa evolve ways to socially integrate inside colonies. Exemplar specialised taxa are shown (left to right): *Myrmoecia confragosa* (Aleocharinae: Lomechusini) representing gland multiplication, with medial gland openings in tergites IV and V labelled with blue arrows (credit: P. Krásenský); *Ecitocryptus* (Aleocharinae: Lomechusini), an ant mimic associated with *Neivamyrmex* (photo credit: K.T. Eldredge) and unrelated to *Aenictosymbia* in Figure 2H, representing parallel evolution of myrmecoid syndrome; *Claviger testaceus* (Pselaphinae: Clavigerini) and *Attapsenius* (Pselaphinae: Attapseniini; photo credit: K.T. Eldredge) together representing the independent evolution of basal abdominal / apical elytral trichomes, which are labelled with blue arrows in each species; both species show antennomere consolidation, via antennomere fusion in *Claviger* and antennomere compaction in *Attapsenius*. Note that cuticular hydrocarbon (CHC) mimicry may not be a general rule for chemical disguise in Aleocharinae and is thus indicated with a dashed line; CHC mimicry has also yet to be demonstrated in the majority of myrmecophilous Pselaphinae although it is strongly suspected. The asterisk indicates that the small, putative defensive gland present in some pselaphines is not thought to be involved in the evolution of myrmecophily in this subfamily.

their strengthened exoskeleton for physical protection (combined with conglobation). This initial strategy has ramifications for subsequent steps: aleocharines continue to rely on chemical-based strategies by modifying tergal gland chemistry, whereas pselaphines are hypothesised to exploit physical contact with hosts to procure the colony odour; synthesis of cuticular hydrocarbons to match hosts may also occur (Fig. 6). Ultimately, in both subfamilies, major phenotypic specialisation has occured through modification of the abdomen. The exposed, flexible aleocharine abdomen has stimulated the evolution of myrmecoid form and the development of novel gland types in different abdominal segments. In pselaphines, the exposed, rigid abdomen has facilitated the evolution of basal abdominal glands with associated trichomes, possibly building on oenocytic progenitors; consolidation of appendages and / or fusion of segments has been an adaptive response to pselaphines physically interacting with hosts.

Secondary preadaptations reveal that core aspects of the morphological innovation of myrmecophiles were already present in ancestral free-living species. To be clear, however, secondary preadaptations are invoked solely to explain parallel evolution of constructed novelties, be they new morphologies, behaviours, or chemical signals. Secondary preadaptations need not be invoked to explain reductive or so-called "regressive" specialisations (Kistner 1979), such as eye loss, aptery, and mouthpart diminution. These modifications are widespread in myrmecophiles (Box 2), and probably represent adaptive "use it or lose it" morphological changes associated with a parasitic lifestyle. Their evolution may be mechanistically straightforward, with removal of purifying selection on the underlying developmental mechanism leading to trait degeneration. The fusion of antennomeres and / or tergites seen in Clavigeritae and Paussini may have arisen similarly.

While preadaptations may promote the evolution of specialisation in some beetle clades, they may act to limit the progression of the relationship in others. For example, if the ancestral saprophagous or phytophagous diets of scarabaeids predispose this family to the exploitation of nest refuse, then there is no historical, genetically-entrenched urge to access the central, better-policed parts of colonies to target the brood. Consequently, major phenotypic characters that mediate contact or communication with hosts, and which are seen repeatedly in aleocharines, pselaphines and histerids, are scarce among scarab myrmecophiles, because the degree of interaction is generally more limited. The plesiomorphic diet that predisposes this clade to myrmecophily in fact favours one kind of myrmecophily, and poses a significant genetic and physiological barrier to evolving alternative modes of colony exploitation. This apparent ceiling to the elaboration of the myrmecophilous relationship is not impassable, however. In the rare instances among scarabaeids where brood predation has evolved, such as in the Cremastocheilini and some Eupariini, heavy cuticular modifications and trichomes can sometimes be observed. With this in mind it is interesting to contrast myrmecophilous scarabs with termitophiles belonging to this family – in particular, those species that frequent the gardens of fungus-growing termites. In these species, trichomes, glandular areas, grasping notches and even physogastric forms may be more common (Vårdal & Forshage 2010, Maruyama 2012a, b). The degree of specialisation therefore appears to depend on how far the beetle translocates into the nest during evolution – a factor contingent on diet, a primary preadaptation inherited from free-living ancestors.

In other cases, the plesiomorphic morphology of a clade may lack readily evolvable secondary preadaptations, which would dampen the capacity of any emerging myrmecophilous lineages to undergo specialisation. For example, despite the large number of scydmaenine myrmecophiles, no socially integrated species have yet been found, and none bear trichomes or other clear morphological hallmarks indicating an obligate dependence on ant colonies. By possessing long elytra, scydmaenines lack the major secondary preadaptation of Aleocharinae and Pselaphinae: the exposed abdomen. This may be an impediment to the evolution of abdominal exocrine glands, which in both aleocharines and pselaphines have been instrumental to evolving more complex associations with ants. This morphological constraint of scydmaenines may be further compounded by an ancestral dietary constraint: many are highly specialised mite predators, and may simply enter nests to target the numerous other microarthropods that live there. In the absence of any impetus to access the colony brood galleries or interact with hosts, there may be little selection pressure for derived morphological or behavioural attributes mediating more intimate forms of myrmecophily.

Ant selection: the Cenozoic rise of ants as a driver of myrmecophily-prone beetle diversification

With this preadaptation-based explanation for the evolution of beetle myrmecophily in mind, it is illuminating to consider the influence ants have had on coleopteran diversity. Comparing the fossil records of the myrmecophily-prone beetle clades to that of ants, a scenario emerges in which these beetle groups existed in their preadaptive, crown-group forms probably long before ants diversified and began to proliferate ecologically. Mid-Cretaceous Burmese amber, dated to 99.8 million years old (Shi & al. 2012), houses the earliest-known definitive ant inclusions, mostly assignable to the extinct stem group subfamily, Sphecomyrminae, and these collectively comprise only a small fraction (far less than 1%) of the total number of insects in this deposit (Engel & Grimaldi 2005, LaPolla & Dlussky 2013, Barden & Grimaldi 2014). Throughout the Upper Cretaceous, ants continue to be rare (as judged by their frequency in fossil deposits), with definitive examples of crown-group ants vanishingly so. Finally, during the Early-Middle Eocene, modern ant subfamilies prevail (and sphecomyrmines no longer persist), and ants as a whole start to increase in frequency relative to other insects, approaching their present day dominance (Grimaldi & Agosti 2000, Wilson & Hölldobler 2005, LaPolla & Dlussky 2013, Barden & Grimaldi 2014). Contemporaneous with the earliest ants, modern-looking scydmaenines (Chatzimanolis & al. 2010) and higher (compact-bodied) Pselaphinae (J. Parker, unpubl.) have been recovered from Burmese amber; so too has a putative histerid (Poinar & A. E. Brown 2009). The antiquity of these beetle groups argues that they were phenotypically outfitted for both general ecological coexistence with ants and exploitation of colonies by the time ants began to dominate terrestrial environments. An aleocharine has also been found in Burmese amber (Cai & Huang 2015), although it belongs to the basal, tergal-glandless tribe Deinopsini. Higher (gland-bearing) aleocharines are thus far not known from the Cretaceous, but are nevertheless relatively common in Middle Eocene Baltic amber, including some that have been assigned to modern genera (taxa listed in Chatzimanolis & Engel 2011). This implies that the higher Aleocharinae may have likewise evolved and undergone substantial diversification some time before the Early-Middle Eocene when modern ants began to dominate.

Not only did all four groups go on to evolve myrmecophily with great frequency, but, given the capacity of these groups for coexistence with ants, their own ecological success and evolutionary diversification may have been favoured by the ascent of ants. By clearing out other arthropods from the forest floor (including would-be predators such as carabids and spiders, which do not fare well in ant-rich habitats, Darlington 1971, Wilson 1990), ants may have permitted these beetle taxa the freedom to diversify in this novel, social insect-dominated world. Through this mechanism of "ant selection" a vast and largely enemy-free space may have been created for these preadapted beetle clades – the entirety of the lowland tropical forest floor. By permitting these clades to radiate in this environment, the now-ubiquitous ants may have been an important driver of these beetles' contemporary species richness.

Future studies on myrmecophily: the value of focusing on preadaptations

The ideas put forward in this article have been synthesised based on a patchwork of biological information documented in a massively dispersed myrmecophile literature. Despite more than a century of study, myrmecophile biology remains very much in its infancy. Yet, exploring how and why myrmecophily evolves is to ask fundamental questions about the starting conditions necessary for interspecies relationships to arise, and the factors leading such relationships to increase in intimacy and phenotypic complexity. Myrmecophily is a form of ecological specialisation, and in its most advanced incarnation represents a paradigm of obligate symbiosis between multicellular organisms. Its repeated emergence in some clades signals the possession of traits that are evolutionarily predisposing to this kind of lifestyle. Identifying what these preadaptations are, and examining how they promote ecological engagement with ants, offers an opportunity to observe the biological phenomena at play as species abandon a free-living existence and begin evolving an increasingly intimate, parasitic symbiosis.

Clades that exhibit repeated evolution have special value in evolutionary biology, because the acquisition of similar traits by independent lineages evolving under comparable selective regimes provides a compelling argument for the non-random nature of evolutionary change (ORD & SUMMERS 2015). Moreover, through comparative analyses of underlying mechanisms governing trait formation, such clades can reveal the extent to which adaptive phenotypic changes are mirrored by parallel genetic and developmental changes (e.g., COLOSIMO & al. 2005, REED & al. 2011, ELMER & al. 2014). In beetles, myrmecophily reaches its phenotypic extreme repeatedly in aleocharines, pselaphines and histerids, with each group showing an element of parallel trait evolution in the more specialised taxa. The recurring ecological transition to myrmecophily, combined with seemingly predictable aspects of phenotypic evolution, distinguishes these taxa as potentially powerful systems for studying the evolution and biological mechanisms of myrmecophily. The implications of studying these clades are broad, not least because they are unusual in containing numerous convergent taxa separated by tens of millions of years. In contrast to more widely studied and evolutionarily young adaptive radiations, myrmecophily-prone clades embody parallel evolution over vast timescales. I suggest that focusing on these clades, and in particular the preadaptations identified in this article, may transform these groups of beetles into important study systems for exploring basic principles of evolution. Crucially, I believe focus should not be limited to the myrmecophiles alone, but should encompass – perhaps even emphasise – related, free-living taxa that embody the ancestral condition from which myrmecophily repeatedly, and convergently, evolves. By studying preadaptations in these species, insight will be gained into the phenotypic and genetic ground state that is poised for myrmecophilous specialisation. Such a comparative approach promises a way in to the adaptive genomic and developmental changes shaping the numerous, fascinating biological dimensions of this beetle-biased way of life.

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