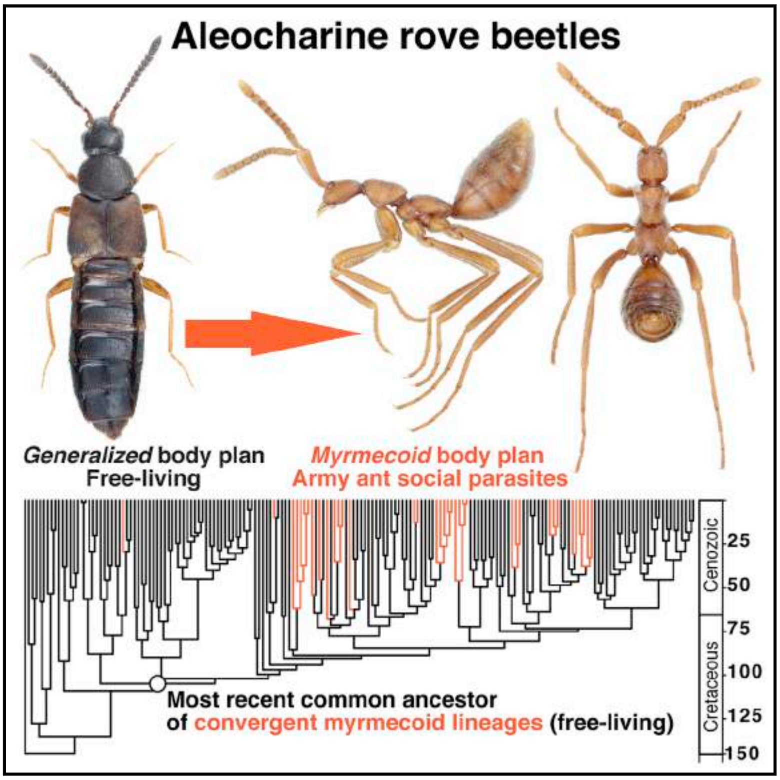
Report

Current Biology

Deep-Time Convergence in Rove Beetle Symbionts of Army Ants

Graphical Abstract



Highlights

- Army ant-parasitic rove beetles comprise an ancient system of complex convergence
- Beetles anatomically mimic and deceive host ants to exploit nest resources
- Convergent clades arose in the Cenozoic and share a Cretaceous common ancestor
- Convergence over deep time challenges the notion of evolutionary contingency

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In Brief

Maruyama and Parker reveal that ant-mimicking rove beetles living symbiotically with army ants evolved at least 12 times. The convergent beetle lineages share a free-living common ancestor in the Early Cretaceous. Discovery of an ancient system of complex convergence challenges the notion of evolutionary contingency over deep timescales.

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Report

Deep-Time Convergence in Rove Beetle Symbionts of Army Ants

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SUMMARY

Recent adaptive radiations provide striking examples of convergence [1–4], but the predictability of evolution over much deeper timescales is controversial, with a scarcity of ancient clades exhibiting repetitive patterns of phenotypic evolution [5, 6]. Army ants are ecologically dominant arthropod predators of the world's tropics, with large nomadic colonies housing diverse communities of socially parasitic myrmecophiles [7]. Remarkable among these are many species of rove beetle (Staphylinidae) that exhibit ant-mimicking "myrmecoid" body forms and are behaviorally accepted into their aggressive hosts' societies: emigrating with colonies and inhabiting temporary nest bivouacs, grooming and feeding with workers, but also consuming the brood [8–11]. Here, we demonstrate that myrmecoid rove beetles are strongly polyphyletic, with this adaptive morphological and behavioral syndrome having evolved at least 12 times during the evolution of a single staphylinid subfamily, Aleocharinae. Each independent myrmecoid clade is restricted to one zoogeographic region and highly host specific on a single army ant genus. Dating estimates reveal that myrmecoid clades are separated by substantial phylogenetic distances—as much as 105 million years. All such groups arose in parallel during the Cenozoic, when army ants diversified into modern genera [12] and rose to ecological dominance [13, 14]. This work uncovers a rare example of an ancient system of complex morphological and behavioral convergence, with replicate beetle lineages following a predictable phenotypic trajectory during their parasitic adaptation to host colonies.

RESULTS AND DISCUSSION

The degree to which biological evolution is idiosyncratic or predictable is a fundamental question in evolutionary biology. Convergence—the acquisition of similar traits in different taxa evolving under comparable selective regimes—provides a compelling argument for predictability in evolutionary change [15]. The most striking convergent systems are recent adaptive radiations, in which independent lineages have followed seemingly parallel evolutionary trajectories. Darwin's finches [1], Hawaiian *Tetragnatha* spiders [2], African lake cichlids [3], and three-spined sticklebacks [4] represent natural experiments, where exposure to similar selection pressures has led to analogous phenotypes in separate lineages. Although predictable evolution is manifestly demonstrated by these systems, the likelihood of convergence may nevertheless be enhanced by the young ages of these clades: the close genetic relatedness of lineages is expected to bias the production of genetic variation, enhancing the probability that similar traits will evolve repeatedly [16, 17]. Molecular studies of such recently descended convergent taxa support this notion, often revealing selection acting on the same loci or signaling pathways [18, 19]. With increasing phylogenetic divergence between taxa, however, the likelihood of such marked convergence has been shown to decrease markedly [6]. Ancient clades displaying equivalently conspicuous repeated evolution are rare, lending apparent credence to Gould's view that evolution is inherently contingent [5] and that adaptive responses to a given selection pressure are likely to be different in distantly related taxa.

Here, we report a novel example of predictable evolution of a highly complex phenotype that has occurred over a deep timescale. We explored the evolutionary origins of specialized rove beetles (Staphylinidae) that live symbiotically with army ants, uncovering an ancient system of marked convergence. Army ants are dominant eusocial predators of the tropics: their colonies are nomadic, with hundreds of thousands of workers that emigrate between temporary nest sites and engage in group foraging (raiding) to harvest invertebrate prey [20]. Although notoriously aggressive, army ant colonies represent major concentrations of resources, attracting numerous myrmecophiles that form obligate symbioses with their hosts [7]. Diverse taxa including mites, silverfish, flies, wasps, and beetles exploit this resource, employing either defensive morphologies, or behavioral and chemical strategies to evade worker hostility. A dramatic manifestation of this lifestyle occurs in numerous genera of the staphylinid subfamily Aleocharinae, where the beetles anatomically mimic their host ants and are recognized and accepted by them [8, 10, 11]. Such species live as behaviorally integrated social parasites—appearing at least partially assimilated into

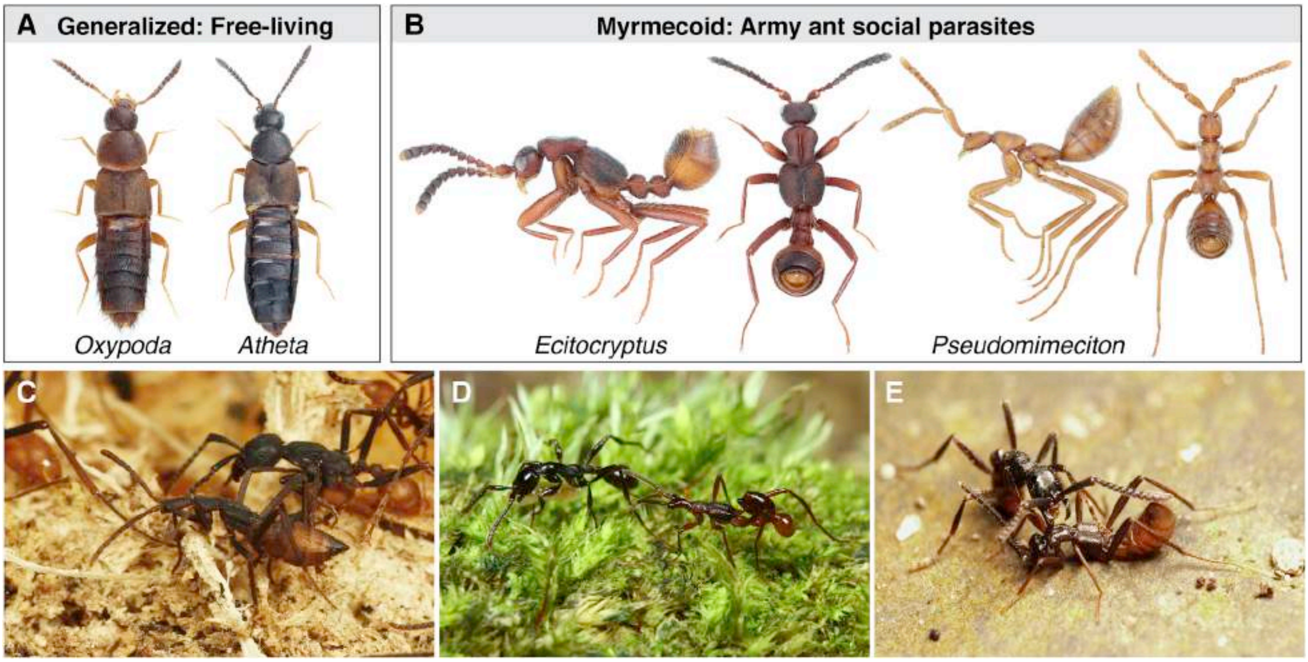


Figure 1. Myrmecoid Syndrome in Aleocharine Rove Beetles

(A) Examples of free-living Aleocharinae with generalized morphology, *Oxypoda* and *Atheta*.

(B) Examples of army ant social parasites with myrmecoid morphology, *Ecitocryptus* (associated with *Nomamyrmex*) and the eyeless, elytra-less *Pseudomimeciton* (associated with *Labidus*).

(C–E) Living myrmecoids with host ants: *Ecitophya* with *Eciton* host (Peru), *Rosciszewskia* with *Aenictus* host (Malaysia), *Beyeria* with *Neivamyrmex* host (Ecuador).

colony life but simultaneously feeding on the ants' brood and raided food. In contrast to the majority of the ~16,000 species of Aleocharinae, which are mainly free-living species with "generalized" staphylinid morphology and extremely similar in body form (Figure 1A), ant-like "myrmecoid" aleocharines are heavily modified (Figures 1B–1E), with a petiolate abdomen (a narrowed waist and expanded gaster), elongate appendages, geniculate (elbowed) antennae, and further similarities to host ant body size, thorax shape, and cuticle sculpturation. The myrmecoid ecomorph is thought to mediate tactile mimicry of nestmate recognition cues [10, 11, 21–23] and is accompanied by a suite of behaviors, including grooming and licking of workers [9], cohabitation of temporary nesting bivouacs, and synchronicity with the colony where the beetles emigrate with hosts and join them on raids, sometimes being carried by or phoretically attaching to workers [10, 24]. Where known, the beetle's cuticular hydrocarbons match those of the host [24], and novel glands on the beetles' cuticles are thought to facilitate chemical integration into the ant society [11].

The myrmecoid morphological and behavioral syndrome presents an evolutionary puzzle: because these beetles are so anatomically modified, their phylogenetic relationships to other aleocharines are obscure. Prominent aleocharine taxonomists have proposed conflicting evolutionary scenarios: Seevers [8] argued for a single principal origin of these beetles within Aleocharinae, forming the large tribe Dorylomimini, and posited an ancient association with army ants followed by codiversification with hosts throughout the tropics. In contrast, Kistner and Jacobson argued for multiple origins [22, 23, 25, 26], splitting Dorylomimini into numerous small tribes and invoking potentially widespread—and extraordinary—morphological and behavioral convergence. Neither scenario has been tested phylogenetically, and to date, the relationships of these beetles have been uncertain. A molecular approach is essential but has been enormously problematic due to difficulties in obtaining specimens. The beetles rank among the rarest and most challenging of insects to find in nature, with many known only from a small number of museum specimens. In this study, we present the outcome of efforts to collect these beetles and explore their evolutionary relationships. Over the course of a decade, we observed army ant colonies across the world's tropics, accumulating myrmecoid aleocharines. In reconstructing their evolutionary history, we uncovered evidence of conspicuous, repeated evolution over deep time that runs counter to the notion of evolutionary contingency and represents a new paradigm for understanding the origins of interspecies relationships.

Parallel Evolution of Myrmecoid Syndrome in Aleocharinae

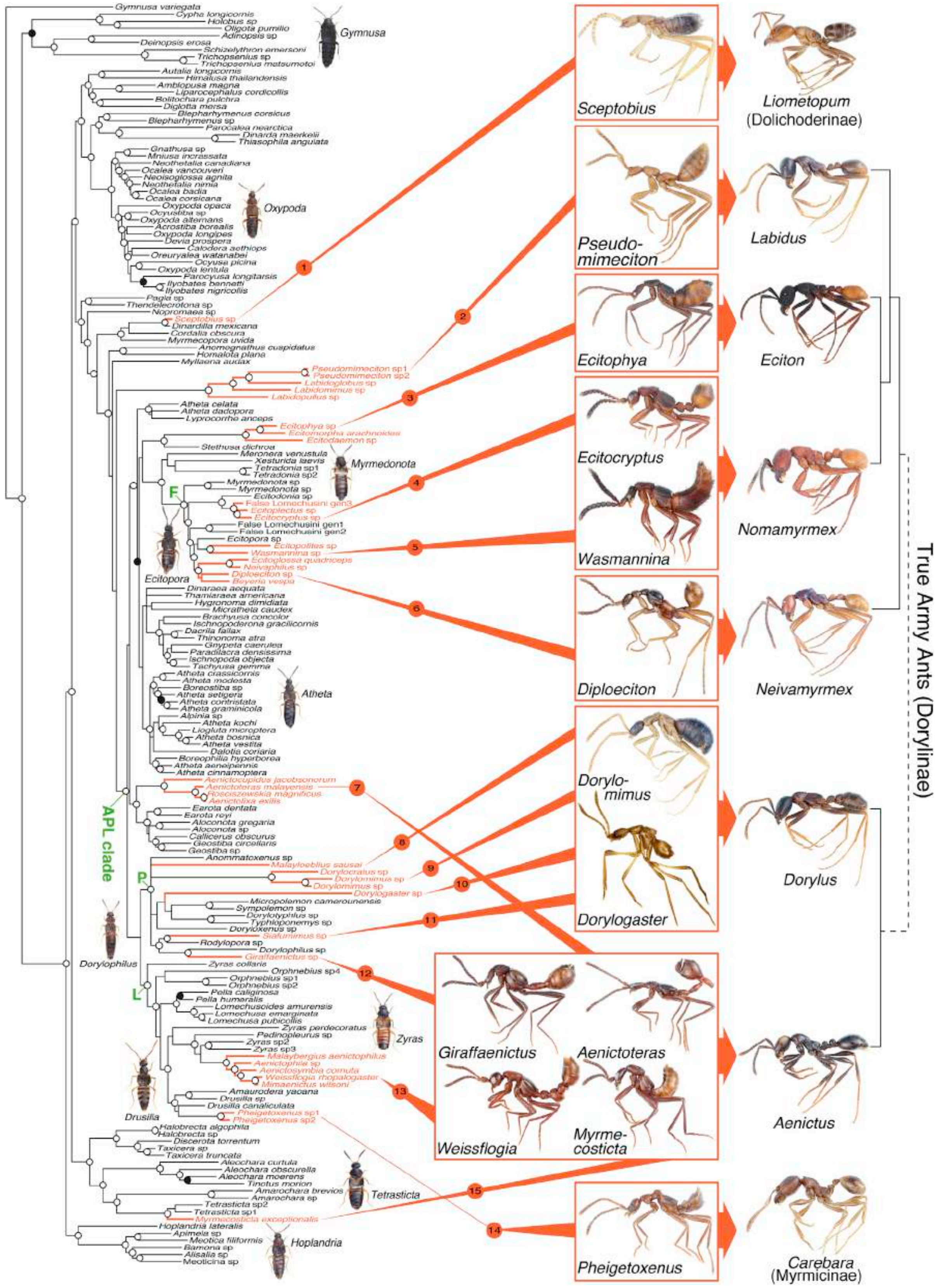
Army ants include the New World genera *Eciton*, *Labidus*, *Neivamyrmex*, *Nomamyrmex*, and *Cheliomyrmex* and Old World *Aenictus*, *Aenictogiton*, and *Dorylus*. These "true" army ants exhibit classical nomadic biology [20] and are split into separate Old and New World clades within the subfamily Dorylinae [12]. We collected aleocharines associated with all genera except the poorly known *Cheliomyrmex* and *Aenictogiton*. Additionally, we collected beetles known to associate with two distantly related ants, *Carebara* (Myrmicinae) and *Liometopum* (Dolichoderinae), which display group-foraging behavior. Both generalized and myrmecoid aleocharines were collected, and to avoid subjectivity on our part, we defined myrmecoid species as those with petiolate abdomens and long legs that previous authors judged to be myrmecoid [8, 22, 23, 25–27] (see "Specimen collection and taxon sampling" in Supplemental Experimental Procedures). Most species collected were new to science, so DNA was extracted non-destructively [28] to permit taxonomic description ([29–31] and ongoing efforts). We sequenced five loci previously used in aleocharine phylogenetics: nuclear *28S rRNA*, *18S rRNA*, and *Topoisomerase 1*; mitochondrial *Cytochrome c oxidase subunit I* and *16S rRNA* [32, 33]. Army ant myrmecophile data were integrated with sequences from free-living, morphologically generalized taxa representing a broad taxonomic spectrum of Aleocharinae including all major tribes, and outgroups from the related subfamily Tachyporinae (see Data S1). We performed Bayesian phylogenetic inference on the resulting 181-taxon matrix (see Data S2). The topology produced by this analysis, along with exemplar beetle and host ant images, is shown in Figure 2.

The pattern of convergence is dramatic and clear to the eye. Generalized aleocharines form an ancestral backbone to the tree, from which numerous elaborate myrmecoid lineages have emerged in parallel (Figures 2, S2A, and S2B; beetles enlarged in Figures S1A–S1O). Each independent origin of the myrmecoid ecomorph is represented by a small clade or single taxon that is host specific on a single ant genus. All host ant genera have been targeted: each of the "true," doryline army ants have their own, dedicated symbiont clade(s) and so too do the group-foraging *Liometopum* and *Carebara*. We estimated the number of origins using parsimony optimization and Bayesian ancestral state reconstruction. For parsimony, we assumed Dollo-type irreversibility of myrmecoid syndrome [34], which may be a valid assumption in this system: the "tippy" distribution of myrmecoid lineages across the tree is consistent with it being a terminal phenotype, and an improbably large number of regains of primitive characters would be required to lose myrmecoid morphology and restore generalized morphology (together with reversion to ancestral behavior). Such a model of evolution produces the 15 origins depicted in Figure 2. However, for a more conservative estimate taking branch lengths and support values into account, and including the possibility of trait reversal, ancestral states were calculated over a Bayesian tree distribution, giving an estimate of 12 origins (Figure S2C). We think 12–15 origins is an underestimate: there remain numerous myrmecoid genera associated with both Old and New World army ants that we were unable to collect, some of which—given the polyphyletic evolution of this syndrome—likely represent additional origins. A detailed anatomical study of myrmecoid taxa and their inferred, non-myrmecoid relatives revealed characters supporting some of our molecular groupings (Figure S3 and "Systematics and Behavior of Myrmecoid Aleocharinae" in Supplemental Discussion, which also summarizes known behavior of each clade).

Importantly, we see no evidence in any of the myrmecoid clades of a lineage promiscuously switching to a different host genus, indicating that all these relationships are highly host specific. The converse of this relationship does not hold, however, with some ant genera—*Aenictus* and *Dorylus* in particular—playing host to multiple beetle clades. The stringency with which each beetle clade associates with its ant genus likely extends to species level, since individual beetle species have generally been recorded living with single ant species [8, 10]. From this evolutionary pattern we determine the following: (1) separate aleocharine lineages evolved to socially parasitize each army ant genus; (2) during subsequent adaptation of these lineages to ants, they specialized and became host specific; (3) most dramatically, their morphology and aspects of behavior followed a predictable evolutionary trajectory, leading to an overtly stereotyped symbiosis. Cumulatively the outcome is an extraordinary system of parallel evolution in the classical sense, where multiple ancestral taxa sharing a relatively conserved body plan have each evolved in the same direction [35]. This degree of conspicuous, repeated parallelism is rare in the natural world and is generally associated with young clades [6, 36]. In contrast, Aleocharinae are ancient, with crown-group fossils known from the mid-Cretaceous and a rich fauna of modern tribes and genera already diversified by the Eocene [37]. Substantial phylogenetic distances should therefore separate many myrmecoid lineages scattered across the tree.

To gauge the timescale over which this system emerged, we dated the tree using a Bayesian lognormal relaxed clock, calibrating nodes with Cretaceous Burmese and Middle Eocene Baltic amber fossils, and a compression from the Jurassic Talbragar Fish Bed (see Supplemental Experimental Procedures for details). Our analysis shows that virtually all myrmecoid clades arose in parallel during the Cenozoic (Figure 3; Figure S2D). This temporal window is consistent with when ants in general (including army ants) are thought to have risen to ecological dominance [13, 14], promoting the diversification of myrmecophiles [38]. Although army ant dating estimates are problematic due to limited fossils (only a single, Miocene Dominican amber *Neivamyrmex* is known [39]), recent dating estimates hypothesize that stem groups of doryline army ants date to the Upper Cretaceous (~80 mya,) radiating into crown-group genera ~35–20 mya [12]. This time frame is broadly consistent with the origins of myrmecoid clades inferred in this study (Figure 3; Figure S2D), although we see no clear relationship between the age of each ant genus and its corresponding myrmecoid clade(s) (data not shown).

Of foremost interest, however, is that we estimate the most recent common ancestor of all myrmecoid clades to have existed in the Early to mid-Cretaceous. In our focal analysis, this ancestor lived ~105 mya (Figure 3; Figure S2D). There is thus an ancient, inherent potential for Aleocharinae to evolve symbioses with army ants, which was realized by multiple lineages in parallel during the Cenozoic and which has led to the repeated evolution of symbionts with matching ecomorphologies and similar behaviors over an extraordinarily deep timescale. We note that origins of myrmecoid syndrome are unevenly distributed across the subfamily: 12 of the 15 myrmecoid lineages are clustered within a clade, "APL" (Figures 2 and 3), comprising the tribes Pygostenini, Lomechusini, and the vast, paraphyletic Athetini, where myrmecoid lineages occur among the "False Lomechusini" (clade F) [32], a group of New World genera formerly placed in Lomechusini. This bias probably represents the tropical dominance of APL tribes relative to other aleocharines, ecologically juxtaposing the beetles with army ants and hence elevating the likelihood of evolving this type of symbiosis. In contrast, no myrmecoid lineages emerge within the speciose



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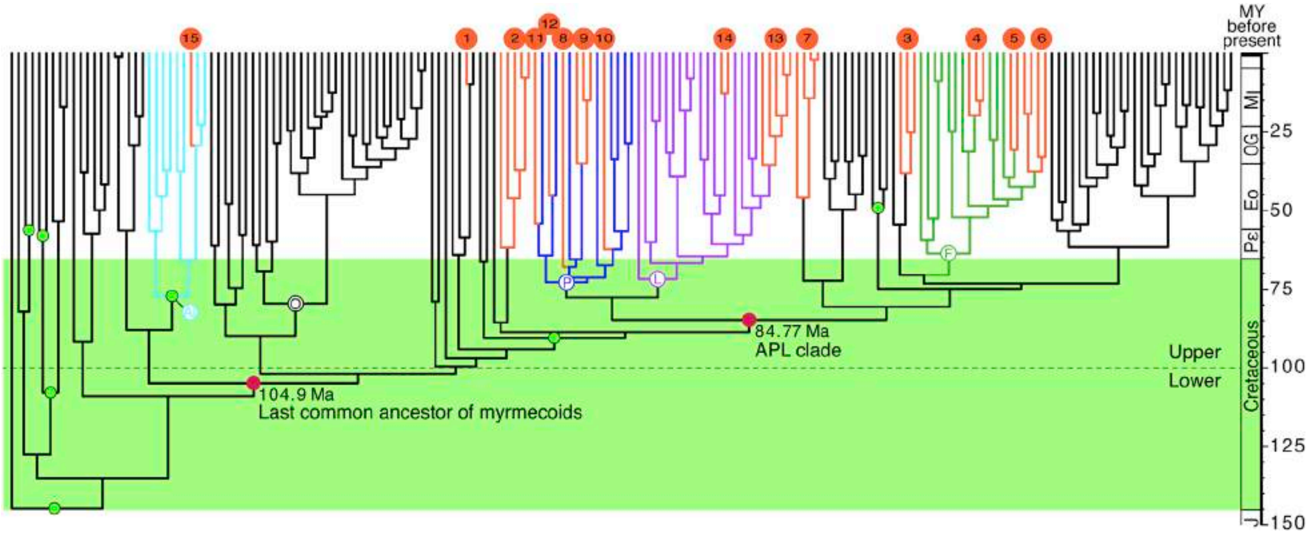

Figure 3. Dating the Evolution and Ancestry of Myrmecoid Clades

Dated phylogeny produced by BEAST2 and eight calibration points under a Bayesian lognormal relaxed clock. Outgroups belonging to Tachyporinae have been removed. Green circles indicate seven out of eight fossil calibration points; all eight calibration points, including the remaining one within Tachyporinae, are shown in Figures S2A and S2B. Myrmecoid clades are highlighted in orange, with clade numbers corresponding to those in Figure 2. The position and age of the APL clade as well as the positions of the P, L, and F subclades are indicated. The O (Oxypodini) and Al (Aleocharini) clades are also highlighted, and the age of the common ancestor of all myrmecoid lineages is indicated. See also Figures S2A, S2B, and S2D.

but largely temperate tribe Oxypodini (clade O; Figure 3). Despite this lineage clustering, the APL clade is itself still comparatively ancient (84.77 mega-annum [Ma]), and three additional origins outside the APL clade (clades 1, 2, and 15) confirm that the potential for evolving myrmecoid syndrome extends broadly across the subfamily (Figure 3).

What circumstances permitted this deep-time convergent system to arise? We deduce that historical selection pressures imposed by different army ant genera on separate aleocharine lineages were likely similar; so too were the adaptive responses of the beetles as they evolved with their hosts. This inherency in the outcome of selection begs the question of why myrmecoid syndrome has evolved repeatedly in Aleocharinae in particular, as opposed to all other groups of beetles, including 31 other staphylinid subfamilies numbering some 45,000 species—most of which have generalized staphylinid morphology similar to aleocharines. We previously argued that aleocharines' predatory habits, small body size, and major defensive capacity in the form of a dorsal abdominal tergal gland constitute a groundplan unique among Coleoptera [11]. This suite of characters predisposes aleocharines to successful entry and exploitation of ant colonies, providing the basis for why myrmecophily has evolved numerous times [10, 11], including repeated associations with army ants [8]. While many army ant associates are morphologically generalized (e.g., multiple APL-clade genera such as *Tetradonia* [40]), such species tend not to be socially accepted in nests. We propose that to gain the selective advantage of unlocking colony resources via social integration, many ancestrally generalized taxa experienced intense selection to conform to the myrmecoid shape, enabling the beetles to pass tactile assessment by workers [10, 11, 21–23]. Myrmecoid aleocharines are associated only with army ants and some other group foraging hosts that may employ such tactile cues to orchestrate collective behavior. If the narrow niche of social acceptance in such colonies demands an ant-like form, then the generalized aleocharine anatomy, comprising short elytra and an exposed, flexible abdomen, is conducive to such developmental remodeling [8, 11, 41]. Consequently, aleocharines are evolutionarily poised for myrmecophily and also for becoming myrmecoid as a major socially parasitic strategy when specializing on army ants. This near-clade-wide preadaptive groundplan may underlie the repeated evolution of myrmecoid syndrome in Aleocharinae.

Documented examples of deep-time convergence are mostly limited to the evolution of single traits with few instances of repeated evolution, and where a narrow range of alternative functional solutions are available. The independent origin of wings in birds, bats, and insects is an example. Similarly, although an expanding body of work has shown parallel genetic changes occurring in widely separated taxa [19, 42], such cases are typically functionally equivalent mutations in single, broadly conserved genes governing relatively simple traits, such as pigmentation [43, 44] or toxin resistance [45]. In contrast, we

Figure 2. Bayesian Consensus Tree of Aleocharinae

Myrmecoid clades are highlighted in orange, with representative taxa shown along with their respective host army ant genera. Clade numbers indicate independent origins of myrmecoid syndrome inferred from Dollo-type parsimony optimization. Anatomically generalized species that embody the ancestral morphology in Aleocharinae are also shown for comparison. Circles on nodes signify posterior probability (PP) values (open circles: PP > 0.95; closed circles: PP > 0.9). "APL" marks the "Athetini, Pygostenini, Lomechusini" clade; "F" labels the "False Lomechusini" clade. Outgroups belonging to Tachyporinae have been removed. The full topology, with PP values and taxonomic groupings indicated is shown in Figures S2A and S2B. See also Figures S2C and S3.

have found that a complex morphological and behavioral syndrome has evolved recurrently over >100 Ma, across a clade approximately equal in species richness to mammals and birds combined. To our knowledge, convergence at this frequency, timescale, and phenotypic complexity is without close precedent. The most comparable convergent system at roughly half the age may be the Caribbean anoles [46], where different ecomorphs share an Eocene common ancestor [47].

Our discovery challenges Gould's view that if the tape of life were replayed, an entirely different assemblage of life would exist [5]. On the contrary, the tape of life appears to be highly predictable whenever aleocharines ecologically coexist with army ants. We note that despite this overarching determinism, however, there is nevertheless an element of contingency: as Seevers appreciated [8], the segmental construction of the abdominal petiole differs among myrmecoid genera; some have unique specializations, such as the gland-associated abdominal lobes of *Aenictoteras*, or the complete loss of eyes and elytra in *Pseudomimeciton*; behavioral differences in how the beetles interact with ants also likely exist [9]. While this spectrum of variation could represent a continuum of specialization, we posit that at least some apparently idiosyncratic elements in this otherwise parallel system stem from clade-specific peculiarities: genetic and phenotypic disparities between ancestors of different myrmecoid lineages, discrepancies in selection pressures imposed by different host ants, as well as mutational and environmental stochasticity. Future studies on these beetles promise to reveal much about the nature of complex phenotypic change and the genetic and evolutionary forces shaping intricate symbioses in the animal kingdom.

ACCESSION NUMBERS

See Data S1 for a full list of NCBI accession numbers used in this study.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Discussion, Supplemental Experimental Procedures, three figures, and two datasets and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2017.02.030.

AUTHOR CONTRIBUTIONS

J.P. conceived and designed the project together with M.M. M.M. collected specimens with help from J.P. M.M. and J.P. sequenced specimens. M.M. photographed specimens and produced illustrations. J.P. performed analyses, made figures, and wrote the paper with input from M.M.

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