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1 **Specialized predation drives aberrant morphological integration and diversity in**
2 **the earliest ants**

3 Phillip Barden^{a,b,*}, Vincent Perrichot^{c,*}, and Bo Wang^{d*}

4 ^aNew Jersey Institute of Technology, Department of Biological Sciences, Dr Martin Luther King Jr Blvd,
5 Newark, NJ 07102, USA.

6
7 ^bAmerican Museum of Natural History, Division of Invertebrate Zoology, Central Park West, New York,
8 NY 10024, USA.

9
10 ^cUniv Rennes, CNRS, Géosciences Rennes - UMR 6118, F-35000 Rennes, France.

11
12 ^d State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology
13 and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, 39 East Beijing
14 Road, Nanjing 210008, China.

15
16 *Correspondence to: barden@njit.edu, vincent.perrichot@univ-rennes1.fr, bowang@nigpas.ac.cn.

17 Lead contact: Phillip Barden (barden@njit.edu)
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1 **Summary**

2 Extinct haidomyrmecine ‘hell ants’ are among the earliest ants known [1, 2]. These eusocial
3 Cretaceous taxa diverged from extant lineages prior to the most recent common ancestor of all
4 living ants [3] and possessed bizarre scythe-like mouthparts along with a striking array of horn-
5 like cephalic projections [4, 5, 6]. Despite the morphological breadth of the fifteen thousand
6 known extant ant species, phenotypic syndromes found in the Cretaceous are without parallel
7 and the evolutionary drivers of extinct diversity are unknown. Here we provide a mechanistic
8 explanation for aberrant hell ant morphology through phylogenetic reconstruction and
9 comparative methods, as well as a newly reported specimen. We report a remarkable instance
10 of fossilized predation that provides direct evidence for the function of dorsoventrally-expanded
11 mandibles and elaborate horns. Our findings confirm the hypothesis that hell ants captured
12 other arthropods between mandible and horn in a manner that could only be achieved by
13 articulating their mouthparts in an axial plane perpendicular to that of modern ants. We
14 demonstrate that the head capsule and mandibles of haidomyrmecines are uniquely integrated
15 as a consequence of this predatory mode and covary across species while finding no evidence
16 of such modular integration in extant ant groups. We suggest that hell ant cephalic integration –
17 analogous to the vertebrate skull – triggered a pathway for an ancient adaptive radiation and
18 expansion into morphospace unoccupied by any living taxon.

19 **Results and Discussion**

20 Extinct diversity is a hallmark of certain lineages but conspicuous only with sufficient fossil
21 evidence. Even among the nine thousand extant species of birds, there are no hints of an
22 ancient array of predatory theropods. Comparisons of marine penguins, flightless ratites,
23 hummingbirds, and albatrosses will not yield reconstructions of ornamented spinosaurids or
24 massive tyrannosaurs. New evidence reveals the same is true for ants. With over 15,500
25 species and subspecies across all post-producer trophic levels and nearly every terrestrial
26 environment [7], modern ants are morphologically diverse [8]. Intraspecific caste specialization
27 amplifies diversity in many species as worker form matches specialized function [9, 10], from
28 foraging and food processing to defense and brood care. In effect there are tens of thousands of
29 ant morphotypes [11]. Even as extant ants represent a remarkable assemblage of adaptive
30 diversity, the boundaries of Recent morphology do not encompass the former expanses of early
31 ants.
32

33
34 The ant fossil record begins with contemporaneous Burmese and Charentese ambers from
35 France and Myanmar dated to the Albian-Cenomanian boundary (~100-99 Ma) [1, 2]. Over 50
36 ant species are known from the Cretaceous – of these, only two are definitively attributable to
37 modern lineages. Most Cretaceous ants belong to extinct stem-group lineages [3]. While the
38 first discovered Mesozoic ants were generalized anatomical composites of living ants and
39 solitary aculeate wasps [12, 13], subsequent discoveries demonstrate the diversity of extinct ant
40 lineages [1, 14, 15, 16, 17]. The most extreme examples are haidomyrmecine ‘hell ants.’
41 Defined by dorsoventrally expanded scythe-like mandibles, these taxa are present in Burmese
42 and Charentese ambers, as well as Campanian-aged (~78 Ma) Canadian amber [18], but do
43 not persist into the Cenozoic [3]. Underscoring their bizarre mouthparts are a variety of horn-like

1 cephalic appendages [4, 5, 6, 19]. The varied mandibles and horns of hell ants have no modern
2 analog.
3

4 Initial phenotypic “explorations” have long been proposed as features of lineage history [20,
5 21]. Early adaptive radiations may give rise to a multitude of morphological innovations, with
6 only a subset of phenotypes persisting into the present [22, 23, 24]. Modern ant morphology
7 operates within the confines of a core set of structural elaborations that relate to niche
8 occupation [25]: spines appear within lineages as cuticular extensions of existing modular
9 elements and relate to defense as well as muscle attachment [26]; setae, ancestrally derived
10 from marine crustaceans, are modified for sense, adhesion, and defense [27, 28]; head
11 capsules and cuticle are broadened and flattened, rendering worker ants into living doors or
12 gliders [8, 29]. Because they dictate many interactions with the environment, ant mandibles are
13 frequently modified for prey capture or task performance through modifications in teeth or
14 margins [30]. Across lineages, specialized mandibles may facilitate the shearing of vegetation
15 [8], the capture or killing of other ant hosts in social parasites [31], or the removal of defensive
16 adaptations in prey [32]. Even with these varied uses, the axis of mandibular movement within
17 modern ants is essentially fixed – extant ant mandibles open in a primarily lateral plane [33].
18 Although unconfirmed until now by direct evidence, hell ant mandibles are suspected to have
19 articulated in an axis perpendicular to that of living species, acting as a trap-jaw mechanism for
20 prey capture [34]. Indirect evidence for this movement includes the presence of hypothesized
21 sensory setae in the path of mandible closure [18, 34]; covariation between elongate mandibles
22 and clypeal projections, which have been proposed to function together [4]; and the
23 reinforcement of cuticle in the region where the mandibles would come into contact with the
24 head capsule [5]. Here, we place haidomyrmecines in an expanded phylogenetic context,
25 demonstrate their unique morphospace occupation linked to evolutionary integration, and report
26 preserved predatory behavior to explain the extinct stem diversity of ants. Our results suggest
27 that an early radiation into disparate morphospace was triggered by an innovation in mouthpart
28 movement for specialized predation. This generated a pathway for phenotypic integration
29 between mandible and head capsule, analogous to the vertebrate skull.
30

31 ***Phylogenetic analysis and comparative morphospace***

32 Our Bayesian and parsimony optimizations of 65 characters across 46 taxa confirm all
33 haidomyrmecine genera as a monophyletic stem group outside of modern ant lineages,
34 potentially sister to all other ants [3] (Haidomyrmecinae [6]). We recover two reciprocally
35 monophyletic hell ant groups, suggesting one origin of horns but two independent derivations of
36 elongate horns (Figure 1). Horns are derived from extensions of the clypeus, a segment of the
37 head capsule that is typically flattened and strictly anteriorly positioned in ants and other
38 aculeates. The clade comprising *Aquilomyrmex*, *Dhagnathos*, and *Chonidris* has a medially
39 raised anterior clypeal margin developed into a furrowed appendage that points anteriorly. The
40 remaining hell ant taxa have a posteriorly-derived clypeal projection resulting from an increase
41 in cuticular elevation and accompanied by a second projection, the frontal triangle. In
42 *Linguamyrmex* and *Ceratomyrmex*, the frontal triangle is fused to the clypeal projection. In taxa
43 where it is not fused to the clypeal projection, such as *Haidomyrmex* and *Protoceratomyrmex*,
44 the function of the frontal triangle is unknown; it may aid in muscular attachment [33]. Scythe-

1 like mandibles and clypeal modifications are synapomorphies for hell ants and represent a
2 ground-plan for the last common ancestor of the lineage. Our comparisons of extant and
3 Cretaceous morphospace consistently recover haidomyrmecines as distinct from other stem
4 and crown ants, even as cephalic morphospace overlaps among other stem ants and living taxa
5 (Figures 2A and S1B). We assessed evolutionary correlation between the clypeus and
6 mandibles in a phylogenetic framework through Bayesian MCMC estimation and regression
7 analyses of phylogenetic independent contrasts. Analyses of subsampled measurements from
8 112 extant and fossil species indicate that the variation in clypeal and mandibular size is
9 uniquely coupled in hell ants, relative to modern ant lineages (Figures 2B and 2C).

11 **Direct evidence of hell ant predation**

12 Specimen NIGP163569 (Figures 3A-D) preserves an instance of haidomyrmecine prey capture
13 in 98.79 ± 0.62 Ma Burmese amber [35]. A single worker of *Ceratomyrmex ellenbergeri* (Figure
14 1D) – a species of hell ant possessing enormous slender mandibles and horn – is restraining a
15 *Caputoraptor elegans* nymph. *Caputoraptor* is known exclusively from Cretaceous Burmese
16 amber and a member of the extinct dictyopteran order †Alienoptera (†Alienopteridae) [36, 37].
17 The mandibles and elongate horn of *C. ellenbergeri* are grasping the narrowed pronotal neck of
18 the nymphal *C. elegans*, acting as a collar, a position which is only possible through vertical
19 movement of the mandibles. *Caputoraptor* possesses an unusual cephalo-pronotal scissor-
20 device, which has been hypothesized to aid in copulation, prey capture, or defense [37, 38].
21 Given the highly specific capture mode reported here, a rapid contraction of the head capsule
22 against the serrated thorax by *Caputoraptor* may have been enough to evade predation by hell
23 ants. Ants and almost all other hexapods have dicondylic mandibles, which limit movement to
24 one axis. It is not yet known if hell ants have lost a condyle or restructured condyle placement,
25 however extant ants notably exhibit modified mandible joints – the dorsal mandibular socket is
26 widened and allows for gliding relative to the more restrictive ball-in-socket joint found in other
27 Hymenoptera [39]. This gliding likely increases range of motion and could be implicated in hell
28 ant prey capture.

30 Diversity in hell ant mandibles and horns likely reflects alternative adaptations for prey
31 capture. Prey were either pinned or pierced between sharp mandibles and head appendages,
32 which would kill on contact or allow for a subsequent immobilizing sting. Taxa with unarmed,
33 elongate horns such as *Ceratomyrmex* apparently grasped prey externally. Others such as
34 *Haidomyrmex* and *Linguamyrmex* are suspected to have impaled prey – potentially feeding on
35 internal liquid released after mandibular strikes as in some extant trap jaw ants [5, 40].

37 **A doomed Cretaceous radiation**

38 Haidomyrmecine “hell ants” were undoubtedly predators. While the postcephalic features of the
39 subfamily are consistent with other ant taxa [1, 14, 34], extreme modifications in cephalic
40 morphology define this enigmatic group. Hell ant mandibles, typified by dorsal expansions and a
41 sharp apical point, are expanded toward the vertex of the head [2, 4] while the clypeus is heavily
42 modified into a variety of nodes and horns in the context of the mandibles (Figures 1A-G and
43 S3). The apex of the mandibles and terminus of the clypeal processes are always in close
44 proximity when mandibles are closed suggesting the two are functionally integrated [4, 18, 34].

1 In at least one haidomyrmecine, *Linguamyrmex vladi*, the clypeal horn cuticle appears to be
2 medially reinforced, potentially with sequestered metals [5]. Accommodating the horn and
3 mandible, the head is dorso-ventrally elongate in most haidomyrmecines, whereby the oral
4 opening faces downward. While not hypognathous in the strict sense, this orientation is similar
5 to that of other aculeate Hymenoptera and many insects [41]. Modern ants are prognathic [42],
6 orienting their mouth forward by keeping the underside of the head parallel with the ground,
7 although the head may be pulled back to nearly flush with the propleuron. Hell ants appear to
8 have had limited head mobility and likely captured prey while keeping the oral opening
9 downward, which positioned the mandibles forward while hunting.

10
11 Extant “trap-jaw” ants provide insight into prey capture in haidomyrmecines. Trap jaw
12 syndromes – with rapidly closing mandibles that are released by a locking apparatus – have
13 evolved at least four times in extant ants [43]. Trap-jaw ants lock their mandibles into a wide-
14 open horizontal position until prey initiate power-amplified closure by stimulating specialized
15 setae, or trigger hairs [44]. Rapidly closing mandibles strike prey, initially killing in some species
16 or grasping until a venomous sting is applied [45]. These mandible strikes are among the fastest
17 animal movements recorded [46]. Most haidomyrmecines have long, fine setae within the
18 hypothesized range of mandibular movement that have been interpreted as trigger hairs
19 (Figures 1A-D) [4, 5, 18, 34]. Some trap-jaw ants feed on fast moving prey such as springtails,
20 but many are generalists, feeding on termites, orthopterans, and spiders [40, 47]. Extant trap-
21 jaw ant mandibles do not make contact with the head capsule but close against each other and
22 so mouthpart specialization reflects mandible-on-mandible contact (Figure 1J).

23
24 The Cretaceous ant fauna was rich, composed almost entirely of now extinct lineages that
25 did not persist beyond the K–Pg boundary [3]. Molecular divergence date estimates indicate that
26 crown ants extend into the Early Cretaceous [48, 49, 50, 51]. Early members of extant ant
27 lineages coexisted with stem taxa, including hell ants, for tens of millions of years. Following
28 their divergence in the Cretaceous, crown ants continued to diversify, with highest rates from
29 the late Cretaceous through the Oligocene [49, 52]. Despite consistent increases in diversity
30 over time among extant lineages [53], there has been no repeated evolution of
31 haidomyrmecine-like morphology. Early expansions in morphological variation are well known in
32 certain extinct taxa [54] but may be uncommon or difficult to measure [55, 56]. The evolutionary
33 pathway for early diversity may also be ambiguous. Hell ants reflect a series of adaptive forms
34 and a pattern of morphological diversity contingent on an innovation in mouthpart movement.
35 Without an initial switch to vertically articulating mandibles, modern ant lineages never infiltrated
36 the morphospace of their extinct counterparts.

37
38 Vertical mandible movement is present in aquatic larvae of some *Hydrophus* beetles [57,
39 58]. The larvae are predators of shelled shrimp, and use their specialized head projection in
40 conjunction with mandibles to grasp prey [59]. Despite staggering anatomical diversity of
41 insects, larval dytiscid beetles and hell ants together appear to represent the only two known
42 instances of mandible-on-head contact used in prey capture [59], both appearing with vertically-
43 articulating mouthparts. In the absence of a mandibular counterforce, mandibles interact with
44 the head capsule [59] and act as a lower jaw analogous to the dentary and cranium of

1 vertebrates. An initial innovation in mandible articulation led to functional and evolutionary
2 integration [60] and feedback between horn and mandible, which provided access to new
3 adaptive space. The modular elements implicated in this syndrome were driven to striking
4 extremes. Such a pattern is visible when comparing *Protoceratomyrmex*, with a weakly
5 developed horn and stout mandibles, with *Linguatomyrmex* and *Ceratomyrmex*, which possesses
6 increasingly co-exaggerated features (Figures 1A-G and S3). A similar, convergent pattern is
7 also present in a sister clade including *Dhagnathos* and *Ceratomyrmex* (Figures 1E-F).

8
9
10 The ecological pressures and developmental requirements that led to vertical mandible
11 articulation are not yet known. Also unclear are the conditions that drove haidomyrmecines to
12 extinction after persisting for a period of at least 20 million years across present day Asia,
13 Europe, and North America. Predatory specialization may have rendered hell ants susceptible
14 to extinction during periods of ecological change. However, generalized stem-group taxa – such
15 as *Gerontofornica* – also disappear from the fossil record toward the end of the Cretaceous,
16 suggesting other factors may have played a role including competition with burgeoning extant
17 ants. While haidomyrmecines and other stem ants were eusocial – evidenced by distinct
18 reproductive castes [2] – perhaps a distinct feature of crown ant sociality provided a bulwark
19 against extinction. Regardless of the conditions leading to their loss, our findings implicate
20 functional integration in shaping the aberrant phenotypic diversity of extinct taxa. Remarkably,
21 this example came as an antecedent to one of the most ubiquitous terrestrial lineages alive
22 today.

23 24 25 26 27 **Acknowledgements**

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36 37 **Author Contributions**

38 Conceptualization, P.B., V.P., and B.W.; Formal Analysis, P.B., and V.P.; Investigation, P.B.,
39 V.P., and B.W.; Methodology, P.B., V.P., and B.W.; Resources, P.B., V.P., and B.W.; Writing
40 P.B., V.P., and B.W.

41 42 **Declaration of Interests**

43 The authors declare no competing interests.

44

1 **Figure Legends**

2 **Fig. 1. Phylogeny and cephalic homology of hell ants and modern lineages.** (Left)
3 Relationships among ant lineages and stem ants from Bayesian optimization of 64 characters
4 with constrained extant topology and divergence dates from Borowiec et al. [51]. (Right) Digitally
5 sculpted 3D reconstructions of hell ant genera: (A) *Haidomyrmex*; (B) *Protoceratomyrmex*; (C)
6 *Linguamyrmex*; (D) *Ceratomyrmex*; (E) *Dhagnathos*; (F) *Chonidris*; (G) *Aquilomyrmex*.
7 Scanning electron microscopy micrographs of extant ants: (H) *Leptanilla*; (I) *Amblyopone*; (J)
8 *Anochetus*; (K) *Aneuretus*; (L) *Nothomyrmecia*; (M) *Tetraoponera*. H-I, K-M courtesy Roberto A.
9 Keller/AMNH; J from Alex Wild. Orange: mandibles; Blue: clypeus; Yellow: labrum; Purple:
10 frontal triangle. See also Figures S1 and S3, Table S1.

11 **Fig. 2. Morphospace and evolutionary integration of living and Cretaceous ants.** (A)
12 Principal coordinate analysis morphospace of cephalic characters (variance: PCo1 30%, PCo2
13 19%). (B) Slope (inset) and R-squared summary of linear regression analyses. Regressions
14 were performed on phylogenetic independent contrasts of scaled clypeal and mandibular area
15 (maximum length x maximum height / head area) in lateral view. Each slope represents one of
16 five subfamilial (n=8-15), three congeneric (n=9), or two Formicidae-wide (n=24, 61)
17 subsamples. Hell ants exhibit a strong positive relationship and high coefficient of determination
18 between these traits ($m=1.3$, $R^2=0.93$, $P<0.001$), a result of integration following an innovation
19 in mandibular function. (C) Posterior distribution of Bayesian estimates of evolutionary
20 correlation between clypeal and mandibular area in extant (n=24, $\bar{x}=0.18$) and hell ant (n=8, \bar{x}
21 =0.72) taxa included in Fig. 1 phylogeny. See also Figures S1 and S2, Table S2.

22 **Fig. 3. Predation preserved in amber.** (A–C), specimen NIGP163569, a worker of
23 *Ceratomyrmex ellenbergeri* grasping a nymph of *Caputoraptor elegans* (Alienoptera) preserved
24 in Burmese amber dated to ~99 Ma. (A) dorsal view; (B) reconstruction of specimen; (C) ventral
25 view of mandibles closed around the pronotal neck; (D) simplified reconstruction from oblique
26 lateral view. Abbreviations: amd, apical portion of *Ceratomyrmex* mandibles; mib, mandibular
27 medioventral blade of *Ceratomyrmex*; e, compound eye of *Caputoraptor*; pg, protruding
28 extension of *Caputoraptor*'s gena.

29 **STAR Methods**

30 **RESOURCE AVAILABILITY**

31 **Lead Contact**

32 Further information and requests for resources and reagents should be directed to and will be
33 fulfilled by the Lead Contact, Phillip Barden (barden@njit.edu).

34 **Materials Availability**

35 This study did not generate new unique reagents.

36 **Data and Code Availability**

37 The phylogenetic matrix and trees generated during this study are available at TreeBase
38 [TB2:S26540]. The published article includes all morphometric data generated and analyzed
39 during this study.

1 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

2 **Studied material for reported predation**

3 Specimen *NIGP163569*. A worker of *Ceratomyrmex ellenbergeri*, exposed in dorsal and ventral
4 views, with an insect nymph (family †Alienopteridae) caught between the mandibles and the
5 cephalic horn. The preservation is average, both syninclusions are coated in small bubbles
6 attached to their exoskeleton. In a rounded piece of clear yellow amber measuring 13×10×6
7 mm. Note: The specimen – from the Hukawng Valley, Kachin State, Myanmar – was deposited
8 in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS)
9 prior to the 2017 military control of some mine regions (work on this manuscript began in early
10 2017). The fossil acquired by NIGPAS was collected in full compliance with the laws of
11 Myanmar and China including Regulation on the Protection of Fossils of China. To avoid any
12 confusion and misunderstanding, all authors declare that the fossil reported in this study was
13 not involved in armed conflict and ethnic strife in Myanmar. The specimen is deposited in the
14 public repository NIGPAS and is available for study.

15 **Specimens for phylogenetic and morphometric data**

16 All sampled specimens were adult female ants in museum collections. Specimens analyzed for
17 phylogenetic coding and morphometric data collection are noted by specimen number in Data
18 S1. All fossil specimens were previously described and are housed in the following collections:
19 American Museum of Natural History (AMNH), Geology Department and Museum of the
20 University Rennes 1 (IGR), Nanjing Institute of Geology and Palaeontology, Chinese Academy
21 of Sciences (NIGPAS), and University of Alberta Strickland Entomology Museum (UASM).
22 Morphometric measurements of extant taxa were obtained through the image database AntWeb
23 [11] with specimen numbers noted in Data S1.

24 **METHOD DETAILS**

25 **Phylogenetic dataset**

26 A recent phylogenetic analysis of Cretaceous and modern ants indicated that hell ants are a
27 monophyletic stem-group [3, 61]. However, at the time of this analysis, only three
28 haidomyrmecine genera were known. We performed a series of expanded phylogenetic
29 analyses under alternate optimality criteria and analytical parameters to assess 1) the internal
30 relationships of the haidomyrmecines as well as 2) the position of hell ants within Formicidae.
31 We constructed a morphological matrix with 65 unordered, discrete characters: 37 were drafted
32 from the matrix of Barden and Grimaldi [3] – indicated with an asterisk* in the character list in
33 Methods S1 – which itself comprised novel characters as well as characters from Keller [62].
34 Some haidomyrmecine taxa are known only from alates or workers. To reduce the impact of
35 caste-specific morphological variation biasing the matrix construction and phylogenetic
36 inference, we did not add any additional caste-specific characters. Taxa with unknown worker
37 castes were coded as missing for worker-specific characters. Because some genera are only
38 known from alate or dealate taxa, which can exhibit significantly different thoracic sculpturing,
39 additional characters were selected primarily from the head and metasoma. Features from
40 these areas vary less significantly among reproductive castes in known congeneric stem ant
41 morphotypes. Eight of the newly added characters included inapplicable states based on
42 contingent character systems (e.g. taxa without any horns were coded as inapplicable for
43 characters representing horn-related states). Characters were coded for a total of 46 terminals:
44 four outgroup taxa, 24 crown ants, and 18 stem ants (Table S1). Nine of the stem ant terminals
45
46

1 are within the Haidomyrmecinae. One of the crown ants, *Kyromyrmex neffi*, is a fossil species
2 included to assess the impact of incomplete data. All haidomyrmecine genera are monotypic,
3 with the exception of *Haidomyrmex* and *Linguamyrmex*, which includes *H. scimitarus*, *H. zigrasi*,
4 and the type species, *H. cerberus* and *L. brevicornis*, *L. rhinocerus*, and the type species *L.*
5 *vladi*, respectively. Coding for *Haidomyrmex* and *Linguamyrmex* was based on chimeric scoring
6 for all congeners, which were not found to be distinct in the context of characters selected here.
7 The matrix included 2.8% missing states and 12.7% inapplicable states. Fossil taxa ranged
8 between 0% missing data in cases where several specimens are known such as species of
9 *Gerontoformica* to 21.5% with *Myanmyrma gracilis* known from a single fragmentary specimen.

11 **Morphometric dataset**

12 We compiled a dataset of clypeal and mandibular dimensions for 112 living and fossil ant
13 species by taking measurements of imaged specimens from AntWeb [11] and fossil specimens
14 (Data S1). Our measurements included:

15 **Head length (HL)** – length from the vertex to the anterior margin of the head capsule at
16 or above the oral opening in lateral view.

17 **Head depth (HD)** – maximum depth of the head in lateral view, comprising the frons
18 or vertex at its dorsal-most and subgenal area at its ventral-most, excluding any clypeal
19 horn in haidomyrmecines.

20 **Clypeal length (CL)** – length of the clypeus in lateral view from the anterior-most
21 expanse of the clypeus to the posterior-most expansion of the clypeus (the posterior-
22 most region may correspond to the epistomal sulcus or the subgenal sulcus, depending
23 on the taxon). In cases where the epistomal sulcus is not visible from a lateral view, the
24 posterior margin of the clypeus was approximated by noting the relative position of the
25 sulcus to the antennal sockets in a frontal view, then measuring to this position.

26 **Clypeal depth (CD)** – maximum depth of the clypeus in lateral view from just above the
27 mandibular insertion at its lowest to the maximum elevational height, taken
28 perpendicular to CL.

29 **Mandible length (ML)** – Lateral length of mandible from insertion to apex.

30 **Mandible height (MH)** – Maximal height of mandible taken in lateral view from ventral-
31 most to dorsal-most margins or teeth.

32
33 Our taxonomic sampling includes representatives of all 17 extant subfamilies (67 genera) and
34 each known extant trap-jaw genus. We also sampled multiple congeners for lineages with highly
35 specialized mandibles including *Dorylus*, *Harpegnathos*, *Mystrium*, and *Protalaridris*. Moreover,
36 we sampled congeners from three trap-jaw genera with known internal phylogenetic
37 relationships: *Anochetus*, *Odontomachus*, and *Strumigenys*. We took measurements for all taxa
38 included in our morphology-based phylogenetic reconstruction (noted with * in Data S1), except
39 for *Brownimecia*, *Haidomyrmodes*, *Myanmyrma*, and *Sphecomyrma* due to poor preservation. In
40 the event that we could not locate suitable images or specimens, we substituted species
41 included in the phylogeny for congeners for which we could collect accurate measurements
42 (noted with ** in Data S1). To evaluate the relationship between traits in haidomyrmecines and
43 extant ants, we created three size-scaled metrics of clypeus and mandible development:

44 **Area** – (Trait Length x Trait Height/Depth) / (Head Length x Head Depth)

1 **Depth/Height** – Trait Height/Depth / Head Length

2 **Length** – Trait Length / Head Length

3
4 **Three-dimensional reconstructions**

5 Models were constructed and rendered in Blender v2.79 (Blender Foundation, Amsterdam,
6 Netherlands) by Oliver Budd, Jackson Fordham, and Victor Nzegwu, led by P.B. and Martina
7 Decker at the New Jersey Institute of Technology (NIJT). To provide an initial foundation for
8 digital sculpting, photomicrographs and a CT scan of *Haidomyrmex scimitarus* specimen AMNH
9 BuFB80 were imported into Blender for side-by side comparison. The head morphology of
10 *Haidomyrmodes* [2] and *Haidotermimus* [18] are largely similar to *Haidomyrmex*; these taxa
11 were not modeled.

12
13 **QUANTIFICATION AND STATISTICAL ANALYSIS**

14
15 **Phylogenetic analyses**

16 The matrix was optimized under both parsimony and Bayesian inference (BI). Parsimony
17 optimization included equal (EW) and implied weighting (IW). We ran tree searches agnostically
18 without any topological constraints, and with the crown ant topology constrained to the results of
19 the latest large-scale molecular phylogenetic hypothesis [51]. Morphological phylogenies have
20 been in significant disagreement with molecular-based hypothesis, so this topological constraint
21 was included to assess the sensitivity of our results to changing character polarity. Our
22 phylogenetic assessment therefore included a total of six searches: EW Parsimony, IW
23 Parsimony, and Bayesian inference each with and without a topological constraint (EWC, IWC,
24 BIC, EWUC, IWUC, BIUC).

25
26 Trees were generated under a parsimony framework in TNT v1.5 (equal and implied weights)
27 [63, 64]. All parsimony optimizations utilized the ‘xmult’ command with tree-drifting, ratchetting,
28 and sectorial searches until the lowest score tree was identified one hundred times
29 independently. Tree support was assessed with 1000 bootstrap pseudoreplicates. Topological
30 constraints were employed with the “Force” command. Our unconstrained EW search returned
31 160 most parsimonious trees of 212 steps with a consistency index (CI) of 0.33 and retention
32 index (RI) of 0.66; the constrained topology EW search resulted in four most parsimonious trees
33 of 242 steps (CI: 0.32, RI: 0.65). Implied weights parsimony reconstructions were performed
34 with the ‘xpiwe’ command with a default k-value of 3 [65]. The implied weights phylogeny was
35 more resolved and supported (Fig. S1A) in both the unconstrained (CI: 0.37, RI: 0.77) and
36 constrained (CI: 0.32, RI: 0.66) searches.

37
38 Bayesian inference was performed in MrBayes v3.2.7a [66]. We excluded character 13,
39 antennal segment number, from Bayesian searches as it comprises a large number of character
40 states. We specified variable coding with a gamma rate distribution i.e. under a Mkv + gamma
41 model [67]. Searches were run for ten million generations with four chains under default
42 parameters of three heated and one cold. We removed 25% of sampled trees as burn-in.
43 Topology was fixed with the “constraint” command for the restricted topology search. We
44 assessed convergence for searches by ensuring that the average standard deviation of split

1 frequencies was less than 0.01, potential scale reduction factors were equal to ~ 1 , and
2 estimated sample size (ESS) exceeded 200. ESS was assessed in Tracer v1.7.1 [68]. Because
3 fossil branches do not terminate in the present, we performed phylogenetic estimation with tip-
4 dating to generate more accurate branch lengths used in phylogenetic comparative methods.
5 Tip dating allows for fossil terminals to calibrate divergence date estimates, which provides
6 temporally informed branch length estimates for fossils [69, 70]. Using the same morphological
7 matrix as in our BI phylogenetic analyses, we generated a phylogeny under a fossilized birth-
8 death model in MrBayes [71]. We constrained monophyly according to the results of our BIC
9 analysis and calibrated the phylogeny through Cretaceous fossil terminal dates. As in our BIC
10 reconstruction, we applied a variable Mk + gamma model for a single morphological partition.
11 We applied a clock-constrained fossilized birth-death model with the flat and fairly agnostic
12 priors of Matzke and Wright [72] for our gamma distribution, clock rate, and birth-death
13 ($\text{igrvarpr}=\text{uniform}(0.0001, 200)$; $\text{clockratepr} = \text{normal}(0.0025,0.1)$; $\text{speciationpr} = \text{uniform}(0,10)$;
14 extinctionpr , $\text{fossilizationpr} = \text{beta}(1,1)$). Our search was run for ten million generations with
15 default chain and temperature settings. We again discarded 25% of sampled trees as burn in
16 and assessed convergence as our BIC and BIUC runs. Our results (Fig. S1C) are not meant to
17 provide divergence date alternatives to those derived from molecular-based phylogenetics, but
18 rather are an attempt to generate another topological hypothesis that incorporates fossil age to
19 assess the impact on comparative methods.

20

21 **Morphospace analyses**

22 To assess the comparative morphospace of hell ants, other stem-ants, crown ants, and non-ant
23 aculeate outgroup taxa, we performed a series of principal coordinate analyses (PCo) and
24 principal component analyses (PCA). Morphospace plots were generated from phylogenetic
25 character matrices used in phylogenetic reconstruction, as in other analyses of morphospace of
26 extinct taxa [73]. However, because inapplicable states can generate artificial positions in
27 morphospace [74], morphological matrices were pruned of characters with inapplicable (-)
28 states for any terminal. In addition, to ensure that morphospaces were not primarily driven by
29 missing data for fossil taxa or anatomical partitioning, we generated three morphospaces: data
30 were subsampled into 1) cephalic-only (Fig. 2A) and 2) all-character datasets (Fig. S1B) for PCo
31 analyses and 3) a matrix with no missing data for PCA analysis (Fig. S1B). We generated
32 euclidean distance matrices in R and PCo analyses with the 'pco' command in the LabDSV
33 library [75]. The outgroup taxon *Heterogyna* possessed a great deal of inapplicable states, and
34 so was removed from PCo and PCA analyses to include more characters. The taxa
35 *Brownimecia clavata*, *Haidomyrmodes mammuthus*, and *Myanmyrma gracilis* contain the
36 greatest number of missing states. These taxa were excluded from the PCA analysis to allow for
37 greater character sampling as PCA analyses cannot incorporate missing data.

38

39 **Phylogenetic comparative methods**

40 To assess the relationship between clypeus and mandible, we performed a series of linear
41 regressions on phylogenetic independent contrast scores informed from different taxonomic
42 sampling treatments. Our taxonomic sampling reflected the match between our phenotypic
43 dataset and available phylogenetic hypotheses. Treatments are outlined in Table S2. We
44 performed two extant "formicidae-wide" analyses: one incorporating our dated morphological

1 phylogeny (pruned to 24 matching terminals) and one incorporating the Bayesian genus-tree of
2 Blanchard & Moreau [76] (pruned to 61 matching terminals). We also generated contrast scores
3 for five subfamily-specific treatments: Haidomyrmecinae (our dated morphological phylogeny
4 pruned to 8 matching terminals), Dorylinae (Blanchard & Moreau [76] pruned to 11 matching
5 terminals), Formicinae (the UCE-100 best loci phylogeny of Blaimer et al. [77] pruned to 9
6 matching terminals), Myrmicinae (Blanchard & Moreau [76] pruned to 15 matching terminals),
7 and Ponerinae (Blanchard & Moreau [76] pruned to 10 matching terminals) as well as three
8 genus-specific treatments, each pruned to nine terminals: *Anochetus* [78], *Odontomachus* [79],
9 and *Strumigenys* [80]. To account for mismatch of species between phylogenies and phenotypic
10 data, we performed analyses at the genus level and did not include multiple congeners in
11 subfamily-specific and formicidae-wide datasets. Generic representatives we included in the
12 Blaimer et al. [77] and Blanchard & Moreau [76] analyses are noted in Data S1 under the
13 column “Data Species”. Contrast scores were generated for all metrics of clypeal and
14 mandibular expansion with the “pic” command in the R package ape [81]: Area, Depth/Height,
15 and Length. We then fit linear models to contrast scores in R using the “lm” command. Resulting
16 summary statistics are presented in Table S2 as well as Figures 2 and S2. Across all metrics,
17 hell ants exhibit increased slopes and R-squared values for the linear relationship between
18 clypeus and mandibles relative to extant ant treatments. Reduced Extant-only and Ponerinae-
19 only analyses of clypeal depth and mandible height as well as our *Odontomachus*-only clypeal
20 area and mandibular area analysis recover significant linear relationships, although with
21 reduced slopes and fit than in the case of hell ants. We presented our area-metric in the main-
22 text as it includes both individual depth/height and length measurement data.

23
24 We also assessed integration between clypeal and mandibular dimensions in a Bayesian
25 framework with the R package ratematrix [82], which can be used to assess correlation between
26 traits across a phylogeny. We pruned our dated molecular phylogeny to terminals for which we
27 had phenotypic data and labeled all tips as either “hell” mandibular syndrome (dorsally
28 expanded to meet clypeal extensions as in all hell ants) for haidomyrmecines and “typ”
29 mandibular syndrome (typical mandibular development reflected in taxa with horizontal
30 mouthpart articulation, i.e. all non-hell ants) for all other ant taxa. Our tip labeling reflected two
31 reciprocally monophyletic groups of “hell” or “typ” taxa. We then generated 100 simulated trees
32 with stochastic character mapping for the two mandibular syndromes with the ‘make.simmap’
33 command in phytools [83]. This sample of trees and our phenotypic data (clypeal and
34 mandibular area, height/depth, and length) were used in two MCMC chain runs employed with
35 ‘ratematrixMCMC’, each spanning five million generations. We discarded 25% of resulting
36 samples as burn in and assessed convergence with the ‘checkConvergence’ command. We
37 then merged the two chain samples and extracted the posterior distribution and degree of
38 overlap for evolutionary correlation with the ‘extractCorrelation’ and ‘testRatematrix’ commands,
39 respectively. We also repeated this process after converting our dated tree to ultrametric with
40 the ‘extend’ method in phytools to assess any impact in differing branch lengths. Our results
41 (Fig. S2D) recover hell ants as consistently exhibiting higher degrees of evolutionary correlation
42 across clypeal and mandibular area, height/depth, and length in both ultrametric and non-
43 ultrametric treatments. We identify a lower degree of overlap in area and height dimensions for
44 non-ultrametric (area: 10.2%; height/depth: 17.1%; length: 48.1%) and ultrametric (area: 24.5%;

1 height/depth: 30.1%; length: 46.3%) treatments, mirroring the results of our PIC analyses but
2 demonstrating a less extreme difference between hell ants and crown ants with this
3 methodology.
4
5

6 **References**

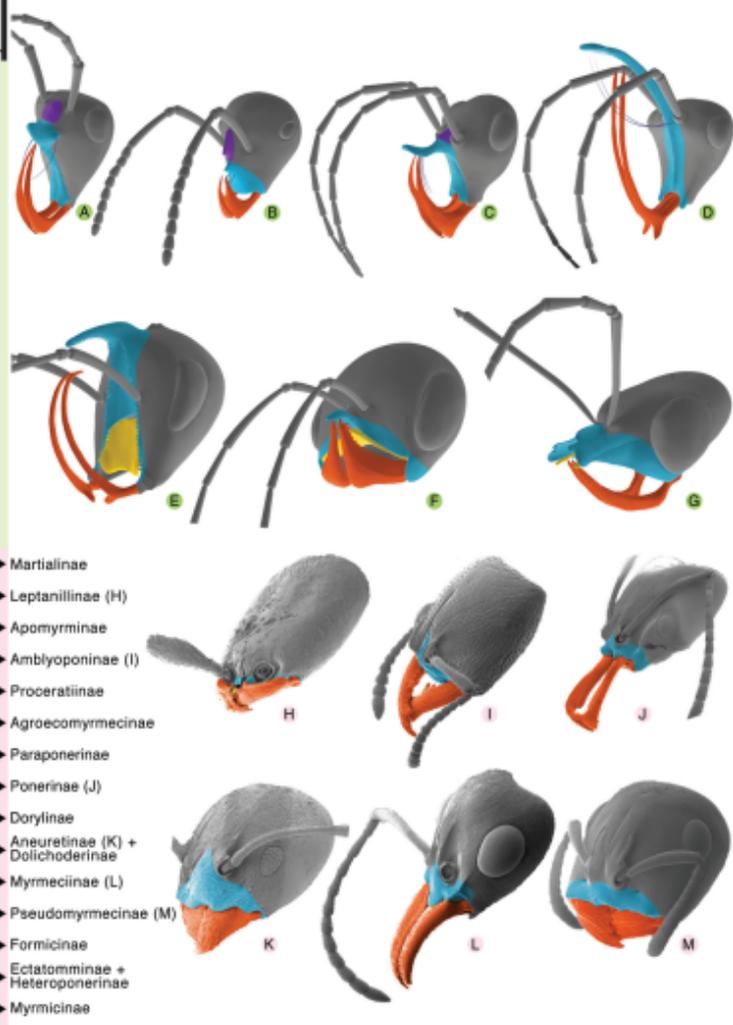
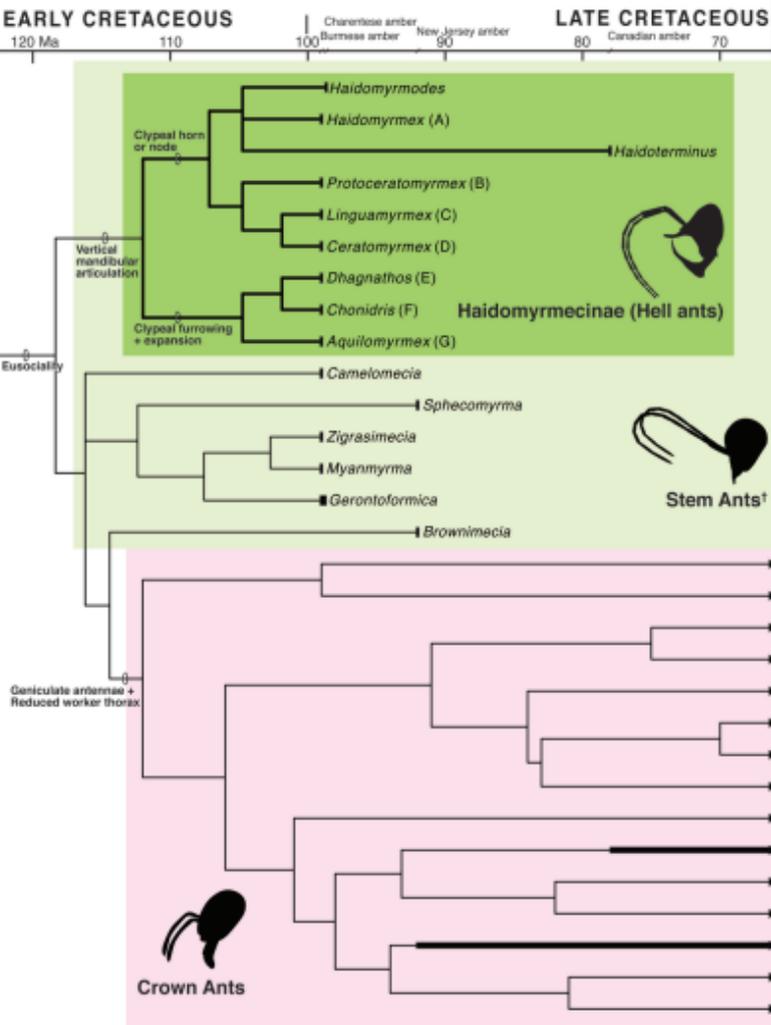
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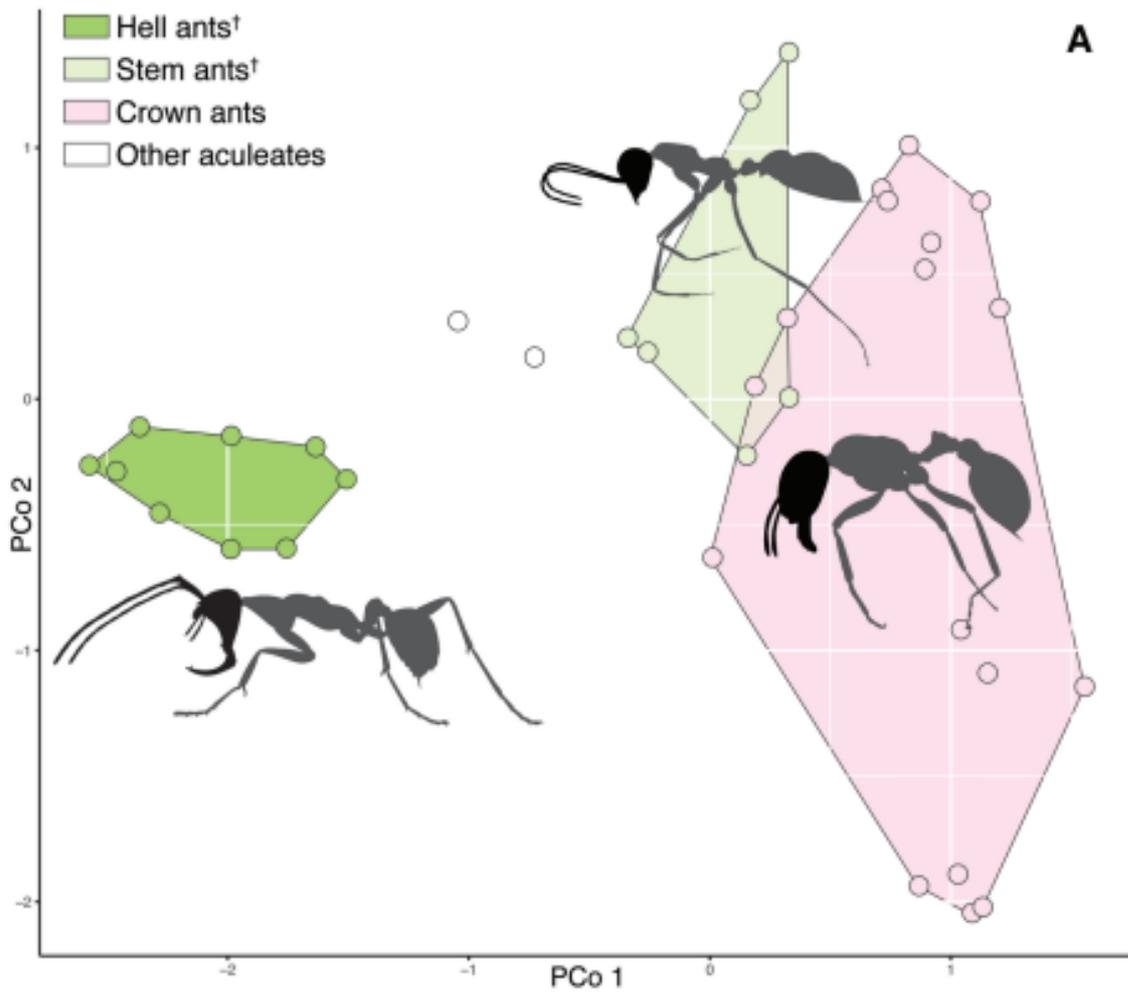
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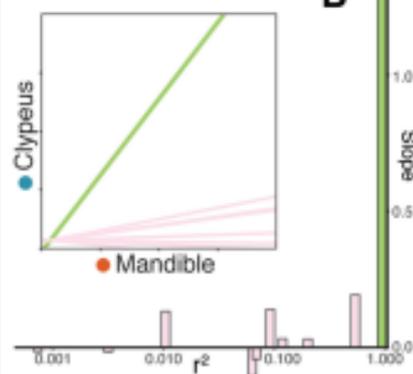
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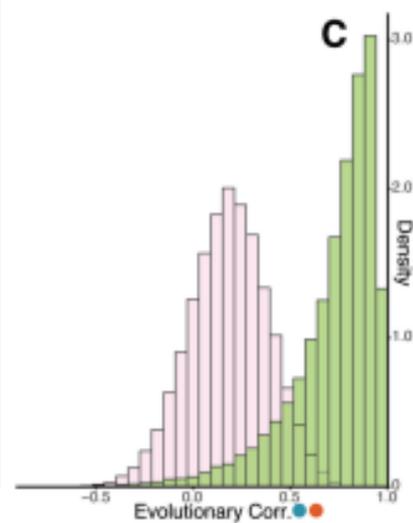




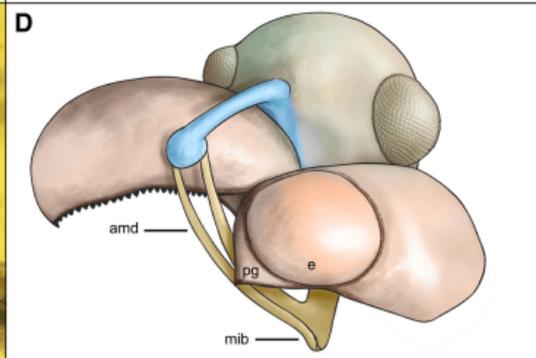
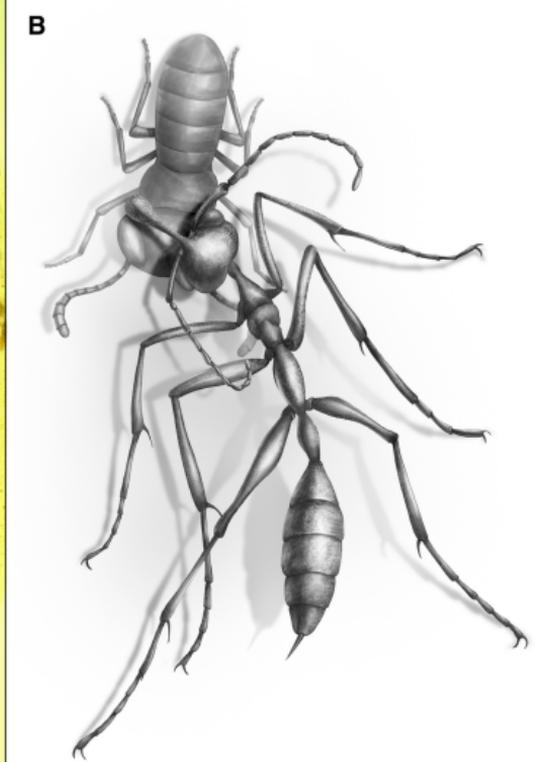
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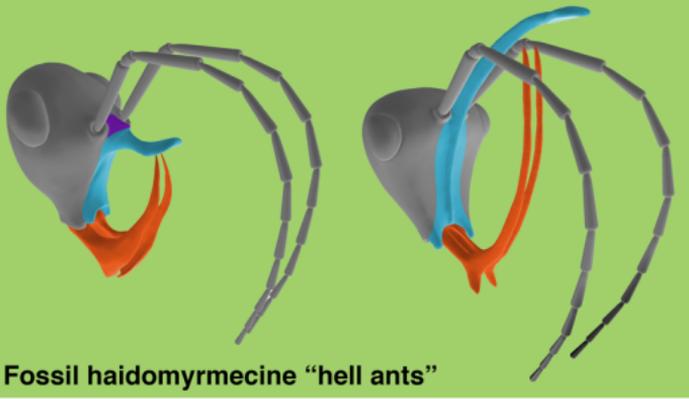


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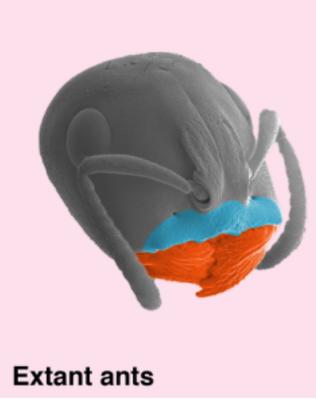


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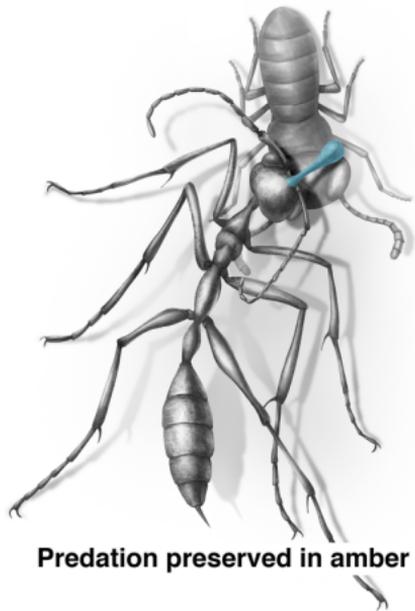




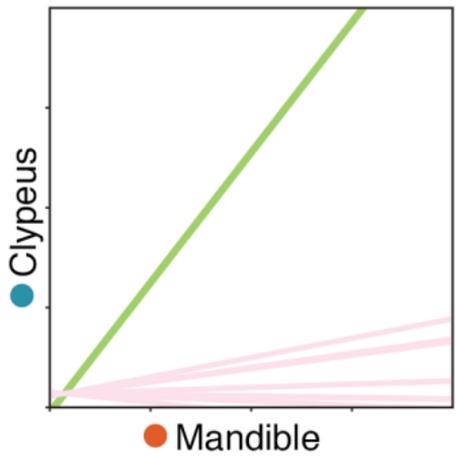
Fossil haidomyrmecine “hell ants”



Extant ants



Predation preserved in amber



The head and mandibles of hell ants are uniquely integrated as a result of specialized prey capture