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Rediscovery of the bizarre Cretaceous ant *Haidomyrmex* Dlussky (Hymenoptera: Formicidae), with two new species

PHILLIP BARDEN^{1, 2} AND DAVID GRIMALDI²

ABSTRACT

The discovery of two distinct, near-complete specimens belonging to the Cretaceous ant genus *Haidomyrmex* Dlussky prompts a detailed description and discussion of a remarkable mandibular morphology. The specimens, preserved in 98 million-year-old amber from northern Myanmar, are described here as *Haidomyrmex scimitarus*, n. sp., and *Haidomyrmex zigrasi*, n. sp., with diagnostic differences provided between them as well as with *H. cerberus* Dlussky (also in Burmese amber). Relationships and comparisons of *H. scimitarus*, *H. zigrasi*, *H. cerberus*, and the recently described *Haidomyrmodes mammothus* Perrichot from Cretaceous French amber are also discussed. *Haidomyrmex* was probably arboreal, cursorial, and a specialized trap-jaw predator, utilizing its enormous mandibles and cranial morphology in concert to capture prey. Mandibles appear to have moved in a plane oblique to the dorsoventral and horizontal axes of the body, unlike the lateral-plane movement of modern ants. The additions of these new fossils provide insight into some of the earliest yet surprisingly specialized ants that roamed the Earth.

INTRODUCTION

Amber from northern Myanmar, commonly called Burmese amber, has held mystique for millennia. Its original use was for ornamental carvings in China, beginning since at least the Zhou dynasty, ca. 600 BC (Xu, 2011). The amber became known to Western geologists at the

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end of the 19th century (Zherikhin and Ross, 2000), and soon thereafter study began of the insects fossilized within it. For 85 years the only collection of fossiliferous Burmese amber was at the Natural History Museum, London (hereafter NHM), which was studied by the prolific entomologist T.D.A. Cockerell (1866–1948). Cockerell published 13 papers on 41 new arthropod species in the NHM collection, and insightfully proposed that the amber could be Cretaceous, not Miocene or Eocene as had been commonly believed. Cockerell was very observant, and he knew Hymenoptera particularly well, but interestingly he did not report what is arguably the most intriguing fossil within the NHM collection: a large ant with bizarre, sickle-shaped mandibles. The description and significance of this ant, *Haidomyrmex*, was instead reported some 80 years later (Dlussky, 1996), based on one partial and one very fragmentary specimen in the same piece of amber in the NHM collection. If Cockerell saw the specimen, was he too perplexed by *Haidomyrmex* to interpret and describe it?

Ants are ubiquitous in nearly every terrestrial environment, exhibit the highest degree of social organization in the animal kingdom, and are keystone members of most ecosystems they inhabit (Hölldobler and Wilson, 1990; Schultz, 2000). It is difficult to picture a world devoid of ants; however, the earliest definitive physical evidence for their presence is approximately 100 million years old, in French and Burmese amber deposits (Engel and Grimaldi, 2005), despite numerous insect-yielding amber deposits of this age and older (Perrichot et al., 2008). It should be noted that the specimens described here, along with the previously discovered *Haidomyrmex cerberus* Dlussky and *Haidomyrmodes mammothus* Perrichot, were recovered from these two deposits, and so are the oldest representatives of the Formicidae. Ants are scarce in Cretaceous amber deposits. Their abundance, measured as a proportion of ants among all individual inclusions, increases from less than 1% during the Cretaceous, to up to 20%–40% of all insects in deposits dating to the Oligocene and younger (Grimaldi and Agosti, 2000), making all Cretaceous discoveries of particular interest.

To elucidate questions regarding the early history of ants, many have turned to molecular phylogenetics. Two large-scale molecular efforts by Brady et al. (2006) and Moreau et al. (2006) suggest that crown-group ants diverged sometime between 115–135 and 140–168 million years ago, respectively. These ranges are incongruent with fossil evidence, the latter predating the oldest aculeate fossils dated at 146 Ma (Rasnitsyn and Quicke, 2002), and, while the discrepancy may be due to incomplete fossil preservation, there is also potential for error in the estimates themselves. These molecular estimates used fossils as calibration points; however, the exact phylogenetic position of the fossils within the Formicidae was not cladistically analyzed. This calibration scheme lends to a possibility imprecise phylogenetic placement, which may adversely affect estimated dates (Brady, 2011). No member of the extinct, purportedly stem-group subfamily Sphecomyrminae—to which each ant discussed here belongs—has been a part of the current molecular-based narrative of ant history. If we are to understand the early history of the ants, it is essential that critical fossils be described and contextualized.

The specimen that Cockerell mysteriously left undescribed was the first in what would be a series of illuminating and unusual amber fossil ants. Dlussky (1996) described *H. cerberus* from the original specimen now known to be approximately 100 million years old, placing it

in the extinct subfamily Sphecomyrminae, along with subsequent authors (Engel and Grimaldi, 2005). A decade after *H. cerberus* was described, similar scythe-mandibled ants were discovered in ~100 myo French amber. These three partially preserved individuals, a gyne and two workers, were determined to be conspecific and described as the aforementioned *Haidomyrmodes mammathus*, demonstrating that this unusual scythiform morphology was not entirely uncommon (Perrichot et al., 2007). The morphological similarities between *Haidomyrmodes* and *Haidomyrmex* led to the placement *H. mammathus* in the tribe Haidomyrmecini, which Bolton (2003) first erected for *Haidomyrmex*. In these new descriptions, this tribe assignment, as well as classification of *Haidomyrmex* within the Sphecomyrminae, is followed as in previous descriptions, based largely on antennal scape length and mandibular morphology. Here, we describe two new species of the genus *Haidomyrmex* from a putative worker and a dealate female, with hopes of offering additional evidence for understanding these unusual animals.

MATERIALS AND METHODS

One specimen is part of a collection of Burmese amber purchased from Federico Berlöcher by the American Museum of Natural History (AMNH); the other is on loan from the personal collection of James Zigras. Both specimens originated in Kachin State, the region of historical and currently active burmite mines (Grimaldi et al., 2002; Cruikshank and Ko, 2003). Modern information on the age of the strata bearing this amber indicated an age of Late Albian to Cenomanian, ca. 105–95 mya, based on palynology, an ammonite, and the insect taxa within Burmese amber (Cruikshank and Ko, 2003; Grimaldi et al., 2002). Most recently, the amber has been dated radiometrically to a maximum of 98.8 ± 0.62 mya (Albian–Cenomanian boundary), based on $^{206}\text{Pb}/^{238}\text{U}$ isotopes in magmatically derived zircon crystals taken from the sedimentary matrix surrounding the amber (Shi et al., in press).

The new specimen of *Haidomyrmex scimitarus*, n. sp., is preserved within a small, prism-shaped piece of dark amber $23 \times 7 \times 7$ mm in size, which had been partially flattened and polished on all sides prior to acquisition. The amber piece is dark orange and contains a suspension of fine bubbles and organic particles, as well as an alate aphid (Aphidoidea). The specimen of *Haidomyrmex zigrasi*, n. sp., is contained within a polished, circular $25 \times 28 \times 17$ mm fragment of amber along with a beetle and a suspension of fragmentary insects, plant trichomes, and pollen. Ant inclusions were studied using conventional light stereomicroscopy (20–200 \times) with fiber optic illumination. However, slight turbidity of the amber obscures some crucial, microscopic details of the external cuticle, so the *H. scimitarus* specimen was also scanned using high-resolution X-ray computer microtomography (CT). In order to scan the amber piece, it was mounted on a steel rod, vertically and in line with the rod, by applying several layers of double-stick carbon SEM tape to the narrow, barren end of the piece distant from the ant, then applying a drop of superglue to the tape surface and the tip of the rod. The other end of the rod was inserted into a customized chuck to allow for a consistent center of rotation in fine increments during X-ray exposure. Scanning was performed on a GE Phoenix vtomex s 240 at 60kV and 180 μA for 5 sec exposures. Resulting images were

4² μm per pixel in resolution, stitched together in Image J, v1.45, and rendered in Volume Graphics Studio Max, v2.2.

After scanning, the amber piece was embedded in a very clear epoxide resin (EpoTek 301-2) using the protocols described by Nascimbene and Silverstein (2000), and then trimmed and polished slightly closer to the ant in order to visualize minute surface structures. Epoxy embedding also stabilizes the amber piece by sealing it against oxidative deterioration and accidental damage.

Measurements were made using two methods: an ocular reticule in a Leitz Wetzlar stereomicroscope, and the calibrated scale on the CT scan images. The amber pieces were repositioned multiple times when measuring with the ocular reticule, by gently pressing the piece into a small piece of dental wax applied to a microscope slide. The advantage of measurements using the CT scale is that the ant image can be rotated for optimal viewing (e.g., longest linear distances); the disadvantage is that thin cuticle and fine structures are not resolved in the CT image.

SYSTEMATICS

Order Hymenoptera Linnaeus, 1758

Family Formicidae Latreille, 1802

Genus *Haidomyrmex* Dlussky, 1996

Haidomyrmex Dlussky, 1996: 449. Type species: *H. cerberus* Dlussky, 1996, by original designation.

DIAGNOSIS: Gracile ants of varied body length (3.5 – 8.0 mm), lacking extensive cuticular microsculpture; ocelli lacking; eyes bulging; antennae long, pedicel very short, ca. 0.20 – 0.12× length of scape; clypeus developed into a setose pad just below antennal insertions, bearing pairs of fine, long trigger hairs laterally; face and gena distended; mandible scythe or L-shaped, with very long apical tooth; mandibles oblique at base and parallel along tips and apparently moved obliquely, with tips of apical teeth meeting clypeus; pronotum with narrow neck; thoracic sutures oblique; legs very long; pretarsal claw with single subapical tooth; propleuron very well developed; articulations between thoracic segments very well developed; propodeum with shallow or steep declivity; pedicel dome shaped, peduncle slender; metasoma with telescoping segments; sting large and entirely retractable.

Haidomyrmex scimitarus, new species

Figures 1–4

DIAGNOSIS: Most similar to *H. cerberus* but distinguished by *H. scimitarus* having slightly larger eyes; mandibles are more curved and scythe shaped (instead of L-shaped), held partially parallel (vs. oblique) to each other, with bases close (vs. bases well separated); vertex of head glabrous (vs. with numerous erect setae); a longer and more slender face and gena; frontal lobe bearing stiff setulae; ventral margin of face above labrum with four upcurved setae; funicular article 2 is twice the length of article 1 (pedicel), article 3 is 4× the length of pedicel (vs. funicular article 2 only slightly longer than pedicel, article 3 twice the length of pedicel); mesonotum longer and more slender, with well-developed propleuron that is dorsally exposed; propodeal

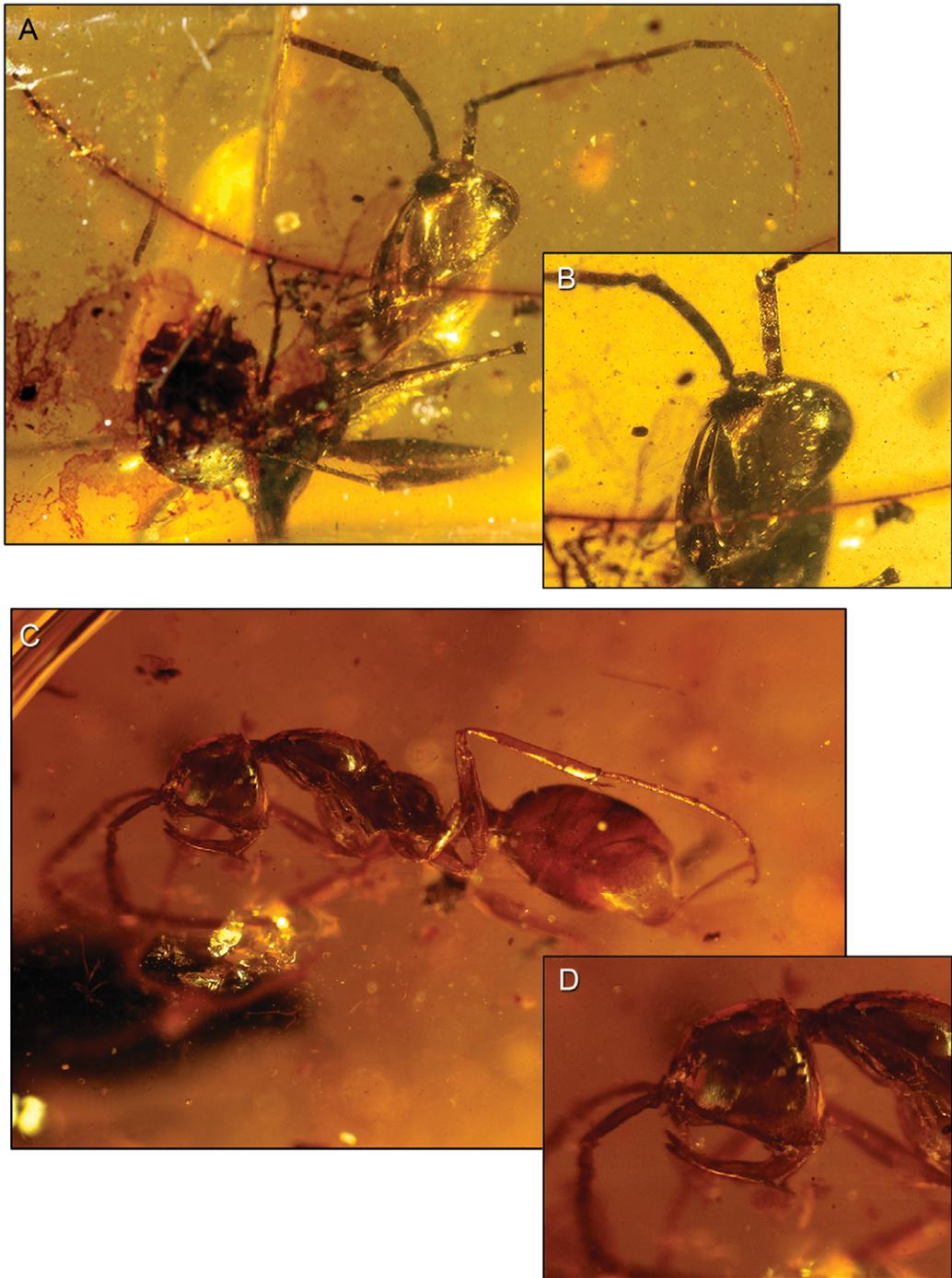


FIGURE 1. Photomicrographs of described specimens. (A) Full view of *Haidomyrmex scimitarus*, n. sp., in Burmese amber holotype AMNH Bu-FB80. (B) Close view of cranial features of *H. scimitarus*. (C) Full view of entire *H. zigrasi*, n. sp., specimen in Burmese amber holotype JZC-BuXX D). Close view of cranial features of *H. zigrasi*.

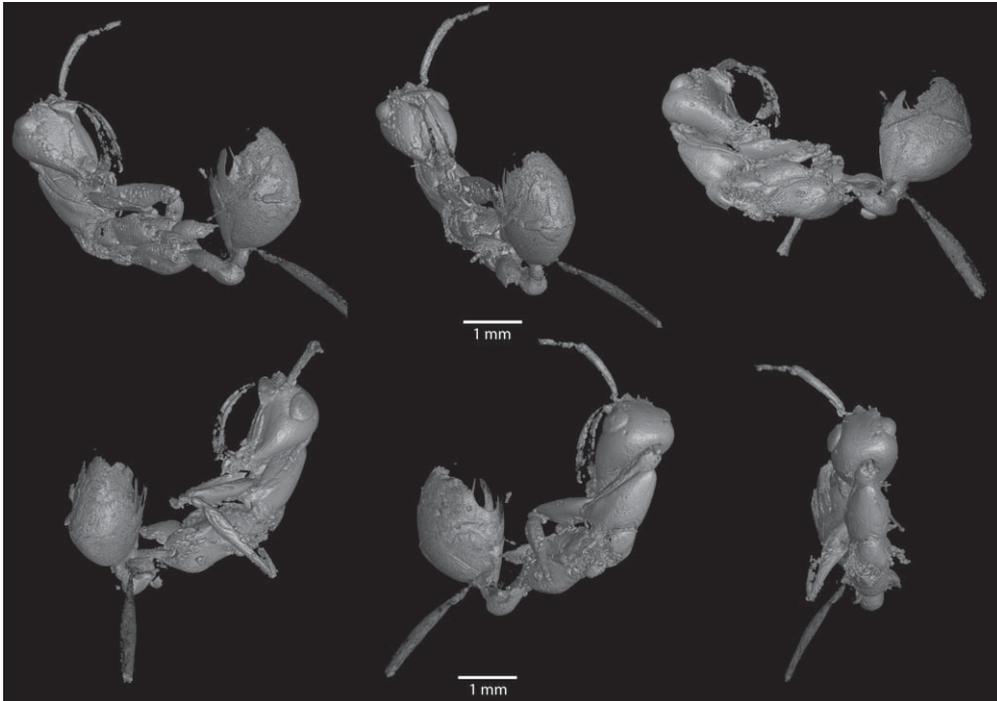


FIGURE 2. Computed tomographic scan renderings of *H. scimitarus*, n. sp., holotype. Multiple views of entire body in various rotations.

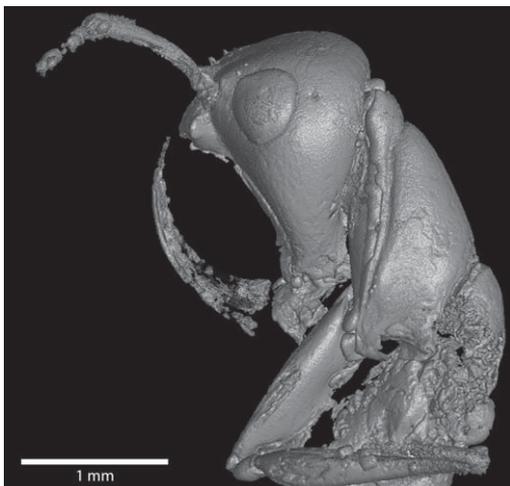


FIGURE 3. CT-Scan rendering of *H. scimitarus* depicting a lateral view of cranial features and propleuron/pronotum.

declivity shallow (vs. steep); procoxae very long, nearly twice the length of metacoxae; metacoxa with very sparse (vs. dense) setae ventrally. Differs from gyne of *H. mammathus* by being more than double total length (8.0 vs. 3.7 mm); lacking ocelli; possession of frontal lobe with stiff setulae; antenna over twice as long (5.66 vs. 2.37 mm); funicular segments are not all homogeneous in length and are relatively longer. Characteristics of *H. scimitarus*, *H. zigrasi*, *H. cerberus*, and *H. mammathus* are summarized in table 1 (see also diagnosis of *H. zigrasi*, n. sp.).

DESCRIPTION: Head: Vertex broad, evenly rounded, glabrous, no ocelli apparent nor traces thereof. Length/depth of head capsule

TABLE 1. Comparison of *Haidomyrmex scimitarus*, n. sp., *H. zigrasi*, n. sp., *H. cerberus* Dlussky, and *Haidomyrmodes mammathus* Perrichot. Preservation details in gray, morphological details in white.

AMNH Bu-FB80 <i>Haidomyrmex</i> <i>scimitarus</i> , n. sp.	JZC-BuXX <i>Haidomyrmex</i> <i>zigrasi</i> , n. sp.	NHM IN. 20182 <i>Haidomyrmex</i> <i>cerberus</i> Dlussky	MNHN ARC 50.2 <i>Haidomyrmodes</i> <i>mammathus</i> Perrichot
Dealate female	Wingless female	Wingless female	Winged female
Antennae complete	Antennae complete	Right antenna with basal 7 segments	Antennae complete
Entire metasoma present	Entire metasoma present	Metasoma with only basal segment	Entire metasoma present
Legs articulated to metasoma	All but one leg articulated to metasoma	Legs detached from specimen	Legs articulated to metasoma
Entire head visible	Entire head visible	Entire head visible	Aspects of head not visible
Total length: 8.0 mm	Total length: 3.5 mm	Total length unknown	Total length 3.7 mm
Clypeal process covered in setae	Clypeal process covered in setae	Clypeal process covered in setae	Clypeal process not present
No ocelli	No ocelli	No ocelli	Two ocelli present
Scythelike L-shaped mandibles, parallel at tips	Mandibles somewhat straight, although gradually curved ventrally, parallel at tips	Mandibles oblique and curved, not parallel	Scythelike L-shaped mandibles, parallel at tips
Flagellomeres variable in length	Flagellomeres variable in length	Flagellomeres variable in length	Flagellomeres all same length, short and broad
Two pairs of trigger hairs visible on clypeus	Two pairs of trigger hairs visible on clypeus	Two pairs of trigger hairs visible on clypeus	No trigger hairs visible
Metapleural gland present	Metapleural gland present	Metapleural gland present	Metapleural gland not seen

1.35 mm. Head-thoracic articulation (occipital foramen) situated very dorsad, near dorsal margin of postocciput. Compound eyes situated high on head capsule, distance between dorsal margins of compound eye and head capsule $0.28\times$ depth of compound eye; compound eye bulging, nearly hemispherical in lateral view, length $0.90\times$ depth; compound eye depth 0.30 mm with longest axis in line with vertical axis of head. Antennal bases exposed, frontal lobes absent; slight, short frontal carinae present just lateral to antennal articulation. Antenna very long, total length 5.66 mm, 10 funicular segments; antennomere lengths (in mm): scape 0.90, pedicel 0.17; flagellomeres, FI 0.35, FII 0.75, FIII 0.57, FIV 0.50, FV 0.47, FVI 0.47, FVII 0.50, FVIII 0.55, FIX 0.52, FX 0.45. Apex of scape slightly broadened, margin ventrally bearing strong, recurved seta; dorsally with pair of stiff setae that point forward; FI with stiff, erect seta on ventral surface near proximal end. Small lobe protruding between bases of antennae, antero-ventral margin with row of six minute, stiff setulae. Clypeus large, protruding, approximately pentagonal in shape in full dorsal view; bearing dense, brushlike vestiture of stiff, black setae arranged in rows, longer setae on ventral margin. Ventral surface of clypeus with two pairs of

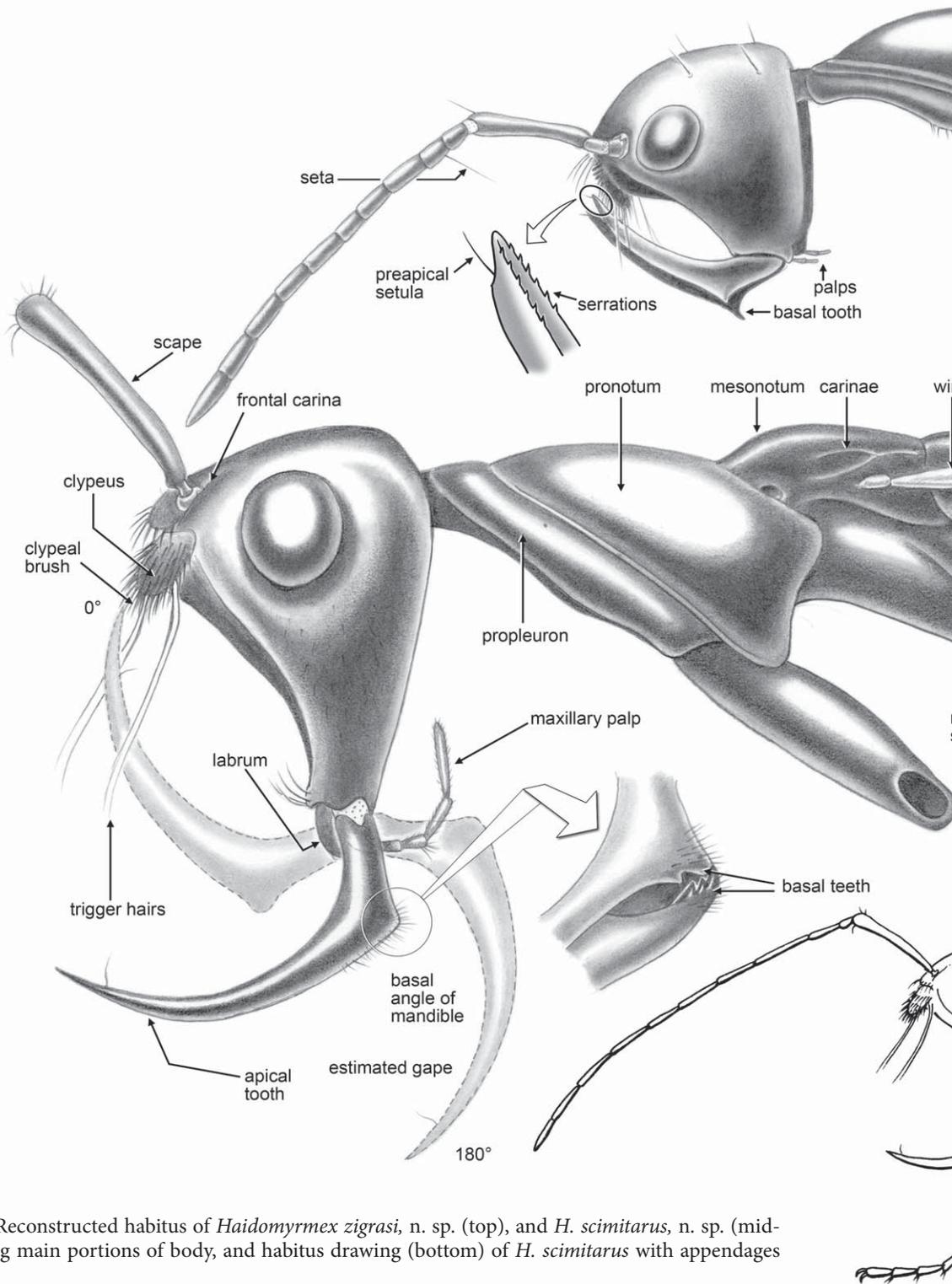
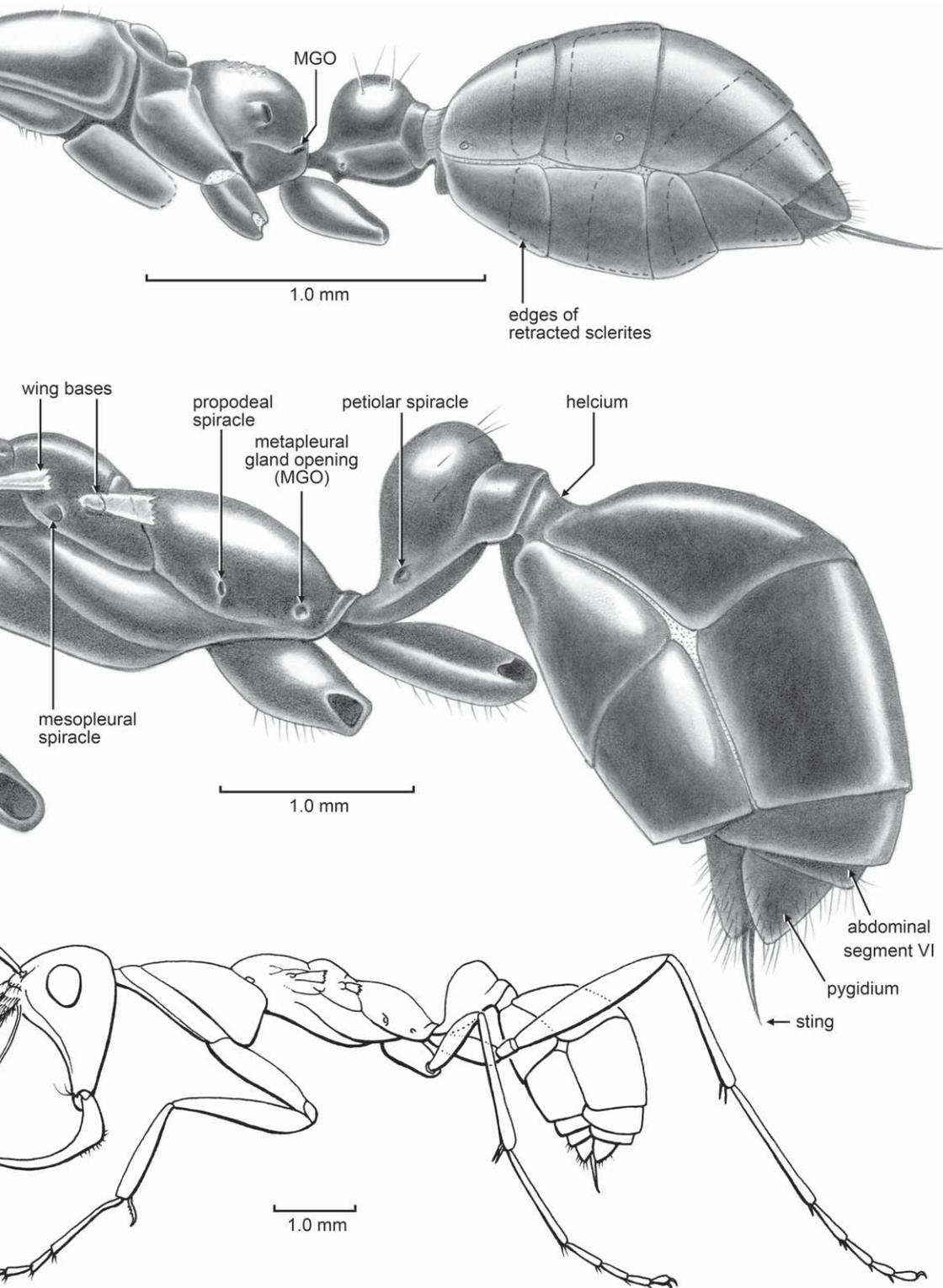


FIGURE 4. Reconstructed habitus of *Haidomyrmex zigrasi*, n. sp. (top), and *H. scimitarus*, n. sp. (middle), showing main portions of body, and habitus drawing (bottom) of *H. scimitarus* with appendages included.



long, fine setae (trigger hairs); each seta slightly bent at basal quarter; each pair of setae flanking tips of mandibles; trigger seta length 0.67 mm. Ventral surface of clypeus attached to pyramidal lobe, with ventral point of pyramid distended into a shallow, median facial carina. Face and gena greatly distended, to twice or more depth of compound eye. Labrum a small lobe dorsal to and between bases of mandibles. Oral margin just above labrum with four fine, upcurved setae. Mandibles long, scythe or sickle shaped, curved upward; bases short, posteroventral corner projecting backward, and main portion of mandible curved and tapered to sharp point. Length of curved portion of mandibles (apical tooth) 1.35 mm. Mandibles very close together, parallel to each other; inner surfaces flat, with shallow concavity along basal half of curved, main portion; deep, mesal concavity at base of main portion of mandible, concavity bearing group of small, stiff setae. Posteroventral portion of mandible, where corner is projected posteriad, heavily sclerotized and bearing 3–4 fine mesal teeth on left mandible, 2–3 slightly larger teeth on right mandible. Base of mandible short, perpendicular to curved portion, not parallel, with V-shaped dicondylic articulation. Tips of mandibles reach (as preserved) to clypeus; near apex of each mandible with very fine, slightly bent seta on dorsal surface. Maxillary palps with at least four palpomeres; most basal visible palpomere shortest, apical one longest (3× length of basal palpomere), second palpomere thickest, with small group of stiff setulae on distoventral margin. **Mesosoma:** Long, slender, length of pronotum through metanotum 2.024 mm (dorsally), propodeal length 1.05 mm, petiole length (from anterior portion of stem to posterior margin, plus helcium) 0.90 mm. Propleuron well developed, with dorsal portions exposed and visible dorsally. Sulci between propleuron and pronotum, pronotum and mesonotum, and the meso- and metanotum/propodeum very well developed (presumably articulated freely), sulci parallel and oblique (lying at an angle of ca. 40° from longitudinal axis of mesosoma). Pronotum with posterior margin having lobe, mesothoracic spiracle lying just above lobe. Meso- and metanota with wing bases intact, distal ends of wings torn/shredded. Two slight carinae lying just above mesothoracic wing base. Metanotum 0.65× length of mesonotum, with short, faint posterior lobe demarcating metascutellum. Metapleuron shallow, no deeper than metanotum. Dorsal level of propleuron, pronotum, mesonotum, and metanotum nearly at same level; dorsal surface of propodeum (declivity) gradually sloped. Propodeal spiracle raised, prominent; metapleural gland opening circular, slightly depressed, without anterodorsal ledge. Legs very long. Procoxa long, length equal to that of propleuron; mesocoxa short, stout, length 0.6× that of procoxa; metacoxa slightly longer than mesocoxa, with dorsal surface flattened, ventral surface with very sparse, fine setulae. Distal (coxal-trochanteral) articulations of meso- and metacoxae on dorsal surface. Trochantellus of pro- and mesothoracic legs barely distinguishable; that of metathoracic leg well defined. Prothoracic leg with well-developed calcar. Meso- and metathoracic tibiae with ventral pair of long apical spurs (lengths 1.3× thickness of tibia), short pair of spurs flanking these (0.5× the length), pair or two of short, stiff dorsal setae on apex. Tibial lengths: prothoracic 1.45 mm, meso- 1.77 mm, meta- 1.80 mm. Femoral lengths (excluding trochantellus): pro- 1.80 mm, meso- 1.85 mm, meta- 1.95 mm. Ventral surfaces of tarsomeres with fine setulae and two longitudinal rows thick, short setae. Pretarsus with claw having single preapical tooth; arolium well developed.

Metasoma: Petiole 0.90 mm, just slightly shorter than propodeum, with dome-shaped dorsal surface, peduncle very narrow (0.25× depth of deepest portion of petiole); petiole with posterior shelf over anterior margin of helcium. Petiolar spiracle between peduncle and expanded part of petiole. Helcium exposed, well developed. Gaster (metasoma minus petiole) short, length 2.4 mm (as preserved), with gastral segments I and II (abdominal segments III and IV) comprising ca. 0.75 length of gaster (as preserved). Gastral tergite II slightly longer than tergite I. Gaster segments III, IV, V (pygidium and hypopygium) telescoping; pygidium and hypopygium setulose. Sting very well developed, fully retractable, length 0.75 mm (base, including venom bulb, not visible in CT scan).

TYPE SPECIMEN: Holotype, dealate female: Amber: Myanmar, Kachin State (nr. Myitkyina) AMNH #Bu-FB80 purchased 2009 ex Federico Berlöcher.

ETYMOLOGY: The species name *scimitarus* derives from the Middle Eastern sword known in English as *scimitar* and whose overall shape is similar to the mandibular morphology observed.

COMMENTS: It is extremely unlikely that all the differences between this new specimen and the holotype of *H. cerberus* are simply due to caste (both specimens are from the same deposit while the dealate *H. scimitarus* is probably a reproductive and the holotype of *cerberus* is a worker). Caste differentiation may account for the larger eye in *H. scimitarus*, since queens of modern species usually have larger eyes relative to head size compared to workers (varying from only slightly to dramatically so). Like males, queens also have the mesosoma dorsally flattened, but typically deeper than in workers (the opposite of the situation in these two *Haidomyrmex* specimens). Also, the size of the queen metasoma is relatively large in proportion to overall body size compared with that of workers due to flight muscles, but the metasoma in *H. scimitarus* is quite small. Lastly, it is highly unlikely that the differences in pilosity as well as the proportions of the coxae, basal funicular articles, head capsule, and mandibles that are observed here are due to caste differentiation, since both workers and a gyne of *H. mammathus* are known and the castes differed only in size and in minor aspects of mandibular morphology (Perrichot et al., 2007).

Haidomyrmex zigrasi, new species

Figures 1, 4

DIAGNOSIS: *H. zigrasi* is distinct from *H. cerberus* and *H. scimitarus* by the following: total size less than one half that of *H. cerberus* and *H. scimitarus*; mandibles not in an L-shape with an initial horizontal protrusion; each mandible with single basal tooth at 0.25× mandible length projecting ventrally; teeth asymmetrical with right tooth 2–3× longer than that of left; trigger hairs shorter; small hairs present on tip of apical tooth, with minute serrations; maxillary palps very short; eyes closer to anterior margin of head not near middle; 10 funicular segments, shorter and stouter than in other *Haidomyrmex* specimens; meso- and metanotum much shorter than in *H. scimitarus*; pro- and mesocoxae not distant; small subpetiole process projecting ventrally near mesosoma; dorsal region of propodeum rugose. Differs from *Haidomyrmodes mammathus* by lack of ocelli, mandibular shape, setose pad projecting between eyes, and funicles of varied lengths.

DESCRIPTION: Head: Vertex broad, gradually but shallowly rounded, four evenly spaced setae dorsally, with no ocelli. Length/depth of head capsule 0.62 mm. Occipital foramen very dorsal, near dorsal margin of postocciput. Compound eye lies in anterior half of head capsule, distance between dorsal margins of compound eye and head capsule approximately same as depth of compound eye. Compound eye length 2.4 mm, depth 2.0 with longest axis oblique to dorsal/horizontal axes of head. Antennal bases exposed, frontal lobes absent. Total antenna length 1.93 mm, funiculus composed of 10 flagellomeres; lengths (in mm): scape 0.40, pedicel 0.08; flagellomeres, FI 0.07, FII 0.08, FIII 0.12, FIV 0.10, FV 0.07, FVI 0.12, FVII 0.12, FVIII 0.13, FIX 0.13, FX 0.19. Dorsally, apex of scape with pair of setae pointed forward; funiculus 2 with stiff, erect seta on ventral surface near proximal end. Small lobe protruding below bases of antennae, anteroventral margin with row of four minute, stiff setulae. Clypeus large, protruding with flattened face, approximately pentagonal in shape from dorsal angle; coated with longer setae on ventral margin and short peglike setae above. Ventral surface of clypeus with two pairs of fine setae (trigger hairs) 0.12 mm in length; trigger hairs flanking tips of mandibles. Ventral surface of clypeus attached to pyramidal lobe, with ventral point of pyramid distended into shallow, median facial carina. Face and gena distended to depth of 1.5× length of compound eye. Mandibles curved upward immediately from base, terminating at a point nearly reaching clypeus. Length of mandibles approximately 0.51 mm. Mandibles close together, parallel to each other; inner surfaces flat. Posteroventral portion of mandible, where corner is projected posteriad, sclerotized and possessing single, ventrally protruding tooth on each mandible. These teeth asymmetrical, with right one 3–4× length of left one. Maxillary palps very small, last two segments visible and approximately equal in length. **Mesosoma:** Slender, length of pronotum through metanotum 0.73 mm dorsally, propodeal length 0.30 mm, petiole length (from anterior portion of peduncle to posterior margin, including helcium) 0.51 mm. Propleuron long, does not extend dorsally, possesses four small, erect setae ventrally. Prothoracic and mesothoracic culcus very well developed. Pronotum extended in the anterior-posterior plane, gradually rounded posteriorly, forming drop shape. Mesonotum possesses two dorsal humps of different sizes, anterior mesoscutum one nearly 3× larger than mesoscutellum. Pronotum, mesonotum, and propodeum gradually descend in height to petiole. Dorsal surface of propodeum with slight rugosity; propodeal declivity steep and abrupt. Propodeal spiracle large and raised I center of propodeum; metapleural gland opening oval shaped, facing slightly ventrally, with faint anterodorsal groove. Legs long. Procoxa length 0.24 mm; mesocoxa 0.15 mm; metacoxa 0.11 mm. Meso- and metathoracic tibiae with ventral pair of long apical spurs (lengths 1.9× thickness of tibia), short pair of spurs flanking these (0.3× the length), several short, stiff dorsal setae on apex. Tibial lengths: prothoracic (slightly obscured) 0.53–0.65 mm, mesothoracic 0.33 mm, metathoracic 0.43 mm. Femoral lengths (excluding trochanter): profemoral (slightly obscured) 0.65–0.75 mm, mesofemoral 0.36 mm, metafemoral 0.40 mm. Ventral surfaces of tarsomeres with fine setulae and two longitudinal rows of thick, longer setae. Pretarsus claw with single preapical tooth; arolium well developed. **Metasoma:** Petiole 0.38 mm, approximately equivalent in size to propodeum, dorsal surface dome shaped, with four stiff, fine setae; small subpetiolar process projecting ventrally as a minute tooth; petiolar spiracle just above

this process, near propodeum. Gaster 1.18 mm in length with gastral segments I and II comprising ~0.50 total gaster length; spiracles present on these segments near median sulci. Gaster segment V setulose. Sting well developed, although disarticulated in specimen.

TYPE SPECIMEN: Holotype, wingless female; amber: Myanmar, Kachin State (nr. Myitkyina) In private collection of James Zigras, specimen available for study through AMNH.

ETYMOLOGY: The species name *zigrasi* derives from James Zigras for his generosity in loaning this and other Burmese amber specimens for study.

COMMENTS: There are strong lines of evidence indicating that *H. zigrasi* is not merely another caste of *H. scimitarus* or *H. cerberus* but in fact a distinct species. First, while there is precious little data in the way of caste differentiation in Cretaceous ants, the one definitive conspecific description from Perrichot et al. (2007) demonstrates that reproductives and workers are only slightly distinct morphologically in *Haidomyrmodes mammathus*—with only major differences in body size and measurements. In the case of *H. zigrasi*, mandibular morphology, propleuron shape, body size, petiole shape, and cuticular sculpturing are all distinctly different from *H. scimitarus* and *H. cerberus*. Perhaps the most curious aspect of this new specimen is the asymmetrical basal teeth located on the mandibles. How did these function with regard to a trap jaw lifestyle? We speculate that the asymmetry allowed to mandibles to lock together as in *H. scimitarus* or aided in mastication after prey were subdued. Still another possibility is that the small teeth enabled these ants to finely manipulate brood and nest substrate, which would otherwise seem very challenging.

DISCUSSION

FEEDING MECHANICS AND BEHAVIOR: In all ants (living and fossil) except *Haidomyrmex* and potentially *Haidomyrmodes*, the mandibles move laterally, with the toothed, masticating surfaces meeting medially. Several lines of morphological evidence indicate that the mandibles of current members of the Haidomyrmecini, particularly those of *H. scimitarus* and *H. zigrasi*, uniquely moved in a vertical plane:

(1) To grasp prey, the mandibles would need to open laterally, vertically, or obliquely. If the mandibles moved only laterally, the mesal surface would have no sharp edges for grasping prey. The sharp tips of the mandibles would seem optimal structures for grasping or impaling prey, in which case they would have needed to move up and down or obliquely. The holotypes of *H. scimitarus* and *H. zigrasi*, as preserved, demonstrate that the tips of the mandibles are capable of nearly touching the brushlike clypeal pad.

(2) The brushlike structure of the clypeus opposes the sharp tips of the mandibles, and so probably functioned as a cushion to absorb the impact of or prevent puncture by the tips. The brush of stiff, sharp setae on the clypeus could also have served to secure prey between the clypeus and mandible tips, pinning them in place for a well-placed sting.

(3) The mandibles in *H. scimitarus* and *H. zigrasi* are very close to each other, and lie parallel along their tips and angled at their base. Moreover, the mesal surfaces of the mandibles are mostly flat, which suggests that the mandibles could be held against each other, with at least some vertical movement, perhaps in unison.

(4) The long, concave face would allow large prey items to be secured for stinging without damaging delicate structures of the ant such as compound eyes or antennae.

(5) If the pairs of long, very fine, stiff setae that flank the mandibles functioned as trigger hairs, the mandibles would need to be either very widely separated laterally (as in modern trap-jaw ants), or cocked backward together. If separated laterally, the trigger setae would be forcefully deflected outward and inward each time the mandibles were snapped open and shut, which could damage the setae over time. The setae were probably triggered by being touched at their tips (as in modern species), but given that they so closely flank the lateral surfaces of the mandibles, they may also have functioned in detecting slight lateral displacement of the tips of the mandibles.

It seems most likely that the mandibles of *H. scimitarus* and *H. zigrasi* were snapped shut in a plane that was oblique to the dorsoventral and horizontal axes of the ant body, and it is even possible that the mandibles were cocked very far back. The occipital foramen is located on the posteroventral portion of the head capsule, indicating that the head could not be held in a prognathous position like modern trap-jaw ants (e.g., *Odontomachus*, *Harpagnathos* [Ponerinae], *Myrmoteras* [Formicinae], Dacetoniini [Myrmicinae]). In these ants, the occipital foramen is located on or near what is actually the vertex of the head, which allows the mouthparts to be held out in front. *Haidomyrmex* was probably hypognathous, supported by the fact that the postmortem head position of *H. scimitarus* is actually under the prothorax. In addition, assuming the trigger hairs are in a fixed position, for the trigger hairs to project forward rather than downward the mandibles would have to be cocked back 140°–180° (with 0° being with the tips of mandibles touching the clypeus). Because of the long legs, there is more than enough clearance for this mandibular positioning. In this position, the mandibles would have an enormous gape of nearly twice the diameter of the head. If the large sting delivered venom of sufficient potency, such a gape would have allowed individual *Haidomyrmex* to subdue rather large prey. A major question remains regarding the processing of food items. How were food sources masticated? Perhaps these ants fed on insects by first impaling them and then funneling hemolymph down their curved mandibles. Indeed there are extant members of amblyoponine ant queens that feed on the hemolymph of their own larvae (Saux et al., 2004). It is difficult to speculate beyond the first moments of trap-jaw hunting as it is unclear whether the basal teeth of *Haidomyrmex* functioned with respect to their proposed feeding lifestyle or as fine-scale manipulators of eggs, larvae, and particulate nest material.

The long, slender mesosoma with oblique sutures, short metasoma, and the very long legs and antennae suggest that *Haidomyrmex* was arboreal. This extreme body structure is found

in unrelated extant ants that are arboreal, specifically *Oecophylla* (Formicinae) and *Leptomyr-mex* (Dolichoderinae). As Dlussky (1996) discussed, it is possible that *Haidomyrmex* nested in natural, preformed cavities, since antennae and mandible structure makes it unlikely that this ant could have manipulated nesting material. In addition, the presence of Haidomyrmecini ants in amber deposits (these being the third and fourth) may be a result of a lifestyle that included foraging along the trunks and limbs of trees.

It is difficult to comment on the sociality of *Haidomyrmex* in the absence of direct evidence; however, the main criticism against social behavior in sphecomyrmine ants has been that individuals would have been unable to perform brood care due to their characteristically short antennal scape (Dlussky, 1996). Perrichot et al. (2007) reported the earliest fossil evidence for ant sociality (i.e., castes) in *H. mammathus*, after discovering both a gyne and two workers in the same deposit. As with all sphecomyrmines, both *Haidomyrmex* and *Haidomyrmodes* possess this shortened scape, and so while, again, there is no direct evidence for sociality in *Haidomyrmex*, there would appear to be none against it at this time. It is also important to note that there are, in fact, modern social ants with relatively short antennal scapes, e.g., army ants (Ecitoninae).

The addition of these two Burmese specimens, which share such unusual cranial features with both *H. cerberus* and *H. mammathus* from French amber, continues to challenge the idea that stem-group ants are morphologically generalized (Hölldobler and Wilson, 1990). This scimitar mandibular morphology and the trap jaw behavior that likely occurred with it must have been at least moderately successful. Not only were some Cretaceous ants very specialized, it appears that their unusual forms were widely distributed across western Laurasia, known thus far from nearly contemporaneous French and Burmese deposits. These early, specialized ants underscore a need for a comprehensive fossil-inclusive phylogenetic analysis so that we may better understand how the extraordinary ants of the past relate to those of today.

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