Extreme Morphogenesis and Ecological Specialization among Cretaceous Basal Ants

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SUMMARY

Ants comprise one lineage of the triumvirate of eusocial insects and experienced their early diversification within the Cretaceous [1–9]. Their ecological success is generally attributed to their remarkable social behavior. Not all ants cooperate in social hunting, however, and some of the most effective predatory ants are solitary hunters with powerful trap jaws [10]. Recent evolutionary studies predict that the early branching lineages of extant ants formed small colonies of ground-dwelling, solitary specialist predators [2, 5, 7, 11, 12], while some Cretaceous fossils suggest group recruitment and socially advanced behavior among stem-group ants [9]. We describe a trap-jaw ant from 99 million-year-old Burmese amber with head structures that presumably functioned as a highly specialized trap for large-bodied prey. These are a cephalic horn resulting from an extreme modification of the clypeus hitherto unseen among living and extinct ants and scythe-like mandibles that extend high above the head, both demonstrating the presence of exaggerated morphogenesis early among stem-group ants. The new ant belongs to the Haidomyrmecini, possibly the earliest ant lineage [9], and together these trap-jaw ants suggest that at least some of the earliest Formicidae were solitary specialist predators. With their peculiar adaptations, haidomyrmecines had a refined ecology shortly following the advent of ants.

RESULTS

The vast majority of Cretaceous ants belong to stem-group Formicidae and comprise workers and reproductives of largely generalized morphologies [8, 13], and it is difficult to draw clear conclusions about their ecology, although recent discoveries from Cretaceous Burmese amber suggest relatively advanced social levels [9]. Remarkable exceptions to this pattern of generalized morphologies are ants with bizarre mouthparts such as Zigrasimecia, Camelomecia, and five species composing the Haidomyrmecini in which both female castes (workers and reproductives; males are unknown) have modified heads and blade-like mandibles that uniquely move in a vertical rather than horizontal plane [9, 14–19]. Haidomyrmecines have puzzled evolutionary biologists as to their specific ecology, the mandibles apparently acting as traps triggered by sensory hairs in a way distinct from that of modern trap-jaw ants [13, 16–19]. Nonetheless, even within haidomyrmecines, there has been relatively little morphological disparity, and their ecology as solitary or social hunters, and as dietary specialists or generalists, remains obscure. Here, we report four individual fossils of a new haidomyrmecine ant species with extraordinary head structures that presumably function as a highly specialized trap for large-bodied prey. The specimens were found in four different pieces of amber from the Hukawng Valley in northern Myanmar, dated radiometrically at 99 mega-annum [20].

Systematic Paleontology

Ceratomyrmex New Genus, Figures 1, S1, S2, and S3C

Diagnosis. Differs from all other extinct and living ants by the presence, in workers, of a long cephalic horn arising from between the antennal insertions and curved forward and by very long, scythe-like mandibles, their tips reaching above head near to the horn’s apex. The horn is spatulate apically, and its undersurface is densely setose, with a semi-circular brush of peg-like spicules along edges. Two pairs of long trigger hairs are each flanking the apical portion of mandibles. The combination of distinct ocelli and subpetiolar process also serves to distinguish the genus from other haidomyrmecines.

Type Species. C. ellenbergeri, new species. See Supplemental Information for description of type and additional material.

Etymology. Derived from Greek “keratos,” meaning “horned,” and “myrmex,” meaning “ant.”

DISCUSSION

Ceratomyrmex has distinctive features of the haidomyrmecines such as the concave face and the scythe-like mandibles moving in a vertical plane, their apical portion flanked by two pairs of long trigger hairs inserted on the clypeus. The most striking feature of Ceratomyrmex is its unique cranio-mandibular system—the horn and trigger hairs evidently operate as a sensory complex to judge the distance of a target before eliciting closure of the oversized...
mandibles, presumably to subdue, puncture, and crush prey or opponents, and alternatively for contact with nestmates without eliciting a strike. Although differently constructed and in no way representing a common evolutionary origin, such trap jaws and their associated trigger hairs are known elsewhere among foragers of three extant ant subfamilies [10] (Figure 2), and such mandibular specializations across those lineages are known in the Cenozoic [21–23]. It is not surprising that predatory behavior should be present among stem-group ants, particularly as related aculeate families are virtually all predatory to some degree or other [24]. The other non-haidomyrmecine stem-group ants are likely to have been mostly generalist predators, except maybe Zigrasimecia and Camelomecia [9, 14, 15]. It is remarkable that among the haidomyrmecines there was an early origin of specialized, trap jaws and that this should be taken to such an exaggerated extreme in Ceratomyrmex. The previously dubbed “clypeal setose lobe” presumably functioned as a stabilizing structure when pressure was applied by the mandibles that braced the prey against the face, offering friction to minimize movement that might cause the victim to be dropped.

Spine-like cuticular expansions are frequent in ants, present in genera of various subfamilies, but are not linked to hunting strategies. These expansions can form short paired spines on the head (e.g., Acromyrmex), paired lateral spines on the pronotum or propodeum (e.g., Polyrhachis), or more rarely a single median spine on the propodeum or petiole (e.g., Acanthoponera). A mediocephalic horn acting as a sensory appendage is a novel organ hitherto never seen among living and fossil ants. This projection is longer than the head and projects high above and forward, with dense long setae on its undersurface and facing the...
Trap jaws have evolved independently at least four times in ants, occurring in 11 genera from four subfamilies (indicated in gray on topology; circled numbers refer to earliest trap-jaw fossils known: 1, *Haidomyrmodes mammuthus*; 2, various *Odontomachus* and *Anochetus* species; 3, *Acanthognathus poinian*). Thick lines denote the temporal range known for each subfamily. Relationships and divergence times among lineages are based on previous molecular and morphological hypotheses [5, 9].

The clypeus appears as a pair of lateral sclerites on each side of an elevated median portion extending longitudinally from above the oral cavity to the ventral base of the prominent, pyramidal frontal triangle (a structure immediately posterior to the clypeus, inserted between antennal sockets, but generally not prominent nor obvious [26]). The elevated median portion of the clypeus consists, in *Haidomyrmex*, of a mushroom-shaped shelf anteriorly with a narrow triangular stem and posteriorly with a hemispheric brushy lobe, while in *Ceratomyrmex*, it consists of a single longitudinal carina posteriorly projecting into the horn, with the brushy lobe moved apically on the horn (Figures 3C and 3D). It is unclear whether the frontal lobe is fused with the dorsal base of the horn or is just not as prominent as in other haidomyrmecines. The trigger hairs are present in a place homologous to that of other haidomyrmecines, slightly below the antennal sockets on the elevated median clypeal portion, and thereby supporting the homology of the entire horn of *Ceratomyrmex* with the setose pad of other Haidomyrmecini. While the trigger hairs are assuredly sensory structures that would make contact with a prey prior to closure of the mandibles, or with a nestmate (without a strike), the clypeal pad likely served a stabilizing function, although it certainly also had a sensory purpose. Its shorter form in other haidomyrmecines would have excluded its ability to receive any tactile information from prey prior to ensnarement. It could have provided information on pressure when prey was appressed against the head. In *Ceratomyrmex*, the typical function of the clypeal pad must have been further elaborated, as the setae are more elongate and the structure itself extends well in front of the ant, suggesting specialization on some large-bodied prey for which a greater grasp was required.

Trap-jaw ants are typically highly predatory and dietary generalists, although some species specialize on particular arthropods, and a few even harvest seeds [10]. The extreme morphogenesis observed in *Ceratomyrmex* implies a unique specialization for predation among this early ant lineage, prior to anything similar among the Formicidae. Indeed, the arrangement of the mouthparts and clypeal structures would have made it challenging for *Ceratomyrmex* to effectively capture small arthropod prey as they would have had a greater chance of escape before the mandibles closed against the face (and thereby presumably with the horn not being capable of playing a role in such entrapment) or would have had an easier time slipping laterally within the large space created by the horn, face, and mandibles. By contrast, the ant could approach larger prey with the mandibles opened, positioned to project beneath the setae are more elongate and the structure itself extends further laterally within the large space created by the horn, face, and mandibles. By contrast, the ant could approach larger prey with the mandibles opened, positioned to project beneath the setose pad of other Haidomyrmecini. While the trigger hairs are assuredly sensory structures that would make contact with a prey prior to closure of the mandibles, or with a nestmate (without a strike), the clypeal pad likely served a stabilizing function, although it certainly also had a sensory purpose. Its shorter form in other haidomyrmecines would have excluded its ability to receive any tactile information from prey prior to ensnarement. It could have provided information on pressure when prey was appressed against the head. In *Ceratomyrmex*, the typical function of the clypeal pad must have been further elaborated, as the setae are more elongate and the structure itself extends well in front of the ant, suggesting specialization on some large-bodied prey for which a greater grasp was required.

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**Figure 2. The Ant Tree of Life and Parallelism among Trap-Jaw Ants**

Trap jaws have evolved independently at least four times in ants, occurring in 11 genera from four subfamilies (indicated in gray on topology; circled numbers refer to earliest trap-jaw fossils known: 1, *Haidomyrmodes mammuthus*; 2, various *Odontomachus* and *Anochetus* species; 3, *Acanthognathus poinian*). Thick lines denote the temporal range known for each subfamily. Relationships and divergence times among lineages are based on previous molecular and morphological hypotheses [5, 9].
defense function is excluded, however, because the horn and setose lobe would then be useless.

Whether Ceratomyrmex cooperated in social hunting or were solitary hunters remains obscure. However, modern trap-jaw ants forage mostly solitarily, and fossils of Ceratomyrmex are exceedingly rare in Burmese amber compared to those of the clearly social genus Gerontoformica [9], which suggests that Ceratomyrmex were likely solitary predators. The new fossil strongly suggests that early following the advent of ant societies in the Early Cretaceous, at least one lineage, the Haidomyrmecini, became adept at prey capture, independently achieving morphological specializations that would be lost for millions of years after the disappearance of this lineage near the end of the Mesozoic. The exaggerated condition in Ceratomyrmex reveals a proficiency for large-bodied carriage, and to the exclusion of smaller, presumably easier-to-subdue prey, and highlights a more complex and diversified suite of ecological traits for the earliest ants.

**EXPERIMENTAL PROCEDURES**

A full systematic description is available in Supplemental Information. Type specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences and the Geological Department of the Université Rennes 1. The study comprised four specimens each preserved in a piece of clear yellow amber from the Cretaceous of northern Myanmar in the State of Kachin. All amber pieces were originally polished in the form of flattened ellipsoid cabochons and, when possible, were further polished into at least two flat surfaces near to the specimens for optimal dorsal, profile, or full face views. The fossils were examined under both incident and transmitted light using a Leica MZ APO stereomicroscope and imaged with the aid of a Canon 5D Mark II camera attached to it. Stacks of photographs taken at different depths of field were merged using HeliconFocus software (Helicon-Soft). Line drawings were made with a camera lucida and digitally processed using Illustrator CS5 software. Measurements were made using the ocular micrometer of the microscope.

**ACCESSION NUMBERS**

Described taxa are registered in ZooBank under LSID: urn:lsid:zoobank.org:pub:748A5E0C-E8F2-4E62-9112-BE4A6E39123C.

**SUPPLEMENTAL INFORMATION**

Supplemental Information includes Supplemental Experimental Procedures, three figures, and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.03.075.

**AUTHOR CONTRIBUTIONS**

Conceptualization, Visualization, and Methodology, V.P.; Investigation, V.P., B.W., and M.S.E.; Writing – Original Draft, V.P. and M.S.E.; Writing – Review & Editing, V.P., B.W., and M.S.E.; Funding Acquisition, V.P. and B.W.

**ACKNOWLEDGMENTS**

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REFERENCES


Supplemental Information

Extreme Morphogenesis and Ecological Specialization among Cretaceous Basal Ants

Vincent Perrichot, Bo Wang, and Michael S. Engel
Figure S1.
Figure S2.
Figure S3.
Supplemental Figure Legends

**Figure S1. New worker ant Ceratomyrmex ellenbergeri, paratype IGR.BU-002.** Related to Figure 1. Top. General profile view. Bottom. Drawing with exoskeletal element identification (left legs omitted for a better clarity).

**Figure S2. Representative workers and head structures of the new ant Ceratomyrmex ellenbergeri.** Related to Figures 1 and 3. A. Specimen SEC-BU39-003, general dorsal view, with gaster masked by sediment-filled cavity at amber surface (white arrow). B. Head of same specimen in semi-ventral view. C. Specimen SEC-BU39-004, general profile view. D. Head in dorsal view, holotype NIGP164022. E. Detailed ventral view of horn and apex of mandibles, with indication of clypeal setation on horn's ventral surface, holotype NIGP164022. Abbreviations: short peglike spicules (pg); long fine hairs (fh); trigger hairs (th).

**Figure S3. Cranio-mandibular structures of Haidomyrmecini.** Related to Figure 3. A-B. Haidomyrmex sp., worker specimen NIGP164023, from Burmese amber. Detail of head in semi-profile view, with indication of the lateral clypeal bands (in blue), the median clypeal elevation and brush (in yellow), and the prominent frontal triangle (in red). C. Ceratomyrmex ellenbergeri, specimen SEC-BU39-004, head in full face view (the apical portions of the horn and mandibles are cut). D. Haidomyrmex cerberus, holotype NHM.In20182, head in full face view. E. Haidomyrnodes mammuthus, holotype MNHN.F.A30162, detail of head in full face view. Abbreviations: amd, apical portion of mandible; clb, clypeal brush; es, epistomal sulcus; ft, frontal triangle; ho, clypeal horn; mce, median clypeal carina; mce, median clypeal elevation; sc, scape; th, trigger hair.
Table S1. Measurements of holotype and paratype (in mm). Related to Figure 1.

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<td>0.50</td>
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* as preserved, with apical segments of gaster missing.

Abbreviations used:
- **BL**: Body length: measured in profile or dorsal view, from anteriormost point of head capsule excluding mandibles and horn to posteriormost point of abdomen excluding sting.
- **HL**: Head length: measured in profile view, from anteriormost point of anterior clypeal margin to highest point of vertex (dorsal surface of head capsule excluding horn).
- **HW**: Head width: the maximum width of the head immediately behind the eyes, measured in dorsal view.
- **HoL**: Horn length: the length of horn from its basal insertion between antennae to apex of blade (or setose pad).
- **HoD**: Horn's blade diameter: the maximum width of blade in dorsal view.
- **EL**: Eye length: in profile, the maximum measurable diameter of the compound eye.
- **Mb**: Mandible, length of basal portion (basally of elbow).
- **Md**: Mandible, length of distal portion (distally of elbow).
- **AL**: Length of antennal segments: scape/pedicel/antennomeres III-XII (= flagellomeres I-X), respectively.
- **WL**: Weber’s length: diagonal length of mesosoma (or alitrunk) in profile, from anteriormost point of pronotum to posteriormost point of propodeum.
- **PrL**: Pronotum length: the length of longitudinal median part of pronotum.
- **PtL**: Petiole length: the maximum length of petiole measured in profile view.
- **PtH**: Petiole height: the maximum height of petiole excluding process, measured in profile view.
- **GL**: Gaster length: the maximum length of gaster (abdominal segments III-VII), measured in dorsal or profile view.
Expanded Systematic Paleontology

Formicidae Latreille, 1809
Haidomyrmecini Bolton, 2003

*Ceratomyrmex ellenbergeri* Perrichot, Wang et Engel, New Species, Figs. 1A-C; S1A,B; S2A-E; S3C

**Diagnosis:** As for the genus.

**Type material:** Holotype NIGP164022, housed at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. A worker missing only the apical portion of left hind leg, and with slight dorsoventral and lateral distortion (Figs. 1A,B; S2D,E). Exposed mostly in ventral and dorsal views. Preserved in a piece of clear yellow amber with a moth fly (Diptera: Psychodidae) and a mite (Acari).

Paratype IGR.BU-002, housed at Geological Department of the University of Rennes 1, France. A worker missing the apical portions of left antenna, left mid and hind legs and the three apicalmost gastral segments, without apparent distortion (Figs. 1C; S1). Specimen exposed mostly in right and left profile views. A large organic debris and another worker ant assignable to *Gerontoformica* sp., the most common genus of ants in Burmite, are located in front of the specimen, which prevent polishing for a full face view.

**Additional material:** Two specimens, both from the Siegardh Ellenberger Collection, Kassel, Germany.
Specimen SEC-BU39.003, a worker missing right antennomeres 7-12, femoro-tibial articulations of mid and hind legs, and with most of gaster truncated by contact with amber surface, resulting in a cavity filled with minerals elements from within the amber bed (Figs.S2A,B). Cuticle darkened and somewhat distorted by local flattening (e.g., compound eyes, apex). Specimen exposed in ventral and dorsal views.

Specimen SEC-BU39.004, a remarkably preserved worker, without distortion, but missing apicalmost portions of the horn and mandibles, and with apex of gaster (abdominal segment 7 with sting) detached, 'floating' at a distance in amber (Figs. S2C; S3C). Specimen exposed in right and left profile views and full face view.

**Deposit and age:** Amber from a mine near Noije Bum Village, Hukawng Valley, Myitkina District of Kachin State, northern Myanmar; Cretaceous, Early Cenomanian (ca. 99 Ma) [S1].

**Etymology:** The specific epithet is a patronym for Sieghard Ellenberger who provided some of the fossils.

**ZooBank LSID:** urn:lsid:zoobank.org:act:CFAA344D-244B-4DFF-AF28-E7134BA1BAE4

**Description (worker):** Body length varying between 4.5 and 5.9 mm. Cuticle with very shallow, tiny punctures widely spaced over head capsule, mesosoma, and coxae; remaining parts of cuticle smooth. Dorsal portion of body with sparse, erect setulae. Head capsule roughly triangular in profile, with vertex rounded, and anterior face (comprising the clypeal surface and genae) elongate, concave. Ocelli small (Figs. 1; S1A,B). Compound eyes situated high on head capsule, ovoid in profile, strongly convex, with longest diameter oblique to longest axis of head, 0.35× head length. Antennae inserted between compound eyes and flanking cephalic horn; with apex of gaster (abdominal segment 7 with sting) detached, 'floating' at a distance in amber (Figs. S2C; S3C). Specimen exposed in right and left profile views and full face view.

**Mandibles:** Very long trigger hairs originating medially on clypeal carina basal to horn, and forming two pairs each flanking curved apical portion of mandibles. Mandibles (Figs. 1B,C; S1; S2B,D,E) a long cuticular expansion gently curved forward, apically with a discoidal blade (diameter 0.2× horn length); setation of horn, on anterior (or ventral) surface, consisting of fine, long, erect setae arranged in a single longitudinal row basally and becoming progressively denser towards blade; ventral surface of blade coated by dense brush of fine, long, erect setae medially and short, peglike spicules disposed in five semi-circular rows along lateral and apical edges of blade (Fig. S2E); dorsal margin of blade rimmed by fine, long setae curved downward. Four very long trigger hairs originating medially on clypeal carina basal to horn, and forming two pairs each flanking curved apical portion of mandibles. Mandibles (Figs. 1B,C; S1; S2B,E) very long, scythe-shaped, parallel and close to each other along basal half, then diverging along apical half; mandibles with inner surface flat or slightly concave, with tips nearly reaching to base of horn's blade; basal portion straight; apical portion 6× as long as basal portion, curved upward and backward, with minute serrations apically; ventral corner (elbow) between basal and apical portions
projected ventrally in a triangular blade bearing one large, basal tooth and one small, distal tooth, these blades symmetrical on each mandible and with the teeth overlapping. Maxillary palps long, with six palpomeres (entirely visible on SEC-BU39.003); palpomeres I-III thickest, III-IV longest. Labial palps with four visible palpomeres, slightly surpassing second maxillary palpomere, with second and third palpomeres the shortest. Maxillo-labial apparatus partly exposed, occupying most of space between basal portion of mandibles, with glossa approximately of same length as galea; outer surface of galea distinctly convex, their apex broadly rounded and bordered by fine, sparse setae.

Mesosoma (alitrunk) elongate and low (Fig. S1), in profile with dorsum distinctly lower than dorsalmost surface of head (vertex). Pronotal neck pronounced, concealing propleuron in dorsal view. Pronotum elongate, dorsally weakly convex, extending laterally to anterior level of mesoscoxae; promesonotal suture present, complete. Mesonotal dorsal outline feebly convex in its anterior third, flat and sloped in its posterior two thirds. Metanotum prominent, convex, with posterior surface steep, separated from propodeum by deep metanotal groove. Propodeum 0.75× as high as long, junction between dorsal and declivitous surfaces broadly rounded; propodeal spiracle slit-like, oriented posteriad, located around midpoint of propodeal sides; metapleural gland bulla a conspicuous, hemispheric concavity oriented posteriad, partly concealed medially by a horizontal cuticular rim. Legs long and slender; all femora and tibiae antero-posteriorly flattened; small trochantellus present on mid and hind legs; protibia with three spurs apically on ventral margin, the largest ("calcar") gently curved, with minute setae apically, two other spurs less than half as long as calcar, straight and simple; mesotibial apex with two subequal, simple, straight spurs and one shorter straight spur (about half as long as other two spurs); metatibial apex with one large, pectinate spur gently curved apically and one small, straight and simple spur; protarsomere I with "antennal cleaner" (strigi), a velvety notch proximally on ventral margin; protarsomeres of all legs with 8–10 pairs of stiff setae along ventral surface; tarsomeres I–IV of all legs with two pairs of stiff setae apically on ventral surfaces; pretarsal claws with minute subapical tooth.

Petiole short-pedunculate (Fig. S1), approximately 0.6× as high as long; petiolar tergite a broadly convex, low node with slightly distinct lateral ridge along ventral margins; subpetiolar process present, in profile a moderately high, transverse, arched lamella pointing anteroventrally.

Gaster with five segments all sparsely covered by fine, long erect setae on their apical half. Absence of constriction between gasteral segments I and II (AII–AIV). First gasteral segment with helcium pronounced, forming a post-petiolar peduncle; anteriormost part of first gasteral sternite with a small mesal process pointing anteroventrally below helcium. Second gasteral segment distinctly larger. Segments III, IV, V telescoping, partially explaining the variation in body length. Sting long but largely internalized, stout, slightly upcurved apically.

The metrics provided in Table S1 for the type material are most accurate from the paratype IGR.BU-002, which has nearly no distortion, while the holotype NIGP164022 is more complete but the mesosoma and metasoma are evidently distorted, resulting in longitudinally elongate and transversely shortened distances.

**Revision of previously described Haidomyrmecini**

In the latest account on *Haidomyrmex*, Barden and Grimaldi [S2] described two species, *H. scimitarus* and *H. zigras*; that they erroneously figured with 11 antennal articles and mentioned with "10 funicular segments", while providing measurements for a full complement of 12 antennal articles (pp. 7, 11-12: measurements for scape, pedicel, and flagellomeres F1-FX). This mistake was overlooked by McKellar et al. [S3] who proposed a key to the genera and species of Haidomyrmecini, and utilized the peculiar antennal count as one of three criteria to distinguish *Haidomyrmex* from their genus *Haidoterminus*. Ironically, *Haidomyrmodes* was also referred to this same misinterpreted condition in the same work, though the genus was correctly described and figured with 12 articles in the original account of Perrichot et al. [S4: p. 92 and figs 2a, e-f]. The presence of 12 antennal articles (i.e., 11 funicular articles, or 10 flagellomeres excluding pedicel) is here confirmed for both *H. scimitarus* and *H. zigras* (Barden & Grimaldi, pers. comm., March 2013). The type species, *H. cerberus*, likely possessed 12 articles as well, but the antennae of the holotype are not preserved beyond the 8th article. Furthermore, *H. cerberus* was depicted by Dlussky [S5] with a posteroventral tooth at the elbow between the basal and apical portions of the mandibles, and with one preserved pair of long, trigger hairs on the right side of the setose pad, but the tooth and trigger hairs were reported absent by Engel and Grimaldi [S6] as these could not been seen during their examination of the holotype in 2002. A re-examination of the holotype by V.P. in 2013 permitted verification of the trigger hairs and tooth’s presence, although scarcely visible (Fig. S3D). Only one large, blade-like tooth can be seen on each mandible in full-facial view, and the presence of smaller teeth could not be assessed.

*Haidomyrmodes mammuthus* was based on three incomplete specimens with some aspects of their morphology obscured by surrounding bubbles and organic debris contained in the amber matrix [S4]. The specimens were embedded in Canada balsam subsequent to the publication and between cover glasses for long-term
conservation. A re-examination of the material for the present study revealed some alterations due to impregnation of the amber by the balsam, i.e., a 'clearing' of the amber matrix and parts of the insect cuticle, for both the holotype (MNHN.F.A30162) and one paratype (MNHN.F.A30163). In addition, a fracture had formed in the piece containing the holotype, which broke at the level of the head in a vertical plane crossing the vertex behind the compound eyes and the apical part of the mandibles. Ironically, and although unfortunate, these alterations resulted in a better view of the facial structures, allowing the present revision of this genus. In the original description of *Haidomyrmodes* [S4], similarities between the French specimens and the Burmese genus *Haidomyrmex* were noted, but a separate genus was justified by the apparent following differences: "part of mandible basal of elbow very short, so that distal part, which is strongly up-curved, is very close to head; mandibles smooth; eyes large (ratio eye length/head length about 0.4 vs 0.2 in *Haidomyrmex*); ocelli well developed; no brush of stiff setae on clypeus; antennal scape with distinct inner apical lobe; all funicular segments of same length and all less than twice as long as broad". Restudy shows that the clypeal pad covered with stout setae and two pairs of trigger hairs are actually present (Fig. S3E), like in all species of *Haidomyrmex* and *Haidotermimus*, and these are assuredly synapomorphies of Haidomyrmecini. Also, the basal tooth at the elbow of the mandibles is actually a serrate, posteroventral lamella of one large tooth and a singular small tooth. Two other features previously used to distinguish *Haidomyrmodes* now appear to range within the morphological variation displayed by species of *Haidomyrmex*: the body length (3.7 mm vs. 3.5 in *H. zigrasi*) and the short part of the mandibles basal to the elbow (observed in *H. zigrasi*). *Haidomyrmodes* may still be distinguished from *Haidomyrmex* by the compound eyes relatively larger, the presence of ocelli, and the antennae with flagellomeres approximately all of similar length, short and broad (as opposed to variable in length).

**Key to genera and species of Haidomyrmecini**

Given the discovery of a fourth genus of haidomyrmecines, a new key to the female diversity in the tribe is provided. The key below is corrected and expanded from that of McKellar et al. [S3].

1. Antenna compact, with flagellar articles short (<2× as long as broad) ........................................................................................................... 2
   – Antenna elongate, with flagellar articles long (>2× as long as broad) ................................................................................................. 3

2. All flagellomeres nearly of same length; clypeal setose pad positioned anterior to antennal bases; basal portion of mandible short, small gap between elongate, apical portion and surface of face; compound eye diameter ca. 0.4× head length; ocelli present; two metatibial spurs .......................................................... ***Haidomyrmodes mammuthus*** [France; Late Albian–Early Cenomanian]
   – Flagellomere I longest of basal four flagellar articles; clypeal setose pad positioned slightly posterior to antennal bases; basal portion of mandible long, large gap between elongate apical portion and surface of face; compound eye diameter 0.2–0.3× head length; ocelli absent; one metatibial spur .......................................................... **Haidotermimus cippus** [Canada; Campanian]

3. Flagellomere I longest; frontal triangle not obvious; clypeal setose pad a long spatulate horn projected forward above vertex; apical portion of mandible very long, reaching above vertex; ventral corner symmetrical between mandibles; ocelli and subpetiolar process present, distinct ................................................................. 4
   – Flagellomere I not longest; frontal triangle prominent, its anterior face more or less elevated and bearing stiff setulae; clypeal setose pad a slightly elevated subantennal shelf; apical portion of mandible not surpassing vertex; ventral corner of mandibles generally asymmetrical; ocelli and subpetiolar process absent or strongly reduced .................................................................................. **Ceratomyrmex ellenbergeri** [Myanmar; earliest Cenomanian]

4. Flagellomere II longest of basal three flagellar articles; compound eye diameter ca. 0.2× head length; frontal triangle moderately elevated; vertex distinctly setose; basal portion of mandible relatively long, ventral corner with at least one large tooth; ocelli reduced to pit-like traces; subpetiolar process a small tooth .......................... **H. cerberus** [Myanmar; earliest Cenomanian]
   – Flagellomere II longest; compound eye diameter ca. 0.2× head length; maxillary palps long; frontal triangle strongly elevated; vertex glabrous; basal portion of mandible relatively long, ventral corner with multiple teeth asymmetrical between mandibles; ocelli and subpetiolar process absent ................................................................. **H. scimitarus** [Myanmar; earliest Cenomanian]
   – Apical flagellomere longest; compound eye diameter ca. 0.35× head length; maxillary palps short; frontal triangle feebly elevated; vertex with few erect setae; basal portion of mandible relatively short, ventral corner a single tooth asymmetrical between mandibles; ocelli absent; subpetiolar process a minute tooth ........................................................................................................ **H. zigrasi** [Myanmar; earliest Cenomanian]
Supplemental References


