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The venom apparatus and other morphological characters of the ant *Martialis heureka* (Hymenoptera, Formicidae, Martialinae)

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ABSTRACT

We describe and illustrate the venom apparatus and other morphological characters of the recently described Martialis heureka *ant worker, a supposedly specialized subterranean predator which could be the sole surviving representative of a highly divergent lineage that arose near the dawn of ant diversification.* M. heureka *was described as the single species of a genus in the subfamily, Martialinae Rabeling and Verhaagh, known from a single worker. However because the authors had available a unique specimen, dissections and scanning electron microscopy from coated specimens were not possible. We base our study on two worker individuals collected in Manaus, AM, Brazil in 1998 and maintained in 70% alcohol since then; the ants were partially destroyed because of desiccation during transport to São Paulo and subsequent efforts to rescue them from the vial. We were able to recover two left mandibles, two pronota, one dismembered fore coxa, one meso-metapropodeal complex with the median and hind coxae and trochanters still attached, one postpetiole, two gastric tergites, the pygidium and the almost complete venom apparatus (lacking the gonostylus and anal plate). We illustrate and describe the pieces, and compare* M. heureka *worker morphology with other basal ant subfamilies, concluding it does merit subfamilial status.*

Keywords: Ant phylogeny; Formicidae; *Martialis;* Ultrastructure; Venom Apparatus.

INTRODUCTION

The ant *Martialis heureka* was recently described by Rabeling and Verhaagh (in Rabeling *et al.* 2008) based on a single worker collected by Christian Rabeling in Manaus (Embrapa Headquarters 02°53'S, 59°59'W), Amazonas state, Brazil, 28 km of Highway AM 010 in May 9, 2003. The specimen was found at dusk in a primary lowland rainforest walking on the leaf litter.

The phylogenetic position of this ant was inferred from several nuclear genes, sequenced from one front leg (Rabeling *et al.,* 2008). On the basis of morphology and phylogenetic evidence the authors suggested this specialized subterranean predator is the sole surviving representative of a highly divergent lineage that

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arose near the dawn of ant diversification. Accordingly they described it as a species of a monotypic genus in the subfamily Martialinae Rabeling and Verhaagh.

This very important ant was regrettably described from a single worker, which thus did not allow for a more detailed morphological study, for instance, under electron scanning microscope, and of the mouth parts or the venom apparatus. The *M. heureka* holotype is deposited in Museu de Zoologia da Universidade de São Paulo. Rabeling *et al.* (2008) briefly mention that five years before the discovery of the holotype of *M. heureka,* two workers of the same species were discovered by M. Verhaagh in a soil sample taken by the SHIFT-project team under the guidance of Marcos Garcia (Embrapa, Manaus) in a different but nearby patch of primary rainforest from where the holotype came from.

Indeed, M. Verhaagh brought several ant samples from Manaus to the Museu de Zoologia at that time, including the one with two *M. heureka* workers and several other ants found in the same spot. The label information found along with this sample says: "Flo. Solo Berl. AN. 06, 02/09/1998, SHIFT 52, Manaus, leg. M. Garcia *et al.*", meaning forest soil submitted to Berlese, sample 06, collection date September 02, 1998. SHIFT project 52. Manaus. M. Garcia *et al.* leg.

Unfortunately, the vial which included the *M. heureka* workers dried up during the trip from Karlsruhe to São Paulo, because the lid opened. Brandão tried to recover the dried specimens by filling the vial with 70% alcohol and adding a drop of detergent; even allowing for several days, the ants did not free themselves from the vial walls and from the other ants that dried up with them. In a desperate move, he gently let the vial with the ants to come in contact with an ultrasound apparatus, just to watch most ants in the vial shatter into small pieces. He collected the pieces and kept them in 70% alcohol until now. This ant proved so important and interesting that we decided to be worthwhile recovering the pieces and studying the different morphological aspects in detail, in order to compare this ant to other formicid subfamilies.

Unfortunately, the pieces we were able to recover did not allow a full reconstruction of the *M. heureka* workers, but we present here details of some parts of the exoskeleton and of the complete venom apparatus, aiming to stimulate future research on this spectacular ant. Finally we compared our observations with those of Ettershank (1966) and Gotwald (1969) on the mandibles, with Kugler's (1978) records of the venom apparatus, with the character coding employed by Bolton (1990), Baroni Urbani *et al.* (1992), Astruc *et al.* (2004), and Brady & Ward (2005).

MATERIAL AND METHODS

Photographs taken under the MZSP scanning electron microscope (SEM) (LEO 440®) were used to record morphological details of *M. heureka* workers. The recovered parts were previously cleaned in acetone, critical-point dried in a Balzer (Bal-Tec® CPD 030), and sputtered over with gold (Bal-Tec® SCD 050). After that, the fragments were fixed on the stubs using silver glue. The images were obtained under several magnifications, according to the size of the observed structure. Finally, the images were edited (Adobe Photoshop CS2®) to enhance brightness and contrast.

We studied also the sting apparatus of one of the fragmented specimens. The apparatus was cleared in NaOH for 12 hours, and then in lactophenol at 45-50°C for 12 more hours (or longer if necessary), rinsing it twice in distilled water, and then transferred to Hoyer's fluid. After the clearing process, the sting apparatus was dismembered, and soaked in Hoyer's fluid for observation and illustration under optical light microscopes. The terms for sting apparatus morphology follow Kugler (1978) and Diniz (1997).

RESULTS

The fragments we were able to recover did not allow for a complete reconstruction of a *M. heureka* worker. Notwithstanding, we recuperated important pieces from the two individuals: two left mandibles, two pronota, a dismembered fore coxa, one meso-metapropodeal complex with the right median and hind coxae with the trochanters attached, and the left median coxa with the trochanter, one postpetiole, one gastric tergite, the pygidium and the almost complete venom apparatus. From the original Automontage picture and description, it is possible to see that the metasoma (abdominal segments IV-VIII visible) is laterally compressed and drop shaped in lateral view (Rabeling *et al.,* 2008).

The pictures (Figs. 1-3) we show do not display similar pilosity in comparison to the original Automontage pictures; summing our information with that presented by Rabeling *et al.* (2008), we can say that in general, pronotum and legs are densely covered with erect to suberect hairs and sparsely with longer erect setae, although most of the hairs were lost during SEM preparation. The scars, however, are perfectly visible under the SEM. Most hairs are erect, thin, flexuous, and follow no definite direction. Dense appressed pubescence is absent from entire body. Special features

of surface sculpture and hairs, when conspicuous, will be described below, in the appropriate sections.

Mandibles (Fig. 1)

As described in Rabeling *et al.* (2008), *Martialis heureka* worker mandibles are forceps-like, slender, extremely elongate, and even longer than the head capsule. The mandibles are inserted at the far lateral sides of head. Mandibular pubescence is dense, consisting of short suberect hairs (better seen in Automontage pictures; Rabeling *et al.,* 2008).

The mandible is not cylindrical in cross section (Fig. 1A); the internal face of the mandible is almost flat throughout its length, vertical, and bears oblique rugulae that arise from the ventral margin and gently curve upwards, although never attaining the dorsal margin (Fig. 1D). The mandibular base is triangular when seen from behind (Fig. 1B); the *mandalus* (MA) is also triangular, and, according to Ettershank (1966) may contain the mandibular gland orifice; the

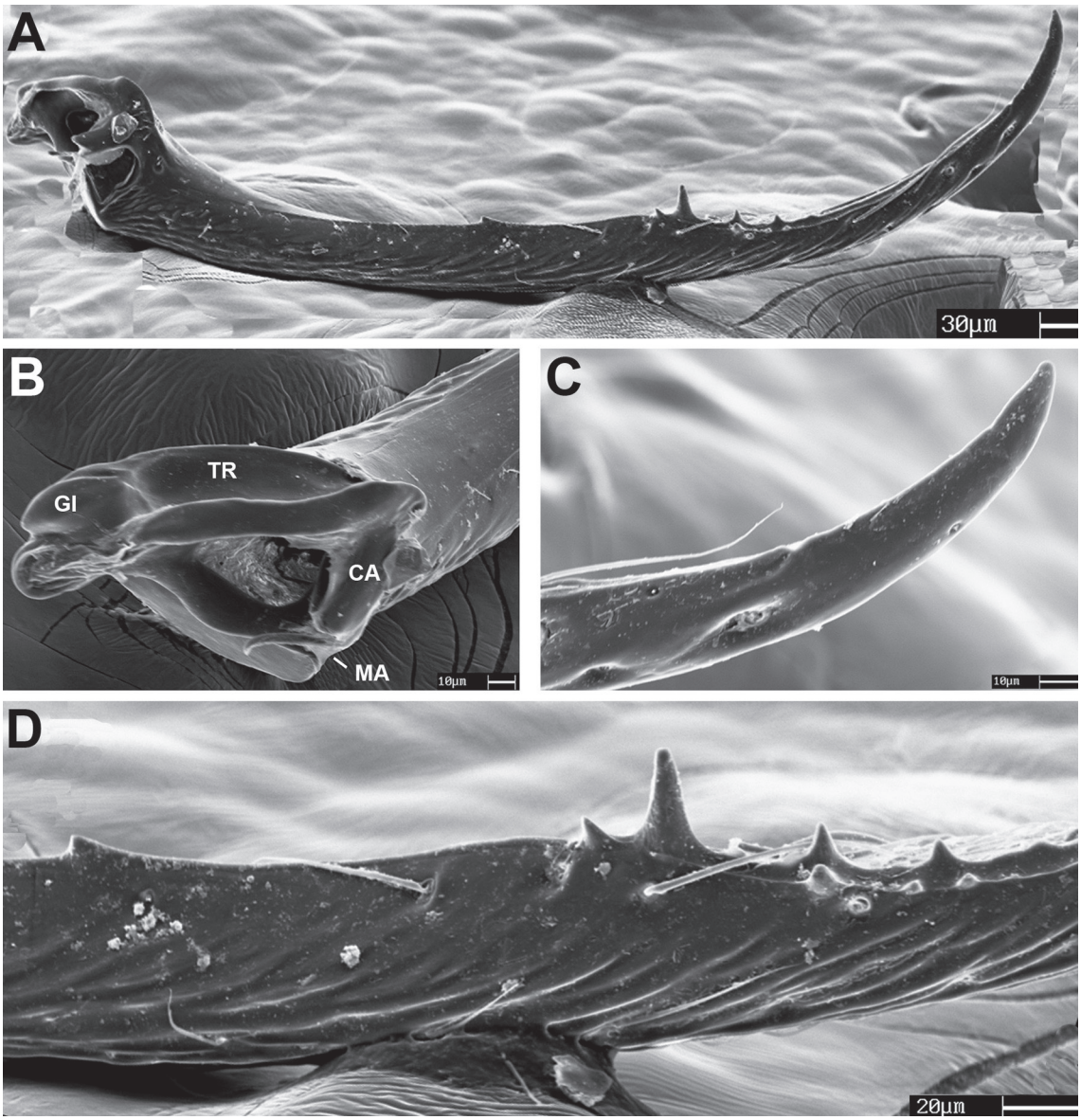

FIGURE 1: Electron micrographs of the left mandible of a *Martialis heureka* worker. **A.** Internal view of the whole mandible. **B.** Detail of mandibular base: CA, canthellus, GI, ginglymus, MA, mandalus, TR, trulleum. **C.** Detail of mandibular apical portion. **D.** Preapical teeth, showing, at left, the beginning of the two dorsal ridges and their teeth.

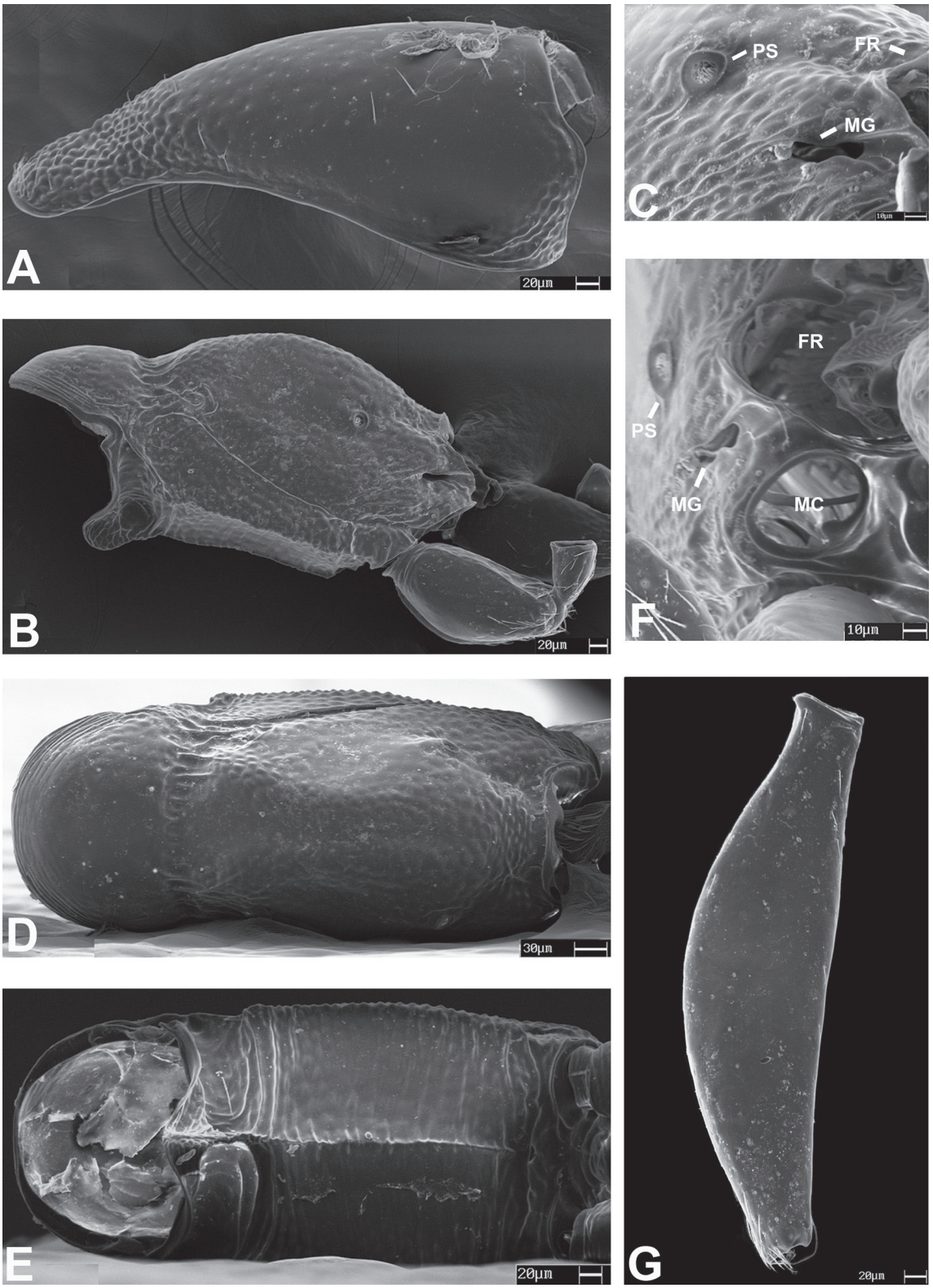

FIGURE 2: Electron micrographs of the mesosoma and legs of a *Martialis heureka* worker. **A.** Pronotum in lateral view. **B.** Meso-metapropodeal complex with middle coxa and trochanter in profile. **C.** Detail of metapleural gland (MG) and propodeal spiracle openings (PS), and petiolar foramen (FR). **D.** Meso-metapropodeal complex in dorsal view. **E.** Meso-metapropodeal complex in ventral view. **F.** Detail of metacoxal cavity (MC), propodeal spiracle opening (PS), and petiolar foramen (FR). **G.** Fore coxa in profile.

trulleum (TR) is open and rather large; the *canthellus* (CA) is free and the *ginglymus* (GI) is small and inconspicuous. From the longest subapical tooth onwards the mandible is falcate (Fig. 1C) and the internal and external blades are flattened.

From the base to the apex, the first denticle in the masticatory border is triangular, minute and directed to the base of the mandibles (Fig. 1D); after a relatively long diastema (1/6 of the mandibular chord length), there are two teeth, the first (second mandibular tooth) is small and obliquely directed towards the base; the second tooth (third mandibular tooth) is the longest of all mandibular teeth, rather pointed and acute, conical. At 5/7 of the mandibular length, at the base of the longest mandibular tooth, the mandibles narrow where, seen from the inside (Fig. 1A), the dorsal (i.e. the masticatory) margin divides into two ridges, each bearing its own sequence of minute teeth (Fig. 1D); from the large tooth on, the diastemas separating the teeth are of similar size and the three triangular and relatively small teeth in each ridge are perpendicular to the mandibles and tend to become smaller in direction of the mandibular apex.

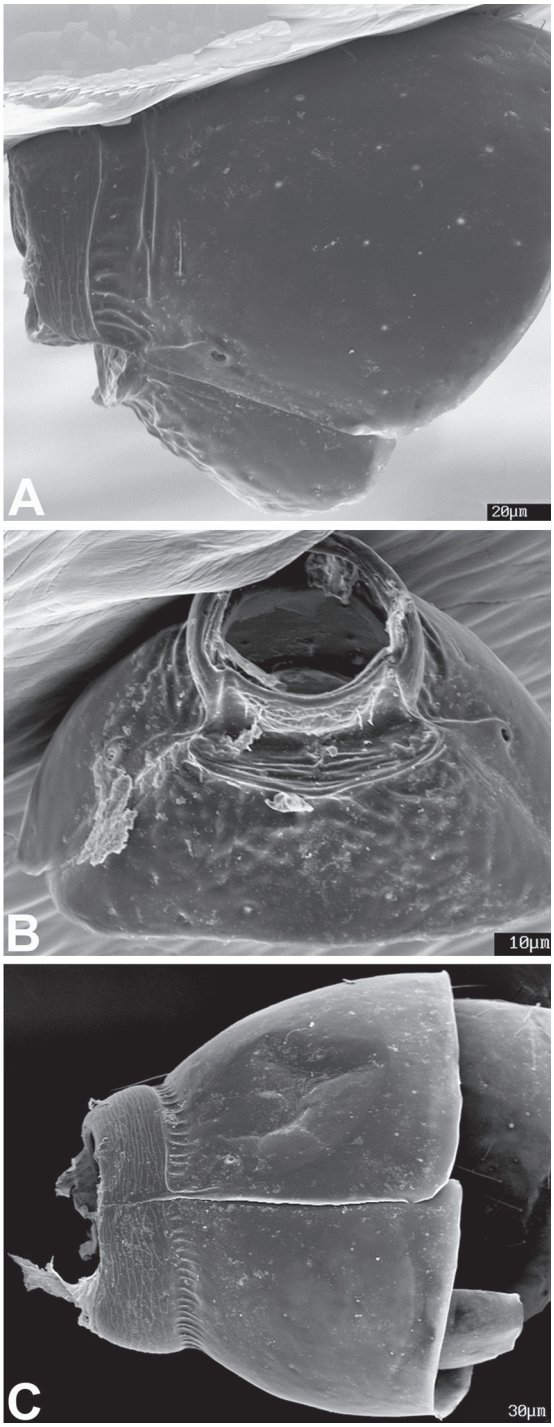

FIGURE 3: Electron micrography of the postpetiole and fourth abdominal segment (1st gastral) of a *Martialis heureka* worker. **A.** Postpetiole in profile. **B.** Postpetiole in frontal view. **C.** fourth abdominal segment (1st gastral) in profile.

Pronotum (Fig. 2A)

The pronotum is bottle shaped, distinctly tapered anteriorly, forming a slender cervix (see Rabeling *et al.,* 2008). The dorsal margin, when seen from the side, is evenly and gently convex; the inferior margin is more convex at the point where the plate expands. The anterior portion is the only part of the segment, which is fully covered by cuniculate sculpture (using Harris, 1979 terminology; "punctate" in Rabeling *et al.* 2008); the posteriormost area shows also some traces of faded similar low sculptures. Anteriorly there is a flange of erect hairs with circa 10 µm coming out of the anterior margin, while over the dorsal disc of the segment there are regularly spaced similar hairs, represented by scars in the SEM images (the preparation for SEM or the previous Ultrasound treatment may have resulted in the loss of hairs, as the original Automontage pictures show many more hairs than the SEM images; see Rabeling *et al.* 2008). Among the covering of smaller hairs, we find also longer hairs (up to 20 µm), still there after the preparation for SEM. At the point where the plate expands, there is also a flange of long hairs. At the base of the segment there are some 10 to 12 long hairs very much scattered in the middle of the plate.

Promesonotal suture unfused, pronotum and mesonotum presumably capable of movement relative to each other (if fused these parts would not have separated from each other during specimen manipulation).

Meso-metapropodeal complex (Fig. 2B-F)

The meso-metapropodeal complex (defined as posterior part of the mesosoma excluding the pronotum) is depicted slightly obliquely in Fig. 2B, giving us the opportunity to observe the mesosternum and the loose anterior tissue resulting from the dismemberment of the segment (see also Fig. 2E). The dorsal face of the mesonotum, when seen in lateral view, is evenly and mildly convex. From the Automontage pictures of the holotype (Rabeling *et al.,* 2008) we learned that only the mesonotum bears comparatively long flexuous hairs. The metapropodeal suture interrupts the dorsal margin of the complex when seen from the side and the suture is covered by gross longitudinal parallel rugae (Fig. 2B; D). The bare mesosternum (Fig. 2E) is extremely long and keeled medially; the keel is produced ventrally and, depending on the angle in which the ant is set for study, can be seen anteriorly when the trunk is observed in side view; the lateral margin of the mesosternum is very sharp and slightly convex. Anteriorly, the mesosternum presents depressions that accommodate the fore coxae. Metapleuron indistinct from propodeum; metapleural gland not covered by a cuticular flange or expansion dorsally. Metapleural gland orifice slit shaped, dorsal orifice margin projecting slightly forward, but not overhanging or concealing opening (Fig. 2C). Metapleural gland orifice posteriorly directed, widely separated from ventral margin of metapleuron (Fig. 2C). Metacoxal cavity closed, with a complete cuticular annulus surrounding the cavity (Fig. 2F); metasternal process absent. The dorsal margin of the propodeum is evenly convex, without a trace of projections or teeth. Dorsal and declivous faces continuous, indistinct. In side view, dorsal margin at the same level of dorsal margin of mesonotum. Cuticular flange over the foramen complete, but without further concentric rugae over the foramen (Fig. 2F). Propodeal lobes absent. Propodeal spiracle round, relatively large and set near the supposed meeting of the propodeum and the metapleuron (Fig. 2B, 2C, 2F). Propodeum without hairs.

Legs

We were able to study in detail only one *M. heureka* free fore coxa (Fig. 2G), one median coxa and trochanter complex, and one hind coxa and trochanter complex (Fig. 2B). Fore coxae as described in Rabeling *et al.* (2008): enlarged, twice as long and wide as median coxae. We did not find any gland orifice in these parts.

Post-petiole (Figs. 3A, 3B)

Helcium small, cylindrical (unconstricted posteriorly), circa one third the maximum width of posttergite in frontal view (Fig. 3B), apparently fused and located high on anterior face of the segment. Presternite very small, almost concealed by the pretergite in lateral view, not bulging ventrad. Posttergite much larger than poststernite, both sclerites fused. Spiracle clearly visible at posttergite, close to the segment constriction. Poststernite with a thickened U-shaped rim below the helcium, which projects ventrad as a lip-like process in lateral view; ventral margin in side view slightly concave anteriorly and straight from thereafter. Seen from the side, the whole segment subtriangular, with the maximum depth of the segment at its posterior margin.

First gastric tergite (Fig. 3C)

The fourth abdominal segment is twice as large as the postpetiole (abdominal segment III) in the sagittal plane, and strongly constricted anteriorly between the pre- and postsclerites. The presclerites (second helcium) of the fourth abdominal segment are collar shaped and rounded, the large pretergite fused with the also large presternite. In the Automontage picture of the holotype (Rabeling *et al.,* 2008), the presclerites appear fully covered by the postpetiole. The posttergite and poststernite are completely unfused; the tergite slightly overlapping the sternite. Fourth abdominal segment spiracle close to the constriction. Dorsal and ventral stridulitra absent.

Venom apparatus (Figs. 4, 5)

Spiracular plate (Fig. 4A) relatively small and pyriform, its ventral margin almost straight. Anterior apodeme very narrow, almost vestigial and non-sclerotized. Relatively small spiracle, occupying at most one sixth of the plate on a virtual transversal line. Dorsal notch, posterodorsal lobe and tubercle on posteroventral corner absent. Median connection attached along the posterior margin of the plate.

Quadrate plate (Fig. 4B) narrower dorsally than ventrally; midplate line vestigial, anterior apodeme weakly sclerotized and rounded throughout its entire posterior length; apodeme narrows at extremities; apodeme area three times smaller than the plate body; anterodorsal corner acute; median and lateral lobes continuous; anterior ridge expanded ventrally, its ventral end notched; dorsal margin convex; posterior margin complete, rounded.

Anal plate not found (see Discussion).

Apodeme of oblong plate (Fig. 4D) relatively short, ill-developed and acute. Subterminal tubercle well developed but non-sclerotized; dorsal ridge relatively narrow, ends before the posterior arm; ventral margin of posterior arm convex. Area of ventral arm similar to that of posterior arm. Post-incision deep although it does not touch the intervalvifer articulation, which bears seven sensillae. Ramus 2 with

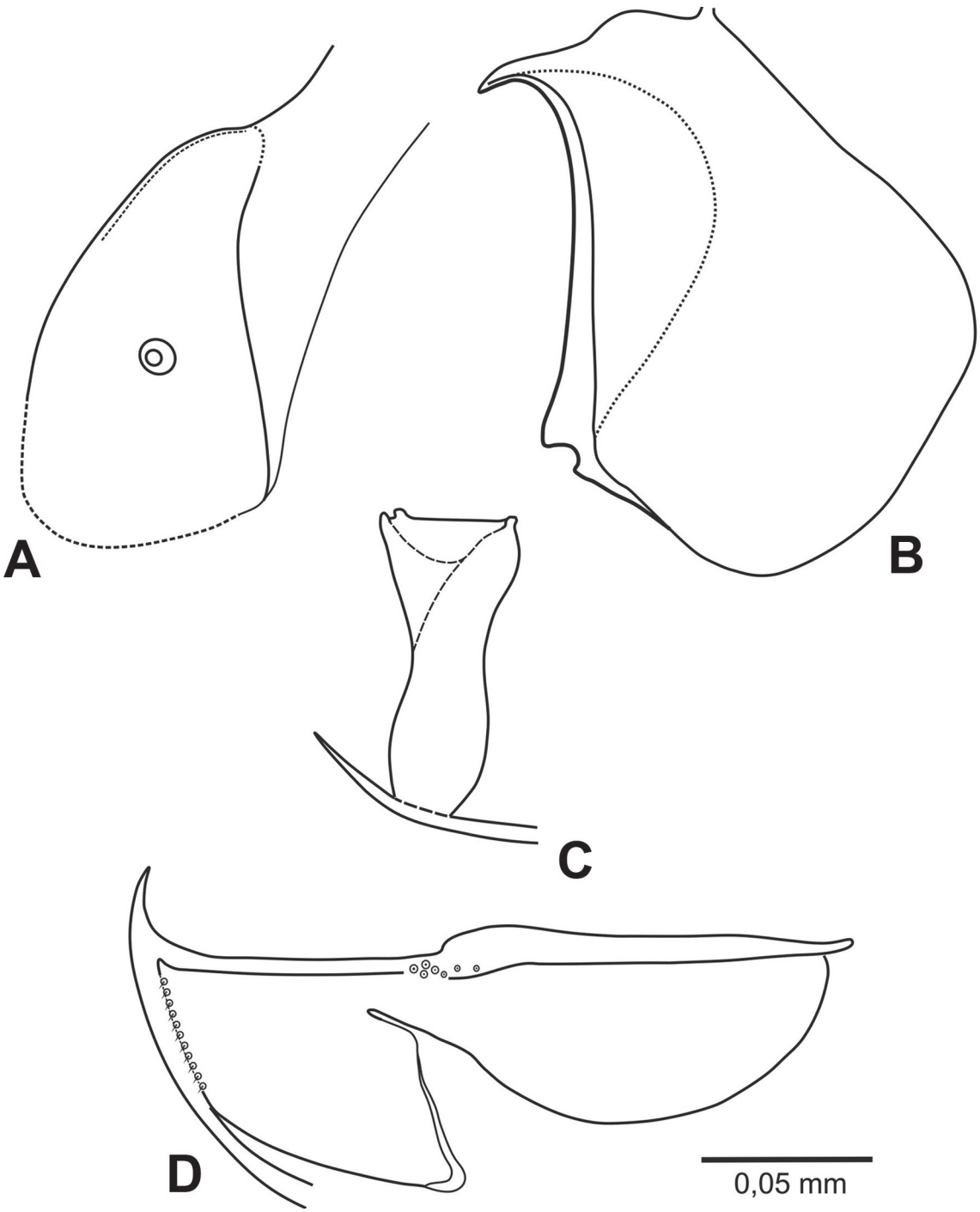

FIGURE 4: Venom apparatus of a *Martialis heureka* worker. **A.** Spiracular plate and part of median connection. **B.** Quadrate plate. **C.** Triangular plate and lancet rami (partially). **D.** Oblong plate.

11 sensillae. Fulcral arm very narrow, without noticeable fulcral sensillae.

Gonostylus lost during preparation or non-observable due to lack of sclerotization.

Triangular plate (Fig. 4C) long, length at least twice its width. Dorsal tubercle absent, lateral tubercle present; dorsoapical and vetroapical processes present.

Sting (Figs. 5A, 5C) with acute shaft, weakly sclerotized, covered by regularly spaced campaniform sensillae. Bulb and valve chamber ill developed, indistinct from the sting shaft, the length of the bulb and valve chamber greater than the length of the shaft. Hemocoele ill developed in lateral view, without dorsal flange. Valve chamber indistinct from the sting base. Internal apophysis developed but relatively short. Basal ridge weakly sclerotized, narrow and straight. Basal notch (arch formed by the curved anterior margin of the sting base in lateral view) uninterrupted (open). Posterior margin of bulb base rounded; the basal ridge and the posterior margin of the bulb in the shape of a D in dorsal view. Anterolateral processes well developed, although relatively short and not sclerotized. Lateral arms of furcula free, gently touching the apex of the anterolateral processes, but not extending beyond; dorsal arm very short.

Lancets (Fig. 5B) with 2 equally developed, separate and conical valves; dorsal lamina very thin throughout its entire length; apical third weakly sclerotized and devoid of barbs. Lancets at rest extend to the end of the sting, and not beyond. Microchetae on the ventral lamina, in special at the valves region.

DISCUSSION

Our investigations show new details of the microsculpture, mandibular dentition, the anatomy of abdominal presclerites, and the venom apparatus in relation to the holotype worker described by Rabeling *et al.* (2008).

Martialis heureka worker mandibles are set very distant from each other in the head capsule, in a similar situation to that encountered in Amblyoponinae, or in the ponerine genera *Thaumatomyrmex* and the isopod hunting species of *Leptogenys. M. heureka* mandibles share with Myrmeciinae the double teeth rows. The specialized mandibles of *Martialis heureka*

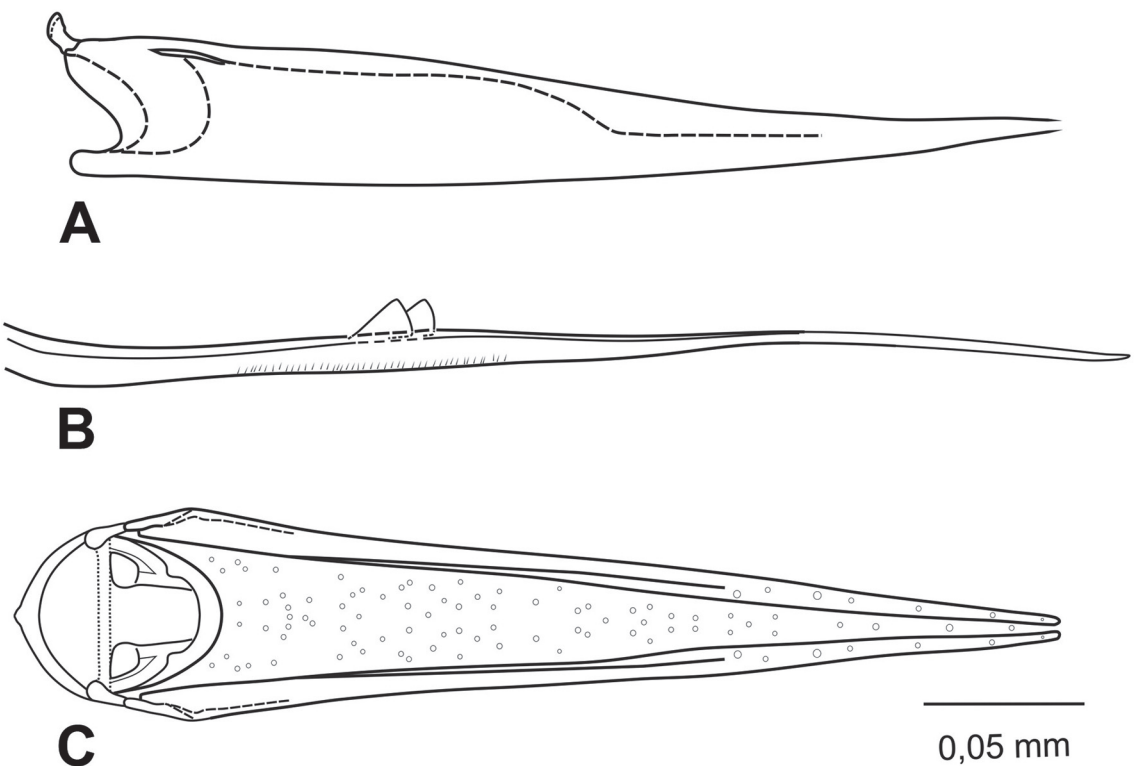

FIGURE 5: Venom apparatus of a *Martialis heureka* worker. **A.** Sting in profile. **B.** Lancets in profile. **C.** Sting in dorsal view, showing the furcula.

are typical for predatory ants. Comparing its mandibles with those of *Thaumatomyrmex* and Dacetini ants, *M. heureka* mandibles may act more similar to those of *Thaumatomyrmex* than to the long-mandibles present in some Dacetini. *Thaumatomyrmex* ants hold their polyxenid prey very carefully, as far as they can from their own bodies (Brandão *et al.,* 1991). The polyxenids are covered by loosely set hollow setae, filled with urticating substances. The ants keep the prey distant from themselves, firmly held by the mandibular tips, and curve up the gaster to sting the prey, which becomes absolutely still right after being stung.

The kinetic trap jaw mandibles of dacetine ants are narrow, sublinear to linear and long, bearing a small number of distally set teeth and enlarged apical teeth, present extremely wide maximum gape; dacetine ants employ the mandibles to dissipate energy which they accumulate in the base of the mandible, and deploy this force in a very rapid and destructive stroke; mandibles snap together very rapidly and are well suited to catch fast prey or to attack arthropods equipped with different defensive mechanisms (Gronenberg *et al.* 1998). The maximum gape of the mandibles is at least 170°. The main mandibular function in this case is to kill the prey by dissipation of the kinetic energy of the initial strike. Prey are generally killed by the closure of the mandibles; in case they are alive after this move, the ants curve the gaster and sting the prey. Rabeling *et al.* (2008) hypothesize that *M. heureka* mandibles are more adequate to drag soft bodied prey out of cavities. The disarticulated mandibles provided us with the chance to study the mandibular base anatomy, according to the definitions and terminology of Ettershank (1966) and Gotwald (1969) although we are not aware of any study on the evolution of the mandibular base characters. So it was not possible to polarize these characters.

It is unfortunate that we were not able to recover the head capsule, as it would have been a good opportunity to study the tuft of hairs the *Martialis heureka* workers display in the clypeus, to ascertain the nature of these structures and whether they are similar or even homologous to other ant structures.

According to Baroni Urbani *et al.* (1992) the unfused condition of the promesonotum is plesiomorphic for ants, a character state Martialinae shares with Formicinae, Dolichoderinae, Aneuretinae, Myrmeciinae, Pseudomyrmecinae, Leptanillinae, Leptanilloidinae and Ponerinae (in the present sense). The *M. heureka* pronotum is otherwise devoid of any singularity.

The orifice of the metapleural gland in *M. heureka* is plesiomorphic in relation to the basic ant plan, according to the interpretation of Baroni Urbani *et al.* (1992), as it does not present a covering flange. The metacoxal cavities of *M. heureka* are completely separated from the cavity in which the petiole articulates (the foramen), and are so called closed (Fig. 2F), an apomorphic condition in relation to the basic ant plan. According to Bolton (1990) the open condition is present in lower aculeates, while in Ponerinae (*sensu* Bolton 1990) these cavities are either open or an annulus is almost complete but interrupted midventrally by a mobile suture or break. The leg pieces we were able to study do not display any gland orifice that could be compared with Billen's (2009) scheme.

Based on the criteria of Baroni Urbani *et al.* (1992) we categorized the helcium of the third abdominal segment (postpetiole) as fused, which is the apomorphic condition for ants in general. Also the helcium III does not protrude ventrally and its sternum is partially enclosed by the helcium tergite, which corresponds, respectively, to state 0 of character 18 and state 0 of character 19 of Baroni Urbani *et al.* (1992).

The *M. heureka* sting apparatus indicates that these ants have a functional sting, which in addition to the specialized mandible morphology suggests they are indeed predators, as hypothesized by Rabeling *et al.* (2008). The fact that the ants are totally blind, relatively soft-bodied and very little pigmented or sclerotized, confirms also the previous impression these ants are subterranean and/or nocturnal. It is interesting to bear in mind that the holotype was collected at dusk and that the specimens investigated in the present study came from superficial soil samples. The sting bears several apparent apomorphies, as for instance, the non-inflated base, the presence of many campaniform sensillae and the very thin apex. The small sting base may indicate the ants are not capable of concentrating too much venom in the apparatus before injecting into the prey, which might suggest further that the prey is not fast-moving; the very thin apex may suggest, by its turn, that the prey are also soft-bodied. It is worth noting the high number of campaniform sensillae of different sizes throughout the whole *M. heureka* sting, a similar situation recorded by Kugler (1997) in *Lordomyrma* (Myrmicinae, see Taylor, 2009), although most probably of different origin. *M. heureka* shares with both Leptanilloidinae genera the presence of two separate conical valves in the lancets (Brandão *et al.* 1999). *M. heureka* also shares with members of Cerapachyinae the presence of numerous microchetae on the ventral lamina of the lancets (JLMD personal observation). However, these character states have not been polarized still.

Rabeling *et al*. (2008) phylogenetic analysis of the ant subfamilies results are congruent with other recent proposals [Brady *et al.* (2006), Moreau *et al.* (2006), Ouellette *et al.* (2006)], and Bolton's (2003) classification, suggesting that the most basal ant lineages are cryptic, hypogeic foragers, rather than wasp-like epigaeic foragers; these analyses suggested also that Leptanillinae, another subfamily of subterranean ant predators, is the sister lineage to all extant ants.

We compared the workers of Leptanillinae to those of Martialinae, as the gynes, larvae and males of *Martialis* remain unknown. *M. heureka* and Leptanillinae share characters that are possibly related to their common predaceous subterranean habits, such as total blindness and loss of pigmentation. Rabeling *et al*. (2008) already pointed out the apomorphic state of Martialinae characters in relation to the ant basal plan. We compared the *M. heureka* venom apparatus with that of Leptanillinae, based mostly on Kugler's description (1992). The *M. heureka* mechanism for venom injection is completely different from that employed by the leptanillines, which have lost the lancet's valves and the corresponding sting's valve chamber, retaining in contrast large barbs on the sting and lancets. Leptanillines inject venom by compression of the poison gland, rather than by shuttling of the lancets; the sting and lancet barbs providing a firm grip of the structure to the prey, enabling the poison transfer. *M. heureka,* in constrast, possesses two lancet valves and a well developed valve chamber, probably injecting venom by means of the rapid back and forth movements of the valves, forcing venom ahead from the valve chamber throughout the sting. The venom apparatus of Leptanillinae and Martialinae also differ in terms of the spiracle position, with those of *M. heureka* in the middle of the spiracular plate, while in leptanillines they are very anterior, and on the junction of the quadrate plates, which are very narrow in *M. heureka* while joining along the entire surface in leptanillines. Contrariwise, Leptanillinae and Martialinae share the lateral tubercle on the triangular plate, spiracular plates reduced dorsally, and oblong plate anterior apodeme relatively short.

In conclusion, the much more detailed morphology of *M. heureka* workers we were able to describe here confirms that the species presents a blend of apomorphic and plesiomorphic character states, although our observations clearly indicate that *Martialis heureka* does not belong to Leptanillinae, Proceratiinae, Amblyoponinae or any other putative basal ant subfamily. If our homology hypotheses for the sting apparatus of *M. heureka* proves true, this ant does merit subfamily recognition, as suggested by the molecular studies by Rabeling *et al.* (2008). We also believe that further studies on the morphology of *M. heureka* ant heads will confirm its subfamilial status.

RESUMO

Descrevemos e ilustramos o aparelho de ferrão e outros caracteres morfológicos da operária da formiga recentemente descrita Martialis heureka, *uma suposta predadora especializada subterrânea, que pode representar o único sobrevivente de uma linhagem altamente divergente que teria surgido no início de diversificação das formigas.* M. heureka *foi descrita como a única espécie de um gênero da subfamília Martialinae Rabeling e Verhaagh, conhecida por uma única operária; como os autores da espécie tinham à disposição um único exemplar, dissecções e microscopia de varredura não foram possíveis. Baseamos nosso estudo em duas operárias coletadas também em Manaus, AM, Brasil, em 1998, e mantidas em via úmida desde então; estes indivíduos haviam sido parcialmente destruídos devido à dissecação durante o transporte para São Paulo e desmembrados pelos esforços subseqüentes para resgatá-los. Ilustramos, descrevemos e comparamos as peças da operária de* M. heureka *com outras subfamílias basais de formigas: duas mandíbulas esquerdas, dois pronotos, uma coxa anterior, um complexo meso-metapropodeal com as coxas e trocanteres medianos ainda conectados, um pós-pecíolo, dois tergitos gástricos mais o pigídio e o aparelho de ferrão quase completo (menos o gonóstilo e a placa anal). Concluimos que Martalinae merece de fato* status *de subfamília.*

Palavras-chave: Filogenia de formigas; Formicidae; *Martialis;* Ultra-estrutura; Aparelho de ferrão.

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