

# A revision of the giant Amazonian ants of the genus *Dinoponera* (Hymenoptera, Formicidae)

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## Abstract

*Dinoponera* Roger 1861 has been revised several times. However, species limits remain questionable due to limited collection and undescribed males. We re-evaluate the species boundaries based on workers and known males. We describe the new species *Dinoponera hispida* from Tucuruí, Pará, Brazil and *Dinoponera snellingi* from Campo Grande, Mato Grosso do Sul, Brazil and describe the male of *Dinoponera longipes* Emery 1901. Additionally, we report numerous range extensions with updated distribution maps and provide keys in English, Spanish and Portuguese for workers and known males of *Dinoponera*.

## Resumen

El género *Dinoponera* Roger 1861 ha sido revisado varias veces. Sin embargo, la distribución geográfica de las especies de este género todavía es cuestionable debido a colecciones limitadas, y a que en general los machos continúan sin descripción. Reevaluamos los límites geográficos de las especies utilizando caracteres merísticos y morfométricos basados en obreras y machos conocidos. Describimos las nuevas especies *Dinoponera hispida* de Tucuruí, Pará, Brasil, y *Dinoponera snellingi* de Campo Grande, Mato Grosso do Sul, Brasil, y describimos el macho de *Dinoponera longipes* Emery 1901. Además, reportamos numerosas extensiones nuevas de las distribuciones geográficas con sus respectivos mapas actualizados, y proporcionamos claves de identificación en inglés, español, y portugués para las obreras y los machos conocidos del género *Dinoponera*.

## Resumo

O género *Dinoponera* Roger 1861, é tem revisados varios vezes. No entanto, a clarificação das especies ainda segue questionável devido a um coleção limitado, e a que em geral os representantes do sexo masculino continuam sem descrição. Reavaliamos os limites de espécies utilizado caracteres merísticos e morfométricos, baseado em operários e machos conhecidos. Descrevemos novas espécies *Dinoponera hispida* de Tucuruí, Para, Brasil e *Dinoponera snellingi* de Campo Grande, Mato Grosso do Sul, Brasil, e descrevemos o macho de *Dinoponera longipes* Emery 1901. Además, reportamos distribuições geográficas com seus respectivos mapas atualizados, e proporcionamos chaves de identificação em inglês, espanhol, e português para operários e machos conhecidos do género *Dinoponera*.

## Keywords

South America, Brazil, taxonomy, gamergate, ponerinae

## Introduction

*Dinoponera* Roger 1861 is a strictly South American genus in the subfamily Ponerinae, tribe Ponerini, commonly called tocandiras or giant Amazonian ants (Zahl 1959, Fourcassié and Oliviera 2002, Haddad et al. 2005). These ants are generally less well known than *Paraponera clavata* (Fabricius 1775), the bullet ant or hormiga bala (Haddad et al. 2005), yet *Dinoponera* workers may surpass 3 cm in total body length, making them the largest in the world. The genus has been found from montane rainforest on the eastern slope of the Andes in Perú, Ecuador and Colombia to savannah and lowland rainforest in Brazil, Guyana, south through Bolivia, Paraguay and Argentina.

Roger (1861) described *Dinoponera* based on *Ponera gigantea* (Perty 1833) and the synonym *Ponera grandis* (Guérin-Méneville 1838). Several authors described additional species (Santschi 1921, Borgmeier 1937, Kempf 1971), subspecies (Emery 1901) and varieties (Santschi 1921, Santschi 1928), resulting in several tetranomials and taxonomic confusion. Kempf (1971) provided a revision of the genus and with additional corrections (Kempf 1975), that formed the basis for the current taxonomy of the genus (Table 1).

Species limits among *Dinoponera* are difficult to define (Kempf 1971). Furthermore, revisionary studies have been hampered by availability of specimens and collection bias. Previous works (Perty 1833, Guérin 1838, Roger 1861, Emery 1901, Santschi 1921, Santschi 1928, Borgmeier 1937) were based on limited numbers of specimens. Most specimens have been collected only at the fringes of the Amazon basin, or along major rivers (Fig. 13). Currently, six species are recognized in the genus *Dinoponera* (Table 1), as well as two questionable subspecies of *Dinoponera australis* based on male coloration (Borgmeier 1937). Kempf (1971) had doubts as to the status of several species largely because uncollected areas suggested that geographic variation was poorly understood. Character integration between what appeared to be distinct species was a possibility, based on the lack of collections in key areas. In particular, Kempf (1971) recognized that because of gaps in distribu-

**Table 1.** Current taxonomy of *Dinoponera* as suggested by Kempf (1971, 1975) and modified by this publication, including known castes of each taxa. <sup>1</sup>This taxa or caste was described by this publication. Female is used instead of the caste designation of gyne and worker because they are morphologically indistinguishable. <sup>2</sup>Validity of these taxa is questionable and could not be addressed in this study as types were unavailable.

Taxa	Described castes
<i>Dinoponera australis</i> Emery, 1901	Male/Female
<i>D. a. bucki</i> Borgmeier, 1937 <sup>2</sup>	Male/Female
<i>D. a. nigricolor</i> Borgmeier, 1937 <sup>2</sup>	Male/Female
<i>Dinoponera gigantea</i> (Perty, 1833)	Male/Female
<i>Dinoponera hispida</i> sp. n. <sup>1</sup>	Female <sup>1</sup>
<i>Dinoponera longipes</i> Emery, 1901	Male <sup>1</sup> /Female
<i>Dinoponera lucida</i> Emery, 1901	Female
<i>Dinoponera mutica</i> Emery, 1901	Female
<i>Dinoponera quadriceps</i> Santschi, 1921	Male/Female
<i>Dinoponera snellingi</i> sp. n. <sup>1</sup>	Male <sup>1</sup>

tional data, character integration was a possibility in the uncollected areas between *D. longipes*, *D. mutica*, *D. quadriceps* and *D. gigantea* where sympatry could exist. If sympatry is demonstrated between different *Dinoponera* species and character integration is not found, this lends support to the recognition of taxa as distinct species. Kempf (1971) suggested that a study incorporating more specimens and quantitative characters could be more effective at defining species limits. Current analyses such as DNA bar-coding or other molecular investigation could solve this dilemma. This study seeks to determine whether the current taxonomy of *Dinoponera* reflects the actual species richness. We re-evaluate the alpha taxonomy of *Dinoponera* using morphological characters (including male genitalia), and interpretation of distribution and sympatry for workers and males.

## Specimens and methods

We examined 345 workers and 11 males of *Dinoponera*, including type specimens for *D. australis*, *D. longipes*, *D. lucida*, *D. mutica* and *D. quadriceps*. We were unable to acquire the type specimens of *Dinoponera gigantea*, *D. australis nigricolor* and *D. australis bucki*. In the material examined section for each species, female workers including possible gamergates are designated with a “w”, and male specimens with a “m” following the number of specimens for each. Collections cited in this study are abbreviated as follows:

- AMNH** American Museum of Natural History
- CASC** California Academy of Sciences Entomological Collection
- CUIC** Cornell University Insect Collection
- FMNH** Field Museum of Natural History

<b>FSCA</b>	Florida State Collection of Arthropods
<b>LACM</b>	Los Angeles County Museum of Natural History
<b>UNAMB</b>	Museo Entomológico Facultad de Agronomía, Universidad Nacional de Colombia
<b>MCSN</b>	Museo Civico di Storia Naturale ‘Giacomo Doria’
<b>MZSP</b>	Museo de Zoologia da Universidade de São Paulo
<b>MCZC</b>	Museum of Comparative Zoology, Harvard University
<b>NHMB</b>	Naturhistorisches Museum Basel
<b>PALC</b>	Paul Alvarado Lenhart personal collection
<b>QCAZ</b>	Pontificia Universidad Católica del Ecuador, Catholic Zoology Museum
<b>USNM</b>	Smithsonian Institution’s National Museum of Natural History
<b>CWEM</b>	William and Emma Mackay Collection at the University of Texas at El Paso

Morphological characters were selected after extensive examination of the material. Previous authors (Roger 1861, Emery 1901, Santschi 1921, 1928, Borgmeier 1937, Kempf 1971) had identified several characters that in combination have been used to distinguish workers. These characters include gular striations, tooth-like antero-ventral pronotal process, pilosity type and color, microsculpturing, petiole profile and stridulatory file shape. The known males possess more discernable character states including compound eye shape, ocelli placement, pygidial spine, volsella and aedeagal shape. Our own examination provided congruence for these characters.

Measurements were made with an ocular micrometer using a Wild stereomicroscope at 64×. A subset of 91 worker specimens including available types were measured totaling 21 *D. australis*, 16 *D. longipes*, 15 *D. gigantea*, 17 *D. quadriceps*, 5 *D. lucida*, 12 *D. mutica* and 5 *D. hispida*. Specimen numbers of *D. lucida*, *D. mutica* and *D. hispida* were limited by availability in museum holdings. In descriptions measurements include the range and in parenthesis the mean. Observations on the *D. longipes* males were made using two specimens and therefore no mean is provided.

A measure of gaster length is not as consistent as other measurements because of differential expansion or contraction of the gastral segments in individual specimens, resulting in a larger range of variation. However, gaster length is useful for a measure of the approximate overall body length which is helpful when identifying *D. australis* which differs notably in size from other species.

Photomicrographs (Fig. 12) were taken using a Carbeco ZDM1 Digital Video Microscope.

Standard myrmecological morphometric parameters were generally selected to best characterize the observed differences and included:

- MDL** Mandibular length. The straight-line length of the mandible from the mandibular apex to the articulation with the clypeus.
- SL** Scape length. Maximum length of first antennal segment not including the articular boss and condyle.

- FL1** First funicular segment length. Maximum length of second antennal segment, for males only.
- FL2** Second funicular segment length. Maximum length of third antennal segment, for males only.
- HL** Head length. Midline measured from the distal edge of the clypeus at the median (not including clypeal teeth) to the occipital margin of the head at its median (not including ocelli in males).
- HW** Head width. Maximum width of the head in full-face view including eyes.
- EL** Eye length. Maximum length of the eye measured along its longer vertical axis.
- EW** Eye width. Maximum width of the eye measured along its shorter horizontal axis.
- OD** Ocelli diameter. Maximum diameter of the medial ocellus, for males only.
- WL** Weber's length. Distance measured between the anterior margin of the pronotum to the posterior margin of the metapleural bulla in lateral view.
- FWL** Forewing length. Maximum length of the forewing measured from the base of the costal vein to the wing apex, for males only.
- HWL** Hindwing length. Maximum length of the hindwing measured from the base of the costal vein to the wing apex, for males only.
- PL** Petiole length. The maximum measurable longitudinal distance between the anterior and posterior extensions of the petiolar node in lateral view.
- PH** Petiole height. Height of the petiole measured laterally from the median of the subpetiolar process viewed laterally to the median of the dorsum of the petiole.
- PW** Petiole width. Maximum width of the petiole measured in dorsal view.
- GL** Gaster length. Maximum longitudinal distance from articulation with petiolar helcium to distal edge of hypopygidium (subgenital plate in males) measured in lateral view.
- HFL** Hind femur length. Maximum length of the posterior femur measured from its basal articulation with the trochanter to its apex at the articulation with the tibia.
- TBL** Total body length (sum of MDL, HL, WL, PL, GL).

Label data were used from all specimens to plot distributions. These data were combined with localities derived from literature (Kempf 1971, Kempf 1975, Araujo et al. 1990, Peeters et al. 1999, Monnin and Peeters 1999, Fourcassié and Oliviera 2002, Monnin et al. 2003, Mariano et al. 2004, Araújo and Rodrigues 2006, Marques-Silva et al. 2006) to supplement specimen distribution data. GPS coordinates were recorded from labels, or estimated from Google Earth (<http://earth.google.com/>) or the Global Gazetteer Version 2.1 Directory of cities and towns in the world (<http://www.fall-ingrain.com/world/index.html>). Maps were constructed using the software package ArcGIS version 9.2 (ESRI 2007). A complete table of localities including estimated geographic coordinates is provided in supplementary file 1.

## Results

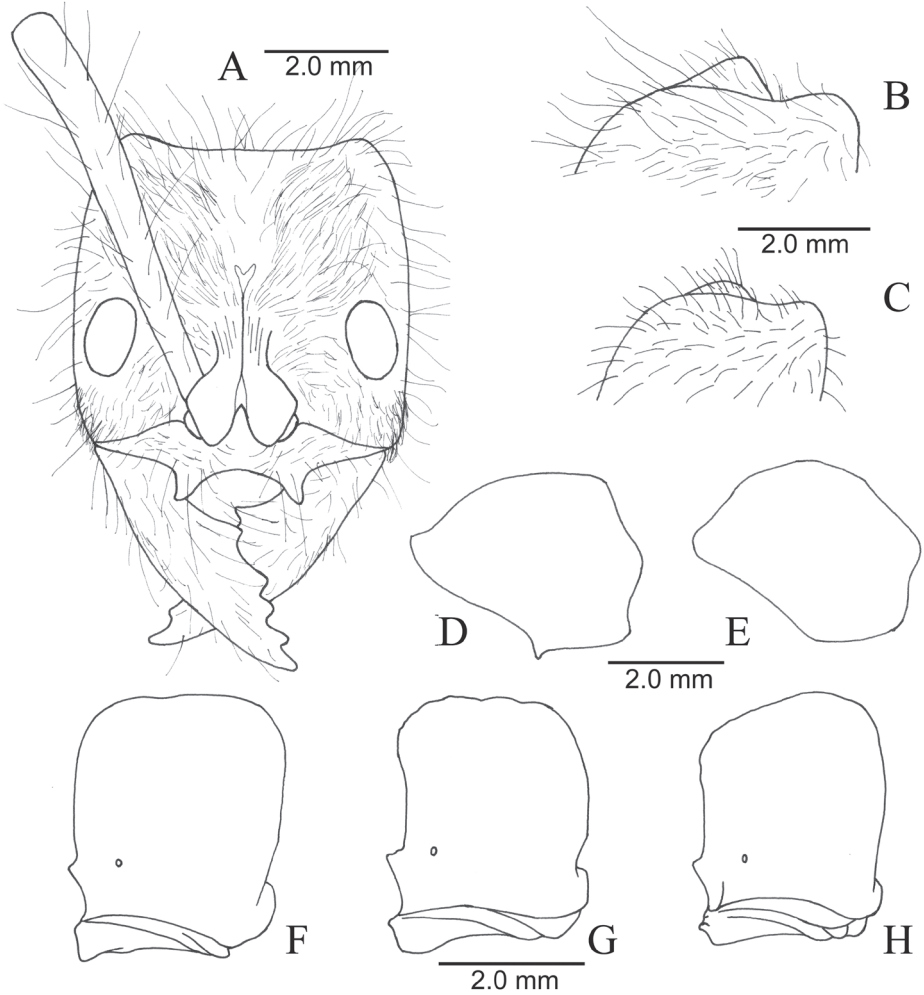
### Genus *Dinoponera* Roger, 1861

<http://species-id.net/wiki/Dinoponera>

Family Formicidae, subfamily Ponerinae, tribe Ponerini. Described by Perty (1833) as *Ponera gigantea*. Defined as a genus by Roger (1861) (Type species: *Dinoponera gigantea*)

**Diagnosis.** Size (TBL > 2.5cm) can easily distinguish *Dinoponera* from other worker ants. Two laterally projecting clypeal teeth (Fig. 1A) and rows of spines on the pygidium and hypopygidium will further distinguish this genus. The gamergates of *Dinoponera* are not distinct from workers in their external morphology (Haskins and Zahl 1971, Araujo et al. 1990, Paiva and Brandão 1995, Monnin and Peeters 1998). True gynes have not been found in this genus.

**Description of the worker.** Abundant setae; black integument, ranges from smooth and shiny with no microsculpturing, to finely micropunctate or scaled depending on species (Fig. 12). Head: Mandibles long and curved posteriorly in side view; seven large teeth; erect setae on dorsum. Ventral surface of head with sparse decumbent and subdecumbent setae; may have fine striations depending on species; Pappal formula 4, 4; large bilobed labrum. Clypeus with two laterally projecting teeth on anterior edge, clypeus bulging medially, extending posteriorly between frontal lobes, anterior edge with row of long setae; sparse appressed setae from distal edges to medial area of clypeus. Area posterior to clypeus with varying amounts of striation. Tentorial pits apparent. Frontal lobes raised and conspicuous, with striations at posterior constriction. Antennae: geniculate, 12 segments, all with flagellate setae; scape long, extending past posterior border of head; funiculus covered in minute appressed pubescence. Gena depressed medially of eye; dense appressed setae on the antero-lateral sides of the head; covered in conflated punctulate sculpturing. Eyes large, elliptical with slight depression (ocular ring) around circumference. Frons with large pads of long flagellate pubescence (lost in older or poorly curated specimens). Median furrow running from posterior termination of clypeus, between frontal lobes to center of frons, terminates in shallow pit in most specimens. Entire head covered in long flagellate subdecumbent setae (Fig. 1A). Mesosoma: in lateral view weakly convex; covered in long subdecumbent to erect flagellate pilosity and dense pubescence; pronotal disc with slight bulges; promesonotal suture distinct, suture between mesopleuron and propodeum distinct; mesonotum fused with propodeum and episternum, separated by slight furrows; basilar sclerite large, ovaloid; propodeum with broadly rounded dorsal outline, dorsal surface gradually curves into posterior face (Fig. 2); propodeal spiracle forms nearly vertical slit; sulcus running from center of propodeum along lower edge of propodeal spiracle to posterior edge of propodeum at dorsal edge of bulla, patches of short white pubescence at curved posterior border of pronotum and basilar sclerite. Legs long, covered in long setae with short, stiff pubescence. One well-developed,



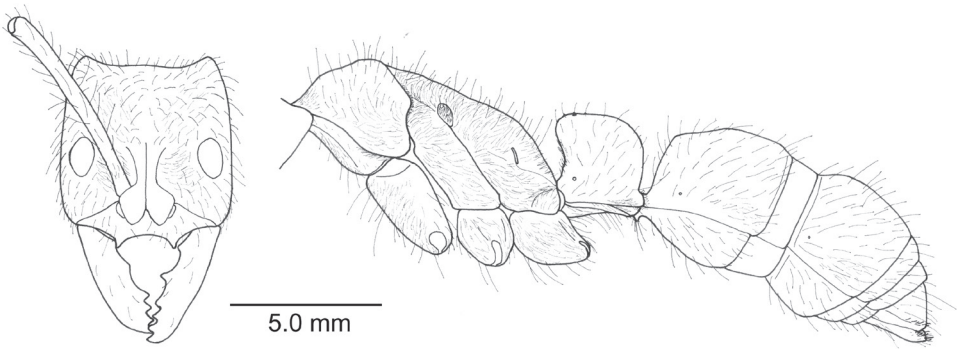
**Figure 1.** Features of *Dinoponera* workers. **A** Head, frontal view **B–C** Occiput of head, oblique anterolateral view **D–E** Pronotum, lateral view **F–H** Petiole, lateral view. **A–B** *D. longipes* **C** *D. hispida* **D** *D. gigantea*. **E–F** *D. mutica* **G** *D. hispida* **H** *D. lucida*.

antennae cleaning, comb-like spur on foreleg; one spine-like appendage and one less developed denticular comb on mesothoracic tibia; one spine and one comb-like spur on hind tibia. Posterior side of fore leg basitarsus with dense pads of golden setae; tarsal claws bidentate. Petiole: node large and tabular in lateral view, narrow attachments at base to propodeum and gaster; in dorsal view largest width less than propodeum and gaster, varies from ovate rectangular to ovate triangular in outline; covered in long subdecumbent to erect flagellate pilosity; pubescence on anterior face and ridges of subpetiolar process; subpetiolar process reduced, slightly variable between species. Gaster: typical of ponerines; covered with flagellate setae with short pubescence; small protuberance at articulation of gastric sternite III and the petiole; stridulatory file of

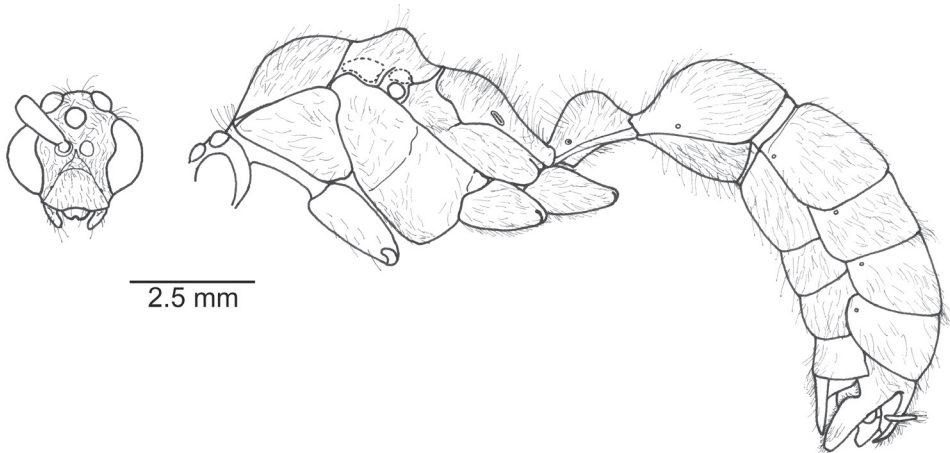


varying size on acrotergite of gastral tergum II; posterior edges of the pygidium and hypopygidium with characteristic rows of minute spines.

**Description of the male.** Integument: smooth and nitid; reddish to dark brown/black. Head: Mandibles greatly reduced, rounded, spoon shaped, lacking teeth; palps elongated, maxillary palps 4 segmented, labial palps 3 segmented; labrum reduced, rounded to truncate, emarginated distal margin in *D. snellingi* and *D. longipes* covered with setae. Clypeus large, triangular, bulging medially; anterior tentorial pits large; frontal lobes absent; antennal sockets almost touching, located at posterior apex of clypeus. Antennae: geniculate, 13-segmented, pilosity varies from fine pubescence to long setae in different species; scape shorter than second funicular segment, but shorter than 1<sup>st</sup>, 1<sup>st</sup> funicular segment reduced. Compound eyes large, along lateral side of head, deeply emarginated medially. Three ocelli at posterior margin of head, bulging beyond margin of head in all species except *D. australis*. Entire head immaculate, covered in fine pubescence and long erect setae (Fig. 3). Mesosoma: pronotum triangular, exposed narrowly dorsally anterior to scutum; scutum large, bulging antero-dorsally,



**Figure 2.** *Dinoponera hispidula* worker. Head in full frontal view; body in lateral view.



**Figure 3.** *Dinoponera longipes* male. Head in full frontal view; body in lateral view with wings not shown.



with 3 longitudinal carina; small tegula over insertion of forewing; scutellum domed, side with vertical carina, dorsal surface smooth; basilar sclerite under hind wing reduced; fused mesopleuron, separated by furrow into anepisternum and katapisternum; metanotum exposed between scutellum and propodeum, reduced; dorsal face of propodeum shorter than posterior face, rounded into posterior face; coxa large, conical (Fig. 3). Wings: covered in minute pubescence, venation as shown in Figure 5. Legs: one well-developed, antennae cleaning, pectinate spur on foreleg; one spine-like and one less developed denticular comb on mesothoracic tibia; one spine and one comb-like spur on hind tibia. Posterior side of fore basitarsus with dense pads of golden setae; tarsal claws bidentate. Petiole: narrow attachments at base to propodeum and gaster; petiolar node humped dorsally, subpetiolar process anteriorly triangular. Gaster: large, cylindrical, covered in fine silvery pubescence; pygidium terminating in spine posteriorly, with short cerci; hypopygidium with long fine erect setae, tabular subgenital plate with posterior end truncated, often emarginated. Genitalia (Figs 6–11): basal ring with dorso-anterior loop structures; parameres long, rounded, with emarginated ventro-basal edge (Fig. 9); volsella articulated with basiparamere along ventral edge, lateral finger-like cuspis volsellaris, medial digitus volsellaris with distal wide toothed cusp, basal medial lobe with tooth-like structures varying with species (Fig. 10); penis valve of aedeagus roughly triangular and rounded, aedeagal apodeme curved horn-like antero-lateral arm structure arising from mid-valve ridge, terminating at interior surface of basiparamere (Fig. 11).

**Description of the larvae.** A basic description of the larva of *D. quadriceps* (cited as *D. grandis mutica*) is present in Mann (1916). A detailed description of the egg and all larval stages of *Dinoponera gigantea* are present in Wheeler and Wheeler (1985). The following generic description of *Dinoponera* larvae is from their work:

*"Profile pogonomymecoid (i.e., diameter greatest near the middle of abdomen, decreasing gradually toward anterior end and more rapidly toward posterior end, which is rounded; thorax more slender than abdomen and forming a neck, which is curved ventrally). Body with numerous (114–160) mammiform tubercles, each with 2–25 short simple hairs; body hairs lacking elsewhere. Cranial hairs lacking. Mandible dinoponeroid (i.e. narrowly subtriangular in anterior view; anterior portion curved posteriorly; with or without medial teeth.)"*

**Discussion.** *Dinoponera*'s status as a genus is validated as several characters differentiate it from other genera. Size (TBL>2.3cm) is the most obvious character distinguishing *Dinoponera*. The only other ants with a worker caste approaching this size are *Paraponera clavata* (Fabricius) and the larger *Pachycondyla* such as *P. crassinoda* (Latreille 1802), *P. impressa* Roger 1861 and *P. villosa* (Fabricius 1804). *Paraponera clavata* is easily separated by its anvil shaped petiole with a spine on the ventral surface, highly sculptured body and deep antennal scrobes. *Pachycondyla* is regarded as the sister taxa to *Dinoponera* (Kempf 1971, Schmidt 2010). *Dinoponera*, in addition to their size, are distinguishable from *Pachycondyla* by the presence of two laterally projecting clypeal teeth (Fig. 1A) and rows of spines on the pygidium and hypopygidium. Several (n=6) specimens have been observed to have a single ocelli in the pit at the termination of

the median furrow. These anomalous specimens were previously thought to be queens (Borgmeier 1937) but as it has been shown that *Dinoponera* lacks queens, the presence of the ocelli is hypothesized to be the result of a *Mermis* Dujardin 1842 nematode parasite (Kempf 1971).

***Dinoponera* biology.** *Dinoponera* is one of the roughly 10 ponerine genera in which some species have secondarily lost the typical morphologically specialized queen caste for a reproductive worker known as a gamergate (Haskins and Zahl 1971, Araujo et al. 1990, Paiva and Brandão 1995, Monnin and Peeters 1998, Peixoto et al. 2008). Conflict over dominance is intense in colonies with younger workers usually joining a linear hierarchy of one to five workers depending on colony size. The gamergate, or alpha female has the highest ranking (Monnin and Ratnieks 1999, Monnin et al. 2003). The alpha female mates with non-nestmate males at night at the entrance of the nest (Monnin and Peeters 1998, Monnin and Peeters 1999). After copulation the female bites through the male's gaster to release herself and pulls out the genital capsule which acts as a temporary sperm plug (Monnin and Peeters 1998). After mating the female is unreceptive to other males and remains monandrous (Monnin and Peeters 1998). The gamergate maintains dominance with ritualized behaviors such as antennal boxing and biting, 'blocking', as well as gaster rubbing and curling (Monnin and Peeters 1999). Lipid stores within *Dinoponera australis* females were found to be strongly related to foraging activity and reproductive status within the colony, ranging from 1–39% of an individual's dry mass (Smith et al. 2011). It is uncertain, however, whether nutritional differences between females is a cause or consequence of rank. Gamergate females possess a higher concentration of a cuticular hydrocarbon (9-hentriacontene, 9-C<sub>31</sub>:1) that indicates rank and is passed onto gamergate-laid egg cuticles (Monnin and Peeters 1997, Monnin et al. 1998, Peeters et al. 1999). Additionally, alpha females may 'sting smear' a competing female with secretions from the Dufour's gland, triggering the lower ranking workers to immobilize the marked female (Monnin and Ratnieks 2001). Subordinate females (beta, gamma, or delta) may produce unfertilized eggs but these are usually consumed by the alpha female in a form of "queen policing" (Monnin and Peeters 1997). Egg recognition in *D. quadriceps* was found to be due to differences in cuticular hydrocarbons, and only workers engaged in brood care could distinguish non-nestmate eggs (Tannure-Nascimento et al. 2009). Cuticular hydrocarbons are also used to distinguish adult nestmates from non-nestmates, however, this is only effective with non-nestmate foragers (Nascimento et al. 2012). Nascimento et al. (2012) found that brood-caring workers from different colonies had very similar hydrocarbon profiles and were more often accepted into alien colonies.

Males are born throughout most of the year in tropical species (Araujo and Jaisson 1994, Monnin and Peeters 1998), however *D. australis* which lives in the more temperate south was found to only produce males in May-July (Paiva and Brandão 1995). When the alpha declines reproductively or dies, she is replaced by a high-ranking worker (Monnin and Peeters 1999).

New colonies are founded by fission, a process in which a beta female is fertilized in the natal nest (Monnin and Peeters 1998). This new alpha female then leaves the

nest with a cohort of workers to found an incipient colony, sometimes employing tandem running (Overal 1980).

Colonies vary in size depending upon species. *Dinoponera australis* colonies have an average of 14 workers (range 3–37) (Paiva and Brandão 1995, Monnin et al. 2003), *D. gigantea* average 41 workers (range ~30–96) (Overal 1980, Fourcassié and Oliveira 2002, Monnin et al. 2003) and *D. quadriceps* has the largest colonies with an average of 80 workers (range 26–238) (Monnin and Peeters 1999, Monnin and Ratnieks 2001). Morgan (1993) excavated two *D. longipes* nests, a possible incipient colony with 7 workers and another mature colony of 120 workers.

The nest consists of large chambers and tunnels in the soil possibly with an earthen mound and can be 0.10–1.2m deep (Araujo et al. 1990, Morgan 1993, Fourcassié and Oliveira 2002, Vasconcellos et al. 2004). Nests are deeper in *D. australis* and *D. quadriceps* than in *D. gigantea*, Monnin et al. (2003) suggests that deeper nests are a possible adaptation to seasons and aridity. *Dinoponera gigantea* nests may have up to eight entrances and can be weakly polydomous (Fourcassié and Oliveira 2002), whereas 1–30 openings with an average of 11 were recorded for *D. longipes* (Morgan 1993). Nesting density and spatial distribution varies depending on habitat (Fowler 1985, Vasconcellos et al. 2004). Density ranges from 15–40 nests per ha<sup>-1</sup> (Vasconcellos et al. 2004) to 80 nests per ha<sup>-1</sup> (Paiva and Brandão 1995). Morgan (1993) measured a spacing between nests for *D. longipes* with a median of 35m (n=22, range 14–69.5m). *Dinoponera australis* and *D. gigantea* usually nest at the base of trees (Paiva and Brandão 1995, Fourcassié and Oliveira 2002). Observations of *D. quadriceps* nests show that in more arid Caatinga and Cerrado habitats, nests are predominantly constructed under trees, whereas in Atlantic forest 60% of nests were 3m away from any tree (Vasconcellos et al. 2004).

Workers lower in the hierarchy forage individually for food items on the substrate and do not recruit other nestmates to assist with food transport (Fowler 1985, Fourcassié et al. 1999, Fourcassié and Oliveira 2002, Araújo and Rodrigues 2006). Although foraging workers do not recruit nestmates, Nascimento et al. (2012) found a positive feedback between incoming food and stimulation of new foragers as well as task partitioning once food was brought into the nest. Lower ranking females processed protein resources while higher ranking females handled small food pieces and distributed them to the larvae. Fourcassié and Oliveira (2002) found *D. gigantea* foraging to be concentrated in the early morning and afternoon but did not sample at night. Morgan (1993) observed the highest activity at night in *D. longipes*. *Dinoponera quadriceps* has a marked seasonal pattern in activity. It is most active in May–August, the late rainy season to early dry season in the semiarid Caatinga (Medeiros et al. 2012). Activity was strongly negatively correlated to temperature and positively correlated to prey abundance (Medeiros et al. 2012). The diets of both *D. gigantea* and *D. quadriceps* have been shown to be predominantly scavenged invertebrates, but include live prey, seeds and fruits (Zahl 1959, Fourcassié and Oliveira 2002, Araújo and Rodrigues 2006). Araújo and Rodrigues (2006) state that the taxonomic diversity of prey is comparable to other tropical ponerines, but has an optimal prey size of 2–3

cm in *Dinoponera*. Diet seems to be very similar across the genus, regardless of habitat (Araújo and Rodrigues 2006).

Despite their large size and strong venom, *Dinoponera* are likely preyed on by many vertebrate and invertebrate species across South America. Like many other ant species, *Dinoponera* can be infected by the entomopathogenic fungi *Codyceps* sp. (Evans 1982). Buys et al. (2010) discovered a *Kapala* sp. eucharitid wasp emerging from the puparia of *Dinoponera lucida*.

Anatomy has been described several times. Marques-Silva et al. (2006) studied of the sensilla and glands of the antennae. Anatomy of the venom apparatus and mandibular glands of *Dinoponera gigantea* is presented in Hermann et al. (1984). Further studies of the mandibular glands and its contents were presented by Oldham and Morgan (1993) and Oldham et al. (1994). Oldham et al. (1994) found that the mandibular gland secretions of workers differed greatly from those of gamergates, which were 98% dimethylalkylpyrazine and lacked the four other pyrazines and 50 times more volatiles than those found in worker secretions. The post-pharyngeal gland morphology was examined by Schoeters and Billen (1997). The cuticular hydrocarbons used in nestmate recognition may be produced by epidermal glands which Serrão et al. (2009) found in the epidermis of abdominal sternites in *D. lucida*.

For subduing large live prey and defense (Morgan, 1993), workers possess a sting that has been known to cause severe pain lasting up to 48 hours, lymphadenopathy, edema, tachycardia and fresh blood to appear in human victim feces are common symptoms (Haddad et al. 2005). In gamergates the venom sac is empty (Monnin et al. 2002). Workers may have 60–75 unique proteinaceous components in the venom (Morgan et al. 2003, Johnson et al. 2010). The convoluted gland within the venom system of *Dinoponera australis* has been found to possess close similarities to those of vespine wasps (Schoeters and Billen 1995). The contents of *D. australis* venom have been found to be similar to those of *Pachycondyla* spp. (Cruz López 1994, Johnson et al. 2010). Billen et al. (1995) studied the morphology and ultrastructure of the pygidial gland of *D. australis*. Due to the high diversity of compounds and systemic effects found by Haddad et al. (2005), venom of *Dinoponera* could be of use to the pharmaceutical industry. For instance, Sousa et al. (2012) demonstrated in mice that venom from *D. quadriceps* had antinociceptive properties. The authors note that the local population of northeast Brazil uses dry crushed *D. quadriceps* ants to treat earaches, and the stings of live ants are administered for back pain and rheumatism.

Several studies of the cytogenetics of *Dinoponera* species have been conducted. *Dinoponera lucida* may have the highest number of chromosomes within the Hymenoptera however the karyotype is variable between populations ( $2n=106-120$ ) (Mariano et al. 2004, Mariano et al. 2008, Barros et al. 2009). Mariano et al. (2008) interpreted the karyotype differences between populations as being due to a division of the species into allopatric populations during the Quaternary. Variability in the karyotype within a described species has been found in the *Pachycondyla* as well, and may represent cryp-

tic species (Mariano et al. 2012). Descriptions of the banding patterns on *Dinoponera* chromosomes are provided by Barros et al. (2009) and de Aguiar et al. (2011).

*Dinoponera* belongs to the tribe Ponerini in the subfamily Ponerinae. The evolutionary position of the genus within Ponerinae was resolved by Schmidt (2010). Based on the phylogenetic analysis of Schmidt (2010) and karyotype analysis by Mariano et al. (2012), *Dinoponera*'s closest living relatives are in the *Pachycondyla* species group consisting of *P. crassinoda*, *P. harpax* (Fabricius 1804), *P. impressa*, *P. metanotalis* Luederwaldt 1918, and *P. striata* Smith 1858. Prior to the generation of well supported phylogenies other associations had been proposed. Carpenter (1930) suggested that the fossil *Archiponera wheeleri* Carpenter from the Miocene Florissant shale of Colorado may be an ancestor of *Dinoponera* and *Streblognathus aethiopicus* Smith 1858. Molecular data has shown that Carpenter's (1930) hypothesis is false (Schmidt 2010). *Streblognathus* is not closely related to *Dinoponera*, and its morphological similarity is purely convergence. The placement of *Archiponera wheeleri* is still questionable.

**Key to the workers of *Dinoponera***

- 1 Antero-inferior corner of pronotum with distinct tooth-like process (Fig. 1D)..... **2**
- Antero-inferior corner of pronotum without tooth-like process (Fig. 1E).... **4**
- 2 Head (Fig. 12B), sides of petiole and terga 1 and 2 of gaster smooth and polished, integument with bluish luster (Fig. 12A); southeastern coast of Brazil ..  
..... ***lucida* Emery**
- Head, lateral sides of the petiole and terga 1 and 2 of gaster finely micro-punctate/scaled (Fig. 12B) ..... **3**
- 3 Total body length under 3 cm; Bolivia, Paraguay, northern Argentina and southern Brazil..... ***australis* Emery**
- Total body length over 3 cm; Brazil, Peru, and Guyana..... ***gigantea* (Perty)**
- 4 Body covered in bristle-like setae which are not flagellate (Fig. 1C); Pará, Brazil ..... ***hispida* sp. n.**
- Body covered in fine and flagellate setae (Fig. 1B) ..... **5**
- 5 Appressed golden yellow pubescence present on frons (Fig. 1A); Colombia south to Perú to northern Brazil..... ***longipes* Emery**
- Pubescence absent from frons or not golden yellow ..... **6**
- 6 Sides of head, lateral sides of the petiole and terga 1 and 2 of gaster finely micro-punctate/scaled (Fig. 12B); in profile antero-dorsal edge of petiole bulging (Fig. 1G); northeast Brazil..... ***quadriceps* Santschi**
- Sides of head, sides of the petiole and terga 1 and 2 of gaster smooth, shiny and polished with no microsculpturing, integument with bluish luster (Fig. 12A); in profile petiole with even dorsal corners (Fig. 1F); eastern Bolivia, northern Paraguay and southwestern Brazil ..... ***mutica* Emery**

### Key to the known males of *Dinoponera*

(couplets 1 and 2 are included to easily separate males of other genera which are likely confused with *Dinoponera*)

- 1 Total body length less than 15 mm ..... *Pachycondyla* and other poneroids
- Total body length greater than 15 mm ..... **2**
- 2 Subpetiolar process in form of spine; pronotum heavily sculptured; palp formula 5:3 ..... *Paraponera*
- Subpetiolar process without spine; pronotum shiny, microsculptured; palp formula 4:3 ..... **3**
- 3 Ocelli protruding on occipital margin of head (Fig. 4A–D) ..... **4**
- Ocelli not protruding on occipital margin of head (Fig. 4E); Bolivia, Paraguay, northern Argentina and southern Brazil ..... *australis* Emery
- 4 Setae on funiculus long and erect (Fig. 4F, G) ..... **5**
- Setae on funiculus short, stiff and subdecumbent, or minute pubescence present (Fig. 4H, I, J) ..... **6**
- 5 Digitus volsellaris with toothless lobe at distal end (Fig. 10C); Brazil, Peru, and Guyana ..... *gigantea* (Perty)
- Digitus volsellaris without lobe at distal end (Fig. 10A); northeast Brazil ..... *quadriceps* Santschi
- 6 Pygidium terminating in narrow, elongate spine (Fig. 4M); penis valve of aedeagus wedge-shaped in lateral view (Fig. 11E); Colombia south to Perú to north western Brazil ..... *longipes* Emery
- Pygidium terminating in short, broad, triangular angle (Fig. 4N); penis valve of aedeagus with distal flange and triangular ventral lobe (Fig. 11B); Mato Grosso do Sul, Brazil ..... *snellingi* sp. n.

### Clave para la identificación de las obreras de *Dinoponera*

- 1 Esquina antero-inferior del pronoto con proceso en forma de diente distinto (Fig. 1D) ..... **2**
- Esquina antero-inferior del pronoto sin proceso en forma de diente (Fig. 1E) ..... **4**
- 2 Cabeza, lados laterales del pecíolo, y tergos 1 y 2 del gáster lisos y brillantes, con reflexiones azules (Fig. 12A) ..... *lucida* Emery
- Cabeza, lados laterales del pecíolo, y las tergos 1 y 2 del gáster finamente punteados o con escamas finas (Fig. 12B), a veces con reflexiones azules ..... **3**
- 3 Largo total menos de 3 cms ..... *australis* Emery
- Largo total más de 3cms ..... *gigantea* (Perty)
- 4 Cuerpo cubierto con pelos gruesos, no flagelados (Fig. 1C) ..... *hispida* sp. n.



- Cuerpo cubierto con pelos finos y flagelados (Fig. 1B) ..... 5
- 5 Frente con pubescencia recostada y amarillo-dorada (Fig. 1A).....  
..... *longipes* Emery
- Frente sin pubescencia recostada y amarilla ..... 6
- 6 Lados de la cabeza, lados del pecíolo y tergos 1 y 2 del gáster finamente punt-  
eados o con escamas finas (Fig. 12B); pecíolo (en perfil) con el borde anterior-  
dorsal hinchado (Fig. 1G)..... *quadriiceps* Santschi
- Lados de la cabeza, lados del pecíolo y tergos 1 y 2 del gáster lisos, y brillantes,  
sin escultura fina, con reflexiones azules (Fig. 12A); pecíolo (en perfil) con  
esquinas dorsales al mismo nivel (Fig. 1F)..... *mutica* Emery

**Clave para la identificación de los machos conocidos de *Dinoponera***

- 1 Largo total menos de 15 mm ..... *Pachycondyla* y otros poneroides
- Largo total más de 15 mm ..... 2
- 2 Proceso subpetiolar en forma de espina; pronoto fuertemente esculturado;  
formula palpal 5:3..... *Paraponera*
- Proceso subpetiolar no en forma de espina; pronoto liso, microesculturado;  
formula palpal 4:3..... 3
- 3 Ocelos muy hinchados en el margen occipital de la cabeza (Fig. 4A–D)..... 4
- Ocelos no muy hinchados en el margen occipital de la cabeza (Fig. 4E).....  
..... *australis* Emery
- 4 Funiculo con pelos alargados y rectos (Fig. 4F, G)..... 5
- Funiculo con pelos cortos, rígidos, y subdecumbentes, o con pubescencia  
diminuta (Fig. 4H, I, J) ..... 6
- 5 Lóbulo del dígito del volsela sin dientes en el ápice (Fig. 10C).....  
..... *gigantea* (Perty)
- Dígito del volsela sin lóbulo en el ápice (Fig. 10A)..... *quadriiceps* Santschi
- 6 Pigidio terminando en un espina, alargada y delgada (Fig. 4M); válvula peneal  
del aedeago en forma de cuña (Visto en perfil) (Fig. 11E)..... *longipes* Emery
- Pigidio terminando en una espina corta y ancha, en forma de triángulo  
(Fig. 4N); válvula peneal del aedeago con una reborde distal y un lóbulo tri-  
angular ventral (Fig. 11B) ..... *snellingi* sp. n.

**Chave para identificação de operários de *Dinoponera***

- 1 Esquina antero-inferior do pronoto com processo em forma de dente distinto  
(Fig. 1D)..... 2
- Esquina antero-inferior do pronoto sem processo em forma de dente  
(Fig. 1E) ..... 4



- 2 Cabeça, lados laterais do pecíolo, e tergas 1 e 2 do gáster lisos e brilhantes, com reflexões azuis (Fig. 12A)..... *lucida* Emery
- Cabeça, lados laterais do pecíolo, e tergas 1 e 2 do gáster finamente ponteados ou com escamas finas (Fig. 12B) ..... 3
- 3 Comprido total menos 3 cms..... *australis* Emery
- Comprido total mais de 3 cms ..... *gigantea* (Perty)
- 4 Corpo cobrido com cogumelos em forma de cerdas, que não são flagelados (Fig. 1C)..... *hispida* sp. n.
- Corpo cobrido com cogumelos finos e flagelados (Fig. 1B) ..... 5
- 5 Frons com pubescencia prendida e amarela-dourada (Fig. 1A) ..... *longipes* Emery
- Frons sem pubescencia amarelo prendido..... 6
- 6 Lados da cabeça, lados do pecíolo e tergas 1 e 2 do gáster finamente ponteados ou com escamas finas (Fig. 12B); pecíolo (em perfil) com o margem anterior-dorsal hinchado (Fig. 1G)..... *quadriceps* Santschi
- Lados da cabeça, lados do pecíolo e tergas 1 e 2 do gáster lisos e brilhantes, sem escultura fina, com reflexões azuis (Fig. 12A); pecíolo (em perfil) com esquinas dorsais ao mesmo nível (Fig. 1F)..... *mutica* Emery

### Chave para identificação de machos de *Dinoponera*

- 1 Comprido total menos de 15mm..... *Pachycondyla* e outro poneromorfos
- Comprido total mais de 15 mm..... 2
- 2 Processo subpetiolar em forma de espinha; pronoto fortemente esculturado; formula palpular 5:3 ..... *Paraponera*
- Processo subpetiolar não em forma de espinha; pronoto liso, microesculturado; formula para palpular 4:3..... 3
- 3 Ocelos na margem occipital da cabeça muito inchados (Fig. 4A–D) ..... 4
- Ocelos na margem occipital da cabeça não muito inchados (Fig. 4E)..... *australis* Emery
- 4 Funículo com cogumelos alongados e retos (Fig. 4F, G) ..... 5
- Funículo com cogumelos curtos, rígidos, e subdecumbentes, ou com pubescencia minuta (Fig. 4H, I, J)..... 6
- 5 Lóbulo do dígito do volsela sem dentes no ápice (Fig. 10C)... *gigantea* (Perty)
- Dígito do volsela sem lóbulo no ápice (Fig. 10A) ..... *quadriceps* Santschi
- 6 Pigídio acabado numa espinha, alongada e delgada (Fig. 4M); válvula penal do aedeago em forma de cunha (visto em perfil) (Fig. 11 E)..... *longipes* Emery
- Pigídio acabado numa espinha apara e alarga, em forma de triângulo (Fig. 4N); válvula penal do aedeago com um reborde distal e um lóbulo triangular ventral (Fig. 11B) ..... *snellingi* sp. n.

***Dinoponera australis* Emery**

[http://species-id.net/wiki/Dinoponera\\_australis](http://species-id.net/wiki/Dinoponera_australis)

Figs 4E, J, O, 5D, 9D, 10D, 11D, 13

*Dinoponera grandis* subsp. *australis* Emery, 1901: 48, worker, BRAZIL: S. Paulo: Avandava [5 syntypes workers examined, MCSN]; additional syntypes from PARAGUAY: Rio Apa, (leg.) Balzan, (leg.); ARGENTINA: Misiones, 1881, Berg (leg.), Giabibiri, Misiones, marzo 1884 G. Bove (leg.); Santschi, 1921: 85 (male); raised to species, Borgmeier, 1937: 227.

*Dinoponera grandis* subsp. *australis* var. *brevis* Santschi, 1928: 416, PARAGUAY: Reichensperger (leg.) [type worker examined, NHMB]. Unavailable name, junior synonym of *D. brevis*: Kempf, 1971: 387.

**Subspecies.** *Dinoponera australis bucki* Borgmeier, 1937:228. BRAZIL: Rio Grande do Sul: Palmeira [types not available].

*Dinoponera australis nigricolor* Borgmeier, 1937:228. BRAZIL: Goyaz: Campinas [types not available].

**Worker diagnosis.** This species is most easily recognized by the antero-inferior corner of pronotum having a distinct tooth-like process (Fig. 1D), the pilosity being short and relatively sparse and the integument being finely micro-sculptured and dull (Fig 12B). In addition the scape length is shorter than the head width and the total body length is under 30 mm. *Dinoponera lucida* could be confused with *D. australis* in that it also has a tooth-like process on the pronotum and can have a TBL under 30 mm, but differs in having the smooth and shiny integument, long flagellate hairs on lobe and forward slanting dorsal edge of petiole.

**Description of the worker.** Measurements (mm) (n=21) TBL: 23.42–29.31 (26.21); MDL: 3.59 – 4.31 (3.88); HL: 4.51–5.64 (4.99); HW: 4.31–5.74 (4.89); SL: 4.31–5.02 (4.73); WL: 6.25–7.69 (7.12); PL: 1.79–2.26 (2.03); PH: 2.56–3.28 (2.90); PW: 1.59–1.95 (1.75); GL: 7.28–9.64 (8.20); HFL: 5.54–6.66 (6.16). A description of the external morphology of the worker is given by Kempf (1971):

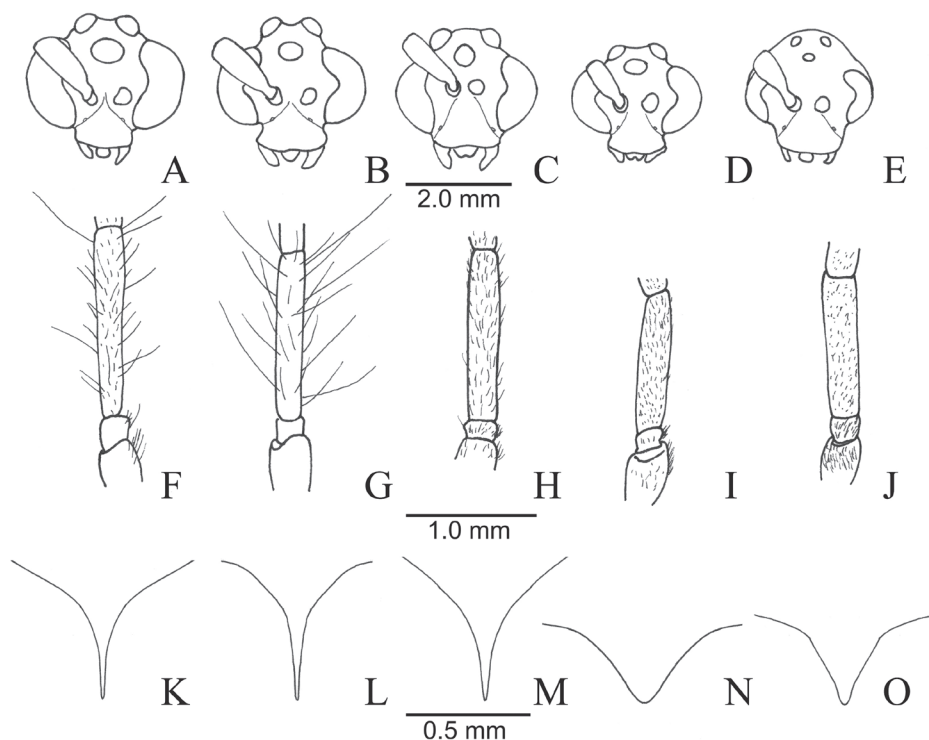
"Antennal scape length equal to, or shorter than head width. Pubescence on front of head short and inconspicuous. Gular face of head subopaque, finely reticulate-punctate throughout; the fine, arcuate striae variably developed from completely covering the undersurface of head to only vestigially shown antero-laterally or nearly absent. Sides of head reticulate-punctate, subopaque. Antero-inferior corner of pronotum dentate. Pronotal disc superficially reticulate and quite shining; paired swellings either feeble or distinct. Length of hind tibia equal to or less than head length. Petiole, in dorsal view, subquadrate, width over length proportion always more than 0.80, notably shorter and broader than in the other species; its shape...resembling that of *mutica*, with the upper anterior and posterior corners equally rounded; finely reticulate, somewhat shining; vertical sulcus on posterior surface either absent or more rarely vestigial to feebly developed. Terga I and II of gaster either reticulate-punctate or more superficially reticulate (in the southern range of the territory) and accordingly either subopaque or somewhat shining: fine appressed pubescence lacking

completely on disc of the terga, present on the sides. Stridulatory file on acrotergite of tergum II of gaster well developed, broad and triangular, extending back to the acrotergite for about one half to two thirds of its length."

**Male diagnosis.** *Dinoponera australis* males are recognized by their rounded head, with compound eyes, reduced ocelli and the posterior margin around the ocelli not protruding as in other species (Fig. 4E). This species is also characterized by the short, broad pygidial spine (Fig. 4O), volsella with tear-drop shaped basal lobe covered in minute teeth (Fig. 10D) and aedeagus with a latero-apical fold, notches and teeth along ventral edge as shown in Fig. 11D.

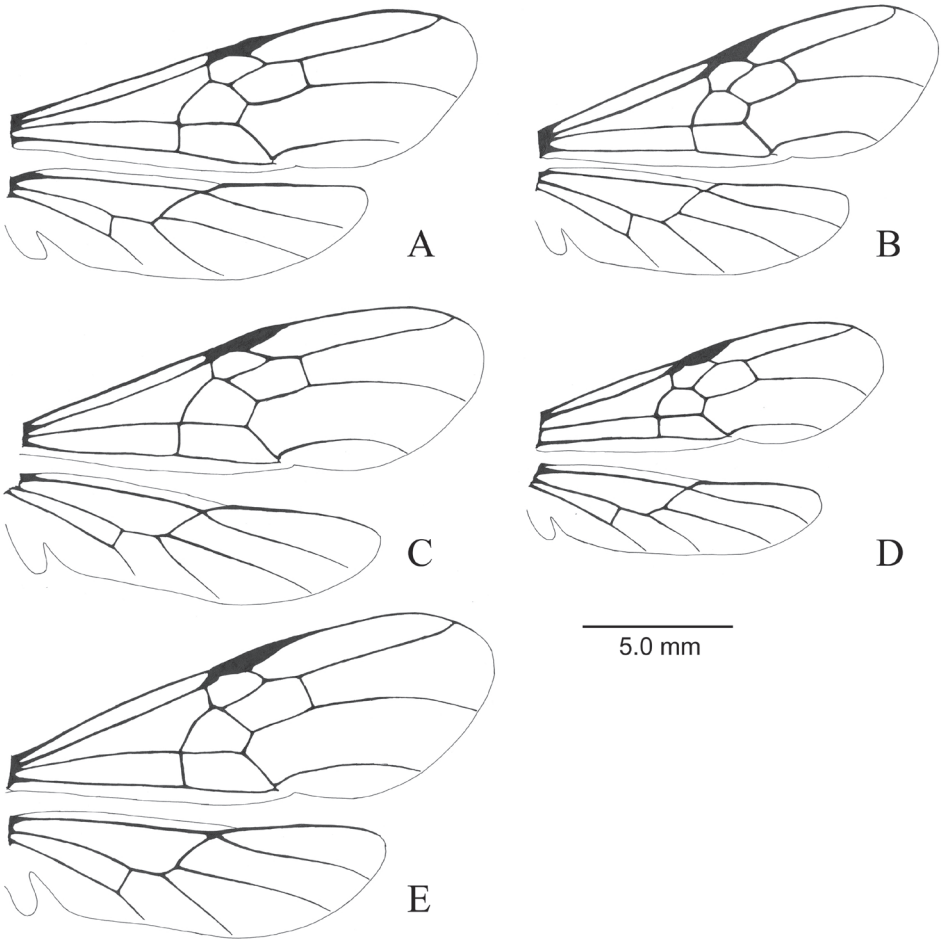
**Description of the male.** A description of the external morphology of the male is given in Kempf (1971):

"Head...with smaller eyes, the maximum interocular width being greater than their diameter; with smaller ocelli not protruding above the posterior border of head when seen in full-face view; antennal scape very short, less than twice as long as broad; funiculi without standing hairs; petiole distinctly shorter although variable in outline...; pygidium with a very short spine, not projecting beyond the long cerci; hypopygidium apically broadly truncate, the truncation either straight, or convex, or concave."



**Figure 4.** Features of *Dinoponera* males. **A–E** Head, frontal view **F–J** Right scape, first and second funicular segments, frontal view **K–O** Pygidial spine, dorsal view **A, F, K** *D. gigantea* **B, G, L** *D. quadriceps* **C, H, M** *D. longipes* **D, I, N** *D. snellingi* **E, J, O** *D. australis*.

**Description of the male genitalia.** Basal ring with thick dorso-anterior loop structures, reduced; parameres short, broad, rounded, small lobe on dorsal edge, emarginated ventro-basal edge (Fig. 9D); cuspis volsellaris with few bumps or teeth, digitus volsellaris with numerous small circular bumps at distal lateral face, tuft of setae on ventro-distal side of broad cusp, large tear-shaped lobe on basal ventral corner, covered in minute teeth (Fig. 10D); penis valve of aedeagus with lateral arm of apodeme at anterior border, no ventral concavity under ridge at base of apodeme, dorsal edge rounded, sloping posteriorly, ventro-anterior triangular projection followed by circular notch, ventral projecting tooth, smaller hemispherical notch with sclerotized border, thin, finely serrated distal edge, noticeable lateral apical fold with slight serration ending ventrally in serrated ridge, rounded un-serrated lobe at distal apex of valve.



**Figure 5.** Wings of known males. **A** *D. quadriceps* **B** *D. snellingi* **C** *D. gigantea* **D** *D. australis* **E** *D. longipes*.

**Distribution.** *Dinoponera australis* has the widest known range of the *Dinoponera*. This species is found in the department of Santa Cruz in Bolivia, southern Brazil in the states of Mato Grosso, Goiás, Minas Gerais, São Paulo, Mato Grosso do Sul, Paraná, Santa Catarina and Rio Grande do Sul, eastern Paraguay in the departments of Itapúa, Alto Paraná and Guairá, as well as the province of Misiones in Argentina (Fig. 13).

**Discussion.** *Dinoponera australis* is the most aberrant of the *Dinoponera* species because of its relatively small size, sparse non-flagellate pubescence, as well as the male characters stated above which distinguish this species. The male coloration difference is the basis for the designation of the subspecies *D. australis bucki* and *D. a. nigricolor*. These may be separate species or the product of intra-specific variation, but this cannot be diagnosed here as the types designated by Borgmeier (1937) were not available to us and the extent of intra-specific variation could not be determined from the limited sample size available.

**Material examined.** ARGENTINA, MISIONES: Iguazú (1 w, 4–10.x.1927, RC and EM Shannon, USNM); Iguazú Falls (2 w, 20–22.i.1920, CUIC); Loreto (1 w, N Kusnezov, USNM); Loreto malaise trap in subtropical wet forest (3 w, i.2001, P Fidalgo, FSCA); Parque Nacional Iguazú (3 w, 24.xii.1988, DH and AC Kistner, LACM); Parque Nacional Iguazú Cantera old gravel pit at forest edge 200m (18 w, 8.xii.1990–6.i.1991, S and J Peck, FMNH); Parque Nacional Iguazú Puerto Canoas hill forest 200m (30 w, 8.xii.1990–6.i.1991, S and J Peck, FMNH); Parque Nacional Iguazú Puerto Canoas river forest 180m (35 w, 2 m, 8.xii.1990–6.i.1991, S and J Peck, FMNH); Puerto Iguazú 100m (1 w, 25.xi–8.xii.1983, A Bordón, MCZC); Santo Pipó (1 w, N. Kusnezov, MCZC); locality not specified (1 w, USNM). BOLIVIA, SANTA CRUZ: Ayacucho (1 w, 13.x.1987, P Bettella, LACM); Buena Vista (1 w, 8.iv.1950, LE Pena, CUIC); Buena Vista (1 w, 20.ii.1999, L Stange, FSCA); Lomas de Arena Biol. Park (4 w, 10.ii.1999, LA Stange, FSCA); Velasco, Santa Cruz de la Sierra (1 w, J Steinbach, MCZC); Santa Cruz de la Sierra (1 w, 23.iv.1989, G Morales, LACM). BRAZIL, GOIAS: Anápolis (1 w, 12.ii.1936, G Fairchild, MCZC); 24 km E Formoso (1 w, 29.v.1956, FS Truzal, LACM); (1 w, 30.iv.1956, FS Truxal, LACM); Parque Nacional da Chapada dos Veadeiros (1 w, 29.xi.1989, J Cuellar, LACM); Parque Nacional da Chapada dos Veadeiros 18–24km N of Alto Paraiso 1400–1500m (1 w, 2–5.x.1985, SE Miller, LACM), Parque Nacional da Chapada dos Veadeiros, 18–24km N of Alto Paraiso 1400–1500m (1 w, 22.iv.1956, FS Truxal, LACM); MATO GROSSO: Rio das Mortes nr. São Felix do Araguaia (1 w, 1944, JV Ca, MCZC); MATO GROSSO DO SUL: 24 km W Campo Grande loose on ground (1 w, 7.xi.1989, WP Mackay, CWEM); 6 km SE Campo Grande nest in soil (2 w, 8.xi.1989, WP Mackay, CWEM); 8 km SE Ponta Purá, loose on ground (2 w, 15.xi.1989, WP Mackay, CWEM); 3 km NW Taunay, loose on ground (1 w, 17.xi.1989, WP Mackay, CWEM); Urucum, Corumbá (1 w, 23–29.xii.1919, CUIC); SÃO PAULO: Corumbataí, loose on ground (1 w, 6.xi.1989, WP Mackay, CWEM); RIO GRANDE DO SUL: Passo Fundo (1 w, 10.iii.1939, PA Berry, USNM). PARAGUAY, ALTO PARANÁ: Villa Encarnación (1 w, 10.i.1905, CASC); GUAIRÁ: Rogue González (1 w, 14.i.1995, B. Garcete and Alex Wild, LACM).

***Dinoponera gigantea* (Perty)**

[http://species-id.net/wiki/Dinoponera\\_gigantea](http://species-id.net/wiki/Dinoponera_gigantea)

Figs 1D, 4A, F, K, 5C, 9C, 10C, 11B, C

*Ponera gigantea* Perty, 1833: 135, pl. 27, Fig. 3. (worker) BRAZIL: Amazonas, Rio Negro [type not found]; Kempf, 1971: 372 (male); combination in *Dinoponera*, Roger, 1861:38.

*Ponera grandis* Guérin-Méneville, 1838: 206 (worker) [type not found]; combination in *Dinoponera*, Roger, 1861:38; junior synonym of *gigantea*: Roger, 1861: 38; Kempf, 1971:371. Emery, 1911: 219 (male); Wheeler, G.C. and Wheeler, J. 1985: 387 (larvae).

**Worker diagnosis.** *Dinoponera gigantea* can be distinguished from other *Dinoponera* species by the following combination of character states: antero-inferior corner of pronotum with distinct tooth-like process (Fig. 1D); integument finely micro-sculptured and not shiny (Fig. 12B); drab pilosity notably dense, long and flagellate; scape length longer than head width; total body length over 30 mm. *Dinoponera gigantea* is the largest species in the genus reaching up to 3.6 cm total body length. *Dinoponera gigantea* can be separated from all but two species by the presence of a tooth-like process on the antero-inferior corner of the pronotum. *Dinoponera lucida* and *D. australis* have a tooth-like process on the pronotum, but are smaller (usually less than 30 mm). In addition *D. lucida* has a shiny integument and *D. australis* lacks the long, flagellate pubescence.

**Description of the worker.** Measurements (mm) (n=15) TBL: 31.62–36.02 (34.34); MDL: 4.59–5.35 (4.92); HL: 5.89–6.65 (6.31); HW: 5.74–6.27 (6.00); SL: 5.95–6.43 (6.30); WL: 8.71–9.94 (9.35); PL: 2.72–3.06 (2.81); PH: 3.08–3.67 (3.59); PW: 1.85–2.07 (1.98); GL: 9.43–12.24 (10.94); HFL: 8.10–9.3 (8.74). A description of the external morphology of the worker is given in Kempf (1971):

"Length of scape exceeding maximum width of head. Pubescence on front of head quite dense yet inconspicuous, not concealing the integument. Gular (ventral) surface of head reticulate-punctate throughout, very finely striate in front, the striae strongly converging mesad toward the anterior border. Sides of head reticulate-punctate, subopaque. Antero-inferior corner of pronotum dentate. Pronotal disc reticulate-punctate, subopaque, the paired swellings rather inconspicuous, but the median impression between swellings distinct, integument irregularly wrinkled. Tarsus I of hind leg longer than maximum head length. Petiole reticulate-punctate and subopaque, rectangular in profile, the anterior surface straight to slightly concave; the anterior upper corner more narrowly, the posterior corner more broadly rounded; posterior surface with the vertical sulcus always distinct; in dorsal view the petiole is decidedly longer than broad, width-length proportion below 0.80. Terga I and II of gaster opaque, sharply reticulate-punctate, densely foveolate (from each foveola arises a short decumbent hair), with scattered, bristle bearing, larger pints. The appressed pubescence, although inconspicuous, is densely spread over the entire terga, stridulatory file on acrotergite (portion of tergum that is normally concealed under the overlapping preceding tergum)



of tergum II short, narrow, inconspicuous, not crossing beyond anterior half of acrotergite (hence not easily seen if entire acrotergite is not exposed)."

**Male diagnosis.** Males of this species are easily recognized by their funiculus which is covered in long standing setae (Fig. 4F), shiny dark reddish brown integument and the combination of a long pygidial spine (Fig. 4K), volsella with two basal teeth, lobed end of digitus volsellaris (Fig. 10C) and deep concavity on the side of the penis valve of the aedeagus (Fig. 11C).

**Description of the male.** A description of the external morphology of the male is given in Kempf (1971). Measurements done by Kempf (1971) are included as only one male *D. gigantea* was examined by us while the measurements of Kempf (1971) most likely represent the means of the four males examined in that study:

"Measurements in millimeters: total length 22.0; maximum length of head capsule 2.48; maximum width of head (eyes included) 3.10; maximum diameter of eyes 1.86; scape length 0.93; length of funicular articles I: 0.21, II: 1.86; Weber's length of thorax 7.12; hind femur length 5.57; hind tarsus I length 5.38; petiole length 2.16, width 1.24, height 1.76; tergum I of gaster length 3.09, width 2.88; fore wing length 15.6; hind wing length 12.15. Chestnut brown, smooth and shining except funiculi, clypeus, front, tibiae and tarsi which are finely punctuate to reticulate-punctate; terga III and following of gaster weakly, superficially and finely reticulate. The entire insect covered with long, subdecumbent, silky pubescence, except funiculi where the pubescence is minute. Standing hairs long and abundant on body, lacking on mid-dorsum of terga II-V of gaster; long hairs on scapes rather numerous, length not much longer than twice the diameter of scape... Anterior border of labrum rounded, not visibly excised... Pygidial spine long and well developed. Parameres (gonostyli) of genitalia in side-view narrow and spear-pointed... Hypopygium (subgenital plate of subandrium) apically rounded..."

**Description of male genitalia.** Basal ring with wide dorso-anterior loop structures, dorsal depression on basal ring posterior to cleft between dorso-anterior loops, ridge extending from anterior of depression to center; parameres long, narrow, rounded spade-shape, emarginated ventro-basal edge (Fig. 9C); volsella with finger-like cuspis volsellaris and broad cusp-like digitus volsellaris, cuspis volsellaris with pointed end, flange extending on dorsal edge, digitus volsellaris with numerous small circular bumps, lobe on postero-dorsal edge, 2 teeth on medial ventro-basal corner of volsella, posterior tooth with lobe on posterior edge; penis valve of aedeagus with lateral arm of apodeme at anterior border, deep, wide, ventral concavity under ridge at base of apodeme, distal edge of valve wedge-shaped, proximal ventral edge of valve ending in tooth descending at roughly 45°, ventral edge with large laterally curved lip, serrated edge (Fig. 11C), serrations facing laterally on either side of aedeagus in dorsal view (similar to penis valve in Fig. 8A).

**Distribution.** *Dinoponera gigantea* has been found on the coast of Guyana, in the Brazilian states of Amazonas, Pará including Marajo Island, Mato Grosso and Maranhão as well as the Loreto Province in Perú. *Dinoponera gigantea* is reported to be common in un-flooded forests in the vicinity of Belém, Pará (Kempf 1971, Overal 1980) (Fig. 13). It is probable that *D. gigantea* is found in French Guyana, Surinam,



Venezuela and southeastern Colombia because these regions are adjacent to known *D. gigantea* localities and have similar lowland rainforest habitat. However, no specimens from these nations are known to us, perhaps as a result of a lack of sampling or the range is absent from Colombia and southwestern Venezuela.

A record from Rio de Janeiro (from the CASC) is puzzling as it is disjunct from the known range of *D. gigantea*. The most southeastern locality for *D. gigantea* is over 1,480 km to the nearest portion of the state of Rio de Janeiro. In addition, Rio de Janeiro is in a well collected area where no other *Dinoponera* have been found. The label reads 'R.d.Janeiro, Brazil, D. Davis' and the specimen agrees in all morphological characters with *D. gigantea*. This locality is omitted from the species' range map (Fig. 13) because of its questionable nature. If other collections can validate this locality it would mean a significant range extension for *D. gigantea*.

**Discussion.** *Dinoponera gigantea* is a valid species with a distinct suite of morphological characters listed in the diagnosis above. The validity of *D. gigantea* is strengthened by range overlaps with *D. longipes* and actual sympatry with *D. hispida*, both with no integration of morphological characters.

**Material examined.** BRAZIL, PARÁ: Belém (6 w, v.1924, FX Williams, LACM, 7 w, vi.1924, FX Williams, LACM, USNM, 1 w, i.1938, GN Wolcott and LF Martorell, USNM, 1 w, 19.ix.1943, MCZC, 1 w, vii.1961, WA Burk, LACM, 1 w, 17.iii.1964, CE and ES Ross, CASC, 1 w, 16.ii.1975, ES Ross, CASC, 1 m, 21.vii.1979, JO Schmidt, LACM); Belém APEG Forest flight trap (1 w, 29.vii-6.viii.1974, DG Young, FSCA); Braganza (1 w, HB Merrill, USNM); Jabaty (1 w, v.1924, JF Illigworth, LACM); Marajo Island (3 w, viii-x.1907, HB Merrill, FMNH); Mocajuba (1 w, 9.xii.1926, EG Holt, USNM); Peixe Boi (1 w, viii-x.1907, HB Merrill, FMNH); Ríó Guamá nr. Belém (20 w, 10.xii.1976, CL Hogue, LACM); Tucuuruí Margem esq. (1 w, 16.iii.1979, WL Overal, LACM); Utinga tract nr. Belém (1 w, 2.viii.1962, PF Darlington, MCZC); Souza (2 w, but the 16.ix.1920, LACM, AMNH); locality not specified (1 w, HB Merrill, LACM); locality not specified (2 w, 1954, WM Mann, LACM, USNM), 4 w, Baker, MCZC, CUIC, USNM, 4 w, Thayer Expedition, AMNH, 1 w, G Franch, AMNH); RIO DE JANEIRO: locality not specified (1 w, D Davis, CASC); State and locality not specified (1 w, HH Smith and T Pergande, USNM). GUYANA, CUYUNI-MAZARUNI: Dist. Bartica Kalacoon (1 w, 1916, AMNH).

***Dinoponera hispida* sp. n.**

[urn:lsid:zoobank.org:act:83696C4B-912A-4833-ACFD-A59E9CCD4D11](http://urn:lsid:zoobank.org:act:83696C4B-912A-4833-ACFD-A59E9CCD4D11)

[http://species-id.net/wiki/Dinoponera\\_hispida](http://species-id.net/wiki/Dinoponera_hispida)

Figs 1C, G, 2, 13

**Worker diagnosis.** Distinguished from other species by the following combination of character states: conspicuous bristle-like setae covering the entire body but most pronounced on the dorsum of the head, mesosoma, petiole and gaster (Fig. 1C); fine striations on dorsum of the head; integument smooth and shiny with bluish luster most

visible on sides of the head (Fig. 12A); antero–inferior corner of pronotum without tooth-like process (Fig. 1E); petiole bulging at antero-dorsal corner; insertions of setae on dorsum of petiole raised, papillate (Fig. 1G).

**Description of the worker.** Measurements (mm) (n=5) TBL: 30.39–31.83 (31.08); MDL: 4.20–4.51 (4.38); HL: 5.64–6.05 (5.86); HW: 5.02–5.33 (5.19); SL: 6.05–6.36 (6.22); EL: 1.23–1.33 (1.27); EL: 0.72–0.97 (0.84); WL: 7.89–8.71 (8.36); PL: 2.5–2.56 (2.52); PH: 2.87–3.18 (3.05); PW: 1.33–1.54 (1.47); GL: 9.69–10.15 (9.95); HFL: 7.89–8.41 (8.14). (See Fig. 2) Entire body with short, thick, stiff, subdecumbent to erect setae (Fig. 1C); integument black, smooth, shiny, appearing polished with bluish luster (Fig. 12A). Head: mandibles long, linear, 7-toothed, large diastema between basal tooth and six apical teeth; clypeus with two laterally projecting teeth on anterior edge, bulges medially, extends posteriorly between frontal lobes, sparse appressed setae from distal edges to disc of clypeus, short stiff setae on anterior edge; large bilobed labrum; ventral surface of head with varying amounts of fine striation, erect bristle-like setae; gena with fine striations running from eye into clypeus; median furrow running from termination of clypeus between frontal lobes to shallow pit in middle of frons (with ocelli in two individuals of type series); frontal lobes raised and conspicuous, with striations at posterior constriction; antennae all with erect bristle-like setae, funiculus covered in minute appressed pubescence; scape long, extending past posterior border of the head, covered in erect bristle-like setae; frons with sparse pads of short appressed setae; entire head covered with erect to subdecumbent bristle-like setae. Mesosoma: antero-inferior corner of pronotum rounded, without tooth-like process; pronotal disc with slight bulges; mesonotum fused with propodeum and episternum, separated by slight furrows; basilar sclerite large, ovaloid; propodeum with broadly rounded dorsal outline; propodeal spiracle nearly vertical slit; sulcus running from center of propodeum along lower edge of propodeal spiracle to posterior edge of propodeum at dorsal edge of bulla; mesosoma and coxae with white pubescence, especially dense on basilar sclerite, appressed white pubescence along dorsal surface facing medially, middle posterior dorsum of pronotum lacking appressed pubescence found on mesonotum and propodeum. Legs: long, femur and tibia with sparse erect bristle-like setae. One well-developed, antennae cleaning, comb-like spur on fore leg; spine-like and less developed denticular comb on mesothoracic leg; spine and comb-like spur on hind leg, posterior side of fore leg basitarsus with dense pads of golden setae; tarsus or mesothoracic and hind leg with short, stiff setae, tarsal claws bidentate. Petiole: large and tabular with narrow attachments at base to the propodeum and gaster, narrow in dorsal view; fine erect setae on anterior surface above articulation with mesosoma; bulging at antero-dorsal corner as in *D. longipes*; integument nitid, papillate at insertion of setae on dorsal surface; keel-like subpetiolar process, anterior triangular projection (Fig. 1G). Gaster: small protuberance at articulation of gastral sternite III and the petiole, covered in erect setae; stridulatory file of varying size on acrotergite of gastric tergum II; covered in bristle-like setae, sparse short appressed setae on terga I and II; polished integument; posterior edges of the pygidium and hypopygidium with characteristic rows of spines.

**Male.** Unknown.

**Distribution.** Known only from the type locality (Fig. 13).

**Discussion.** *Dinoponera hispida* is considered a valid species based on the above mentioned morphological characters, as well as its sympatry with *D. gigantea* without any visible character integration. Based on the morphological character states *D. hispida* is most similar to *D. longipes* and *D. mutica*. *Dinoponera longipes* differs greatly in the setae which are flagellate and golden, completely lacks gular striations and lacks the raised insertions of setae on the petiole. *Dinoponera mutica* also differs in pilosity, possessing drab-colored flagellate pubescence and lacks the bulging antero-dorsal corner and papillate dorsum of the petiole.

**Etymology.** *hispida*, from the Latin *hispidus*: bristle, referring to the conspicuous bristle-like setae covering the frons and body.

**Type series.** Holotype worker (MCZC) BRAZIL, Pará: Tucuruí, I.1979, Coll. M. Alvarenga; Paratypes (CASC, CWEM, LACM, MZSP) BRAZIL, Pará, Tucuruí, I.1979, Coll. M. Alvarenga" (1 worker). "Brasil Pará Tucuruí Margem esq. 21.II.1979, Brasil Pará, WL Overall, Várzea" (1 worker). "Pará Tucuruí, 20.VIII.1979, Brazil PA, R B Neto" (1 worker). "Pará Tucuruí, 19.VIII.1979, km 28, Brasil Pará WL Overall" (1 worker).

### *Dinoponera longipes* Emery

[http://species-id.net/wiki/Dinoponera\\_longipes](http://species-id.net/wiki/Dinoponera_longipes)

Figs 1A, B, 3, 4C, H, M, 5E, 8, 9E, 10E, 11E, 13

*Dinoponera grandis* subsp. *longipes* Emery, 1901: 48 Holotype worker PERÚ: Cumbase (MCSN) [examined]. Raised to species: Kempf, 1971: 375.

**Worker diagnosis.** This species can easily be recognized by the golden luster of its conspicuous long, flagellate hairs especially on the frons. In addition this species has the following combination of character states: pronotal corner rounded without tooth-like process (Fig. 1E), no gular striations, a reflective, smooth and shiny integument (Fig. 12A). All specimens have a petiole which bulges on the dorso-anterior edge except for those from the Rio Madeira and Rio Negro in Brazil.

**Description of the worker.** Measurements (mm) (n=16) TBL: 30.85–34.75 (32.83); MDL: 4.61–5.33 (4.89); HL: 5.48–6.87 (6.12); HW: 5.23–5.84 (5.57); SL: 5.54–6.56 (6.23); WL: 7.84–9.33 (8.51); PL: 2.46–2.82 (2.64); PH: 2.77–3.59 (3.28); PW: 1.44–1.85 (1.67); GL: 9.02–12.20 (10.67); HFL: 7.48–8.87 (8.36). A description of the external morphology of the worker is given in Kempf (1971):

"Antennal scape from slightly shorter to slightly longer than maximum head width (index: scape L/head W × 100 = 94–103). Pubescence on front of head (as well as on thorax and dorsum of gaster) golden brown, very dense and rather long. Gular face of head smooth and shining, without vestiges of striae antero-laterally. Antero-inferior corner of pronotum obtusely angulate, not dentate. Pronotal disc smooth and shining, but densely covered with piligerous punctulae;

paired swellings from faint to distinct; integument not wrinkled. Tarsus I of hind leg decidedly longer than maximum length of head capsule. Petiole smooth and shining; shape resembling that of quadriceps. . . , dorsal surface faintly to distinctly slanted backwards; width-length proportion distinctly lower than 0.80: vertical sulcus on posterior surface present in specimens from Acre Territory, Brasil, absent in specimens seen from Perú. Terga I and II of gaster smooth and shining but densely covered with punctulae from which arises the long and dense pubescence that covers the entire segments. Stridulatory file on acrotergite of Tergum II of gaster very short but broadly triangular, not extending backwards beyond the anterior half of acrotergite."

**Male diagnosis.** Distinguished from other *Dinoponera* by the following combination of character states: funiculus of antennae with short, thick decumbent setae (Fig. 4H); pygidial spine (Fig. 4M) shorter than in *D. gigantea* and *D. quadriceps* but longer and narrower than in *D. australis* and *D. snellingi*, volsella with broad basal lobe covered in minute teeth (Fig. 10E).

**Description of the male.** Previously undescribed. Measurements (mm) (n=2) TBL: 19.78, 21.12; HL: 2.10, 2.26; HW: 2.67, 2.77; SL: 0.92, 0.92; EL: 1.49, 1.59; EW: 0.923, 0.923; WL: 6.66, 6.66; FWL: 17.43, 15.38; HWL: 13.12, 11.48; PL: 1.90, 2.05; PH: 1.38, 1.54; PW: 0.97, 1.03; GL: 9.12, 10.15; HFL: 5.23, 5.54. (See Fig. 3) Integument: smooth and shining reddish brown, mesosoma slightly darker than head, petiole, gaster. Head: Mandibles reduced, rounded and broad, lacking teeth; palps elongated; labrum reduced, emarginated on distal margin, covered with setae. Clypeus large, triangular, bulging medially, covered in appressed to subdecumbent setae; anterior tentorial pits large; frontal carinae reduced to slight ridge along antennal socket; antennal sockets close, located at posterior apex of clypeus. Antennae reddish brown; funiculus covered in minute appressed pubescence with thicker bristle-like decumbent setae; scape shorter than second funicular segment, 1<sup>st</sup> funicular segment reduced. Compound eyes large, along lateral side of head, deeply emarginated border medially, ocelli bulging beyond margin of head, depressed area between posterior ocelli. Entire head covered in short decumbent to erect setae, longer hairs on clypeus and around ocelli (Fig. 4C). Mesosoma: covered in long dense suberect to decumbent setae; pronotum triangular, exposed narrowly dorsally below scutum; scutum of mesonotum large, bulging antero-dorsally, with 3 longitudinal ridges; small tegula over insertion of forewing; scutellum domed, sides with vertical ridges, dorsal surface smooth; basilar sclerite under hind wing, reduced; fused mesopleuron, separated by furrow with mesosternite; metanotum, exposed between scutellum and propodeum, reduced; mesoepimera, mesoepisternite and propodeum fused, rounded; coxa large, conical, covered in long, dense subdecumbent to decumbent setae. Wings: covered in dense minute setae, venation as shown in Fig. 5E. Legs: dark reddish brown integument; covered in minute subdecumbent to decumbent stiff setae; one well-developed, antennae cleaning, pectinate spur on fore leg; spine-like and less developed denticular comb on meso-thoracic leg; spine and comb-like spur on hind leg; tarsal claws bidentate. Petiole: dark brown, narrow attachments at base to propodeum and gaster; petiole humped dorso-posteriorly; subpetiolar process reduced, bulging slightly posteriorly, covered in long erect setae. Gaster: large, cylindrical; covered in fine silvery suberect to

subdecumbent setae, longer on first tergite and all sternites; first gastric tergite rounded, elongated; pygidium terminating in short spine with a broad base, narrow tip, shorter than in *D. gigantea*; cerci short, covered in erect setae; tabular subgenital plate with posterior truncate and slightly emarginated with rounded corners. Genitalia: (Fig. 8) basal ring with wide, thin dorso-anterior loop structures; parameres long, narrow, rounded distally, emarginated ventro-basal edge (Fig. 9E); cuspis volsellaris finger-like with slight raised rounded bumps, digitus volsellaris broad cusp with numerous small circular bumps, roughly triangular lobe at ventro-basal corner of volsella covered in minute teeth (Fig. 10E); penis valve of aedeagus with lateral arm apodeme at anterior border, ventral concavity under ridge at base of apodeme, ridge recurving dorsally near distal edge of penis valve, distal edge wedge-shaped, proximal ventral edge of valve ending in downward facing tooth, ventral edge serrated with large dorsally curved lip (Fig. 11E), serrations facing laterally on either side of aedeagus in dorsal view (Fig. 8A).

**Distribution.** *Dinoponera longipes* have been collected in eastern Perú in the departments of Loreto, Amazonas, Huánuco, San Martín and Pasco, as well as Ecuador in the province of Pastaza. In Colombia it has been recorded near the Peruvian border in the department of Amazonas. In Brazil, *D. longipes* has been found in Acre, Amazonas as far east as Manaus, as well as along the Rio Madeira in Rondônia (Fig. 13).

**Discussion.** Doubt was raised by Kempf (1971) as to whether *D. longipes* was a valid species. Since few specimens have been collected from western Brazil a clinal variation in character form with *D. gigantea* or *D. mutica* was a possibility (Kempf 1971). The specimens we have examined from Brazil show no such integration. Additionally, evidence of species validity comes from the unique morphology of the male. Among the holdings at the CASC, males were located with 20 worker specimens from Tingo María, Departamento de Huánuco, Perú; all *D. longipes*. The nearest known locality of another species is *D. gigantea* 550 km away at Estirón Rio Ampiacu in the Departamento de Loreto, Perú. There is a possibility that these could be males of a yet undiscovered species. However, relatively intensive collecting of *Dinoponera* in the area by numerous collectors has not revealed any other form.

**Material examined.** BRAZIL, AMAZONAS: Uypiranga Rio Negro, 14 km from Manaus, 81 m (1 w, x.1941, A Rabaut, AMNH); Tabatingo (2 w, MCZC, CUIC); União Rio Madeira (1 w, iii.1921 or 1922, WM Mann, USNM); RONDÔNIA: Porto Velho, Rio Madeira (1 w, Mann and Baker, USNM). COLOMBIA, AMAZONAS: 18 km N Leticia (1 w, 25.ii.1974, Sand J Peck, MCZC); Leticia (1 w, x.1977, F Castaño, CWEM); Leticia, Rio Tacana, loose on ground (1 w, 3.viii.2002, L Mejia, UNAB); 5 km N Zaragoza (1 w, 18.ix.1988, F. Fernández, CWEM); El Encanto, (9 w, 25.viii.1920, CUIC, LACM, MCZC, AMNH);, La Sombra to El Encanto, (2 w, 23.viii.1920, CUIC, AMNH). ECUADOR, PASTAZA: Moretecocha Ex. Barrido plataforma (1 w, 1–7. vi.1996, J Naranjo, QCAZ). PERÚ, AMAZONAS: Km 292–296 E of Montenegro Olmos-Maranón Hwy 700–800m (3 w, 21.i.1964, PC Hutchison and JK Wright, CASC); Montenegro, Bagua 350m (3 w, 29.ix–2.x.1963, Wygodzinsky, AMNH); MADRE DE DIOS: Cueva de Castillo nr. Tingo María 600 m (3 w, 7.viii.1982, JM Wilson, LACM, 1 w, 31.x.1970, J Schuster, LACM); Tingo María 670 m (1 w, Weyrauch, MCZC);



Tingo María 2200 ft. (1 w, 8.x.1946, JC Pallister, AMNH) (3 w, 12.x.1946, JC Pallister, AMNH, 1 w, 28.x.1946, JC Pallister, AMNH, 1 w, 23.v.1947, JC Pallister, AMNH, 1 w, 1.vi.1947, JC Pallister, AMNH, 1 w, xii.1949, HA Allard, USNM, 2 w, 27.ix.1952, NA Wells, CASC); Tingo María, Monson Valley (1 w, 18.ix.1954, EI Schlinger and ES Ross, CASC, 3 w, 23.ix.1954, EI Schlinger and ES Ross, CASC, 1 w, 8.x.1954, EI Schlinger and ES Ross, CASC, 2 w, 10.x.1954, EI Schlinger and ES Ross, CASC, 1 w, 19.x.1954, EI Schlinger and ES Ross, CASC, 1 w, 21.x.1954, EI Schlinger and ES Ross, CASC, 1 m, 2.xi.1954, EI Schlinger and ES Ross, CASC, 1 w, 3.xi.1954, EI Schlinger and ES Ross, CASC, 1 w, 9.xii.1954, EI Schlinger and ES Ross, CASC, 1 m, 11.xii.1954, EI Schlinger and ES Ross, CASC, 3 w, 15.xii.1954, EI Schlinger and ES Ross, CASC, 1 w, 23.xii.1954, EI Schlinger and ES Ross, CASC, 1 w, 13–17.ix.1956, C Gregoire, USNM, 1 w, 11.viii.1960, DA Young, USNM, 1 w, 16.v.1964, CE and ES Ross, CASC, 1 w, 9–12.iii.1967, WL Brown, MCZC); Parque Nacional de Tingo María, Cueva de las Lechuzas tropical rainforest window trap (1 w, 8–16.i.1983, A Newton and M Thayer, MCZC); Parque Nacional de Tingo María, Cueva de las Lechuzas, sweeping (1 w, 11.viii.1985, JF Cornell, LACM); 14 km N Tingo María (1 w, 7.ii.1984, WN Mathis, USNM); Parque Nacional de Tingo María, 6 km W Tingo María (1 w, 9.ii.1984, WN Mathis, USNM); 12km SW Tingo María (1 w, 12–15.viii.1985, JF Cornell, LACM); Parque Nacional de Tingo María, 660 m (3 w, 11–17.iv.1987, JE Eger, FSCA); Tambello Chico Canyon, 13km S Tingo María, 800 m (1 w, vi.1983, CM Stevens, FSCA); LORETO: Amazon Camp Rio Momón, nr. Iquitos, 97.5 m (1 w, 1–10.xii.1982, ES Ross, CASC); Amazon Conservatory for Tropical Studies, 70 km NE Iquitos, extracted from nest, lowland tropical wetforest (1 w, 9.vii.2002, RC Morgan, CASC); Amazon Safari Camp Nr. Iquitos (1 w, 25.vi.1980, CL Hogue, LACM); Aventurama Camp Rio Napo/Rio Yagua (2 w, one infected with fungus, CL Hogue, LACM); Boquerón 500m (5 w, 7–14.vii.1965, J Schunke, LACM); Explornapo Camp 100mi NE Iquitos (1 w, 15.vii.1990, S Dunkle, FSCA); Rio Napo at Sucusnui (1 w, 13.vii.1985, CL Hogue, LACM); PASCO: Río Iscozazin (1 w, 8–19.vii.1961, FS Truxal, LACM); SAN MARTIN: Tarapoto (9 w, A Vasquez, AMNH); UCAYALI: Balta Rio Curanja (2 w, vii.1966, A Gardner, FSCA); department not specified, Upper Rio Huallaga (1 w, 29.x.1925, H. Bassler, AMNH, 1 w, 30.x.1925, H. Bassler, AMNH, 1 w, xi.1930, H Bassler, AMNH); DEPARTMENT NOT SPECIFIED, Upper Rio Marañon (2 w, Orton, CASC, MCZC), Rio Marañon (1 w, 10.vii.1930, AMNH); Rio Santiago (1 w, 15.ix.1923, AMNH, 1 w, 17.xi.1923, AMNH); Middle Rio Ucayali (3 w, 1.x.1929, H Bassler, AMNH).

### ***Dinoponera lucida* Emery**

[http://species-id.net/wiki/Dinoponera\\_lucida](http://species-id.net/wiki/Dinoponera_lucida)

Figs 1H, 13

*Dinoponera grandis* subsp. *lucida* Emery, 1901: 48. Syntype workers BRASIL: Espírito Santo, ex coll Fruhstorfer. (MCSN) [examined]. (specific locality of Vila Velha (Cidade do Espírito Santo) proposed by Kempf (1971). Raised to species: Kempf 1971: 376.

**Worker diagnosis.** This species can be recognized by the following combination of character states: anterior inferior pronotal corner with tooth-like process (Fig. 1D), pilosity long and flagellate with white luster, integument smooth and shiny with bluish luster (Fig. 12A), scape length longer than head width, petiole slanting obliquely on dorsal edge (Fig. 1H). Total body length ranges from 27–30mm which is between the lengths of *D. australis* and the other larger species.

**Description of the worker.** Measurements (mm) (n=5) TBL: 27.01–30.39 (28.64); MDL: 3.79–4.31 (3.97); HL: 4.92–5.64 (5.34); HW: 5.02–5.13 (5.07); SL: 5.23–5.64 (5.42); WL: 7.33–8.20 (7.84); PL: 2.25–2.51 (2.39); PH: 3.18–3.28 (3.26); PW: 1.54–1.90 (1.72); GL: 8.00–10.05 (9.10); HFL: 6.87–7.28 (7.18). A description of the external morphology of the worker is given in Kempf (1971):

"Antennal scape distinctly longer than head width. Pubescence on front and vertex of head variable, either short and inconspicuous or longer, denser and quite visible. Gular surface of head finely striate either throughout or at least on anterior half; very seldom the striae are confined to a narrow stripe along the anterior border and obsolescent yet still discernible. Sides of head smooth, not quite glossy but with a silky sheen on account of the superficial reticulate microsculpture. Antero-inferior corner of pronotum dentate. Pronotal disc smooth and shining, lacking wrinkles and dense, fine punctulae; paired swellings quite distinct. Hind tarsus I decidedly longer than head length. Petiole...smooth and polished, its anterior face not excavate, its dorsal face slanted forward; vertical sulcus on posterior face either present or absent; width-length proportion well under 0.80; anterior face lacking dense pubescence. Terga I and II of gaster smooth, highly shining, lacking dense, fine punctulae; pubescence loosely scattered on sides, entirely absent on disc. Stridulatory file on acrotergite of tergum II well developed, nearly crossing the entire tergite."

**Male.** Unknown.

**Distribution.** This species inhabits fragments of Atlantic rainforest in the Brazilian state of Espírito Santo, across the border into Minas Gerais, the southern portion of Bahia and São Paulo (Fig. 13). It is possible that *D. lucida* exists in Rio de Janeiro but we are not aware of any specimens from this area. Refer to Mariano et al. (2008) for information on the biogeography of this species. With the locality data available *D. lucida* is the only species with no known range overlaps with other *Dinoponera* species.

**Discussion.** *Dinoponera lucida* appears to be a valid species based on the unique suite of characters including a tooth-like process on the pronotum, smooth and shiny integument, long and flagellate pilosity and petiole slanting forward on the dorsal edge. However, the limited sample size (n=5) restricts the certainty with which we can assert that *D. lucida* is a separate species because a broad spectrum of intraspecific variation may not be represented. There may be a possibility of character integration with *D. australis* in the area between the states of São Paulo and Rio de Janeiro. *Dinoponera lucida* is only slightly larger than *D. australis* but differs in its integument micro-sculpturing and pilosity type (see the diagnosis above). *Dinoponera lucida* can be confused with *D. australis* but is distinguished by its shiny integument and whitish setae, as opposed to the micro-sculptured integument and dull tan setae of *D. australis*.

*Dinoponera lucida* has been classified as endangered in Brazil by the Ministério do Meio Ambiente (Campiolo et al. 2003) due to habitat destruction in the Atlantic forest.



**Material examined.** BRAZIL, BAHIA: Itabuna, Itapebi 177 m (1 w, ii.1999, JRM Santos, CASC); ESPÍRITO SANTO: Santa Tereza (1 w, 24.xi.1954, A Ruschi, MCZC); MINAS GERAIS: Ataléia (1 w, 27.i.1994, I Cardoso, LACM).

***Dinoponera mutica* Emery**

[http://species-id.net/wiki/Dinoponera\\_mutica](http://species-id.net/wiki/Dinoponera_mutica)

Figs 1E, F, 12B, 13

*Dinoponera grandis* subsp. *mutica* Emery, 1901: 48 Syntype workers, BRAZIL: Mato Grosso, Germain (leg.) (MCSN) [examined] (specific locality of Rondonópolis proposed by Kempf (1971); Wheeler, G.C. and Wheeler, J. 1952: 607 (larvae.); raised to species Kempf, 1971: 378.

**Worker diagnosis.** *Dinoponera mutica* is identified by its smooth and shiny integument with a bluish luster (Fig. 12A), a rounded pronotal corner lacking a tooth-like process (Fig. 1E), gular striations on the ventral surface of the head, long and flagellate pubescence, scape length longer than head width and petiole with even dorsal corners (Fig. 1F).

**Description of the worker.** Measurements (mm) (n=12) TBL: 29.42–32.34 (30.99); MDL: 4.10–5.48 (4.71); HL: 5.13–6.30 (5.65); HW: 5.13–5.64 (5.39); SL: 5.43–6.05 (5.72); WL: 7.53–8.61 (8.20); PL: 2.26–2.67 (2.41); PH: 2.82–3.38 (3.17); PW: 1.54–1.90 (1.76); GL: 8.61–11.99 (10.06); HFL: 7.18–8.00 (7.60). A description of the morphology of the worker is given in Kempf (1971):

"*Antennal scape remarkably longer than head width. Pubescence on front and vertex generally longer and denser than in gigantea, but lacking the golden luster on longipes. Gular face smooth and shiny, with fine, more or less distinct striation antero-laterally and antero-mesially (sometimes nearly effaced). Sides of head smooth and shining in spite of the very fine, superficial microsculpture which is reticulate-punctate. Antero-inferior corner of pronotum obtusely angulate or rounded. Pronotal disc smooth and shiny, lacking irregular fossae and wrinkles; the paired swellings rather weakly expressed. Tarsus I of hind leg decidedly longer than head width. Petiole of distinctive shape..., shorter than that of gigantea and longipes, but width-length proportion still under 0.08; anterior and posterior upper corners subequally rounded; smooth and shining; vertical sulcus on posterior face usually obsolete, present only in one Bolivian specimen. Terga I and II of gaster very indistinctly, superficially and finely reticulate-punctate yet quite smooth and shining, lacking the dense foviolae of longipes on disc where the pubescence is likewise scarce. Stridulatory file well-developed, triangular but short, visible only when acrotergite of tergum II is fully exposed.*"

**Male.** Unknown.

**Distribution.** *Dinoponera mutica* is found in central South America in the Brazilian states of Rondônia, Mato Grosso, Goiás and Mato Grosso do Sul, in eastern Bolivia and northwest Paraguay (Fig. 12).

**Discussion.** *Dinoponera mutica* is a valid species based on our study. *Dinoponera quadriceps* is the closest to *D. mutica* in terms of morphological characters and is not synonymized in this work because of the differences stated in the diagnosis above. Males of *D. mutica* may provide further support for separation from *D. quadriceps*. *Dinoponera quadriceps* has a finely micro-sculptured integument which is not shiny (Fig. 12B), lacks gular striations and has a petiole which bulges on the dorso-anterior edge. *Dinoponera longipes* and *D. hispida* may also be confused with *D. mutica* but this species lacks the dense golden pubescence of the former, or the short, stiff setae and forward bulging petiole of the latter.

**Material examined.** BRAZIL, MATO GROSSO DO SUL: Corumbá (1 w, MCZC); Urucum, Corumbá (3 w, 23–29.xii.1919, LACM, CUIC); RONDÔNIA: 7 km NW Costa Marques (1 w, 16.xi.1986, R Wilkerson, FSCA); Schmitt Ranch (1 w, ix.1996, R. Rogers, PALC). BOLIVIA, SANTA CRUZ: Perseverancia (1 w, 18.iii.1990, P Bettella, LACM). PARAGUAY, BOQUERÓN: Enciso (1 w, T. del Sinne, CWEM).

### *Dinoponera quadriceps* Kempf

[http://species-id.net/wiki/Dinoponera\\_quadriceps](http://species-id.net/wiki/Dinoponera_quadriceps)

Figs 4B, G, L, 5A, 6A, 10A, 11A, 12B, 13

*Dinoponera quadriceps* Kempf, 1971: 380, first available use of *Dinoponera grandis* st. *mutica* var. *quadriceps* Santschi, 1921: 84; unavailable name, BRAZIL: Pernambuco: São Lourenço da Mata, Tapera (NHMB, examined).

*Dinoponera mutica* var. Mann, 1916, male

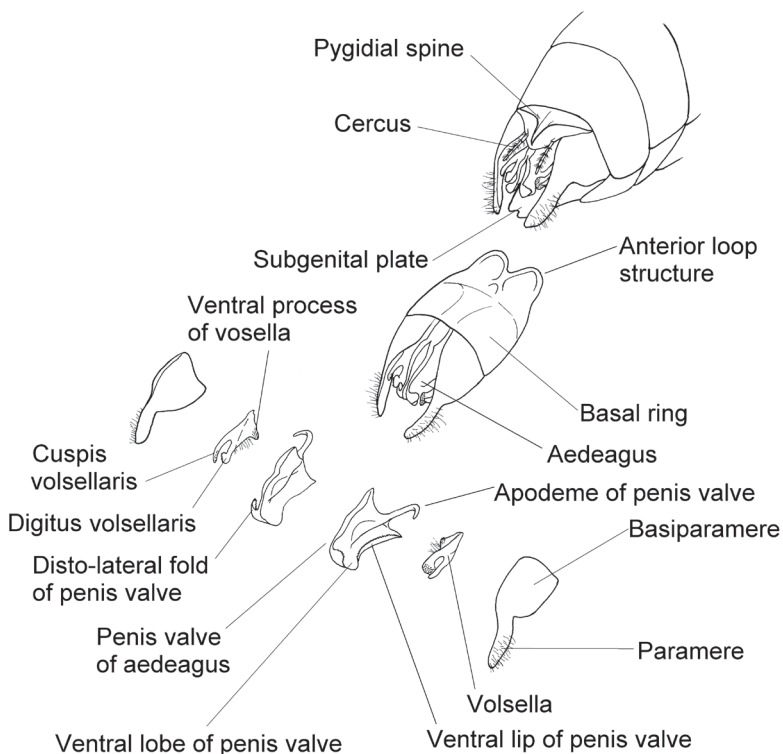
*Dinoponera gigantean mutica* var. *quadriceps* Borgmeier 1937 male designated BRASIL: Pernambuco, Tapera.

*Dinoponera opaca* Santschi, 1921. Holotype worker BRAZIL: Rio Janeiro (Goeldi) (1 w NHMB, examined); junior synonym of *D. quadriceps* Kempf 1975: 344

**Worker diagnosis.** This species is recognized by its finely micro-sculptured integument which is not shiny (Fig. 12B), rounded anterior inferior pronotal corner lacking a tooth-like process (Fig. 1E), ventral side of the head lacking any gular striations and long/flagellate pilosity.

**Description of the worker.** Measurements (mm) (n=17) TBL: 28.09–33.73 (30.60); MDL: 4.10–5.05 (4.53); HL: 5.23–6.04 (5.58); HW: 5.33–5.97 (5.56); SL: 5.54–6.12 (5.80); WL: 7.38–9.03 (8.20); PL: 2.26–2.68 (2.50); PH: 3.06–3.52 (3.26); PW: 1.64–1.99 (1.80); GL: 8.20–11.93 (9.80); HFL: 7.18–8.11 (7.65). A description of the worker is given in Emery 1911, Mann 1916, Borgmeier 1937, Kempf 1971. Presented below is that of Kempf (1971):

"Antennal scape notably longer than head width. Pubescence on front and vertex of head short and inconspicuous. Gular surface of head reticulate-punctate, subopaque, but lacking arcuate striae except for some cases when a few short and vestigial striae appear



**Figure 6.** Schematic drawing of generalized *Dinoponera* male genitalia *in situ*; genitalia capsule and disarticulated aedeagus, volsella and parameres.

antero-laterally, just behind the mandibular insertion. Sides of head reticulate-punctate, subopaque. Antero-lateral corner of pronotum obtusely angulate (very seldom subdentate). Pronotal disc reticulate-punctate, subopaque, occasionally slightly wrinkled, bristle pits irregular in outline; paired swellings very faint and obsolete. Hind tarsus I longer than head length. Petiole... of distinctive shape, the anterior surface being slightly inclined forward and often a bit excavate; anterior upper corner narrowly, the posterior corner very broadly rounded; integument minutely reticulate-punctate and subopaque; sulcus on posterior surface always distinct. Terga I and II of gaster reticulate-punctate and opaque; piligerous pits for pubescence discally greatly scattered (in a few southern specimens from Bahia State, these pits are stronger and denser, almost as in *gigantea*); coarse bristle-bearing pits greatly scattered: pubescence rather scarce on dorsum, denser and more conspicuous on sides. Stridulatory file on tergum II of gaster weakly developed, arising from the anterior border of acrotergite and running streak-like across the anterior half of the same (visible only when acrotergite is fully exposed; observed in five specimens)."

**Male diagnosis.** Males of this species are distinguished by the long fine setae of the second funicular segment (Fig. 4G), light brown coloration, long narrow parameres (Fig. 9A), volsella with two small basal teeth and lacking a lobe on the distal edge of digitus volsellaris (Fig. 10A).

**Description of the male.** Total length 21mm (Mann 1916) 22 mm (Borgmeier 1937). A description of the male is given in Emery (1911), Mann (1916), Borgmeier (1937), and Kempf (1971). Mann (1916) described the male as follows:

"Head, including the mandibles, as broad as long, very convex behind. Eyes very large and long occupying the entire sides of head, the inner border deeply emarginate; ocelli very large and convex. Clypeus convex, the anterior border truncate. Mandibles small, pointed at apex, with a small tooth at middle of inner border. Antennae a little shorter than the body; first funicular joint twice as broad as long; joints 2–11 very long, cylindrical, each slightly shorter and more slender than the preceding. Thorax [= mesosoma] robust; scutellum short, triangular, broadly rounded at apex. Epinotum [= propodeum] evenly rounded, without distinct base or declivity, unarmed. Petiole nearly twice as long as broad, narrowed in front, with nearly straight sides; in profile longer than high, flattened above...the anterior slope gradual, more abruptly sloping behind, the antero-ventral surface with a broad, triangular projection. Gaster long and slender, the three times the breadth. Genitalia prominent; the valves broad, rounded at apex; cerci long and slender...Wings large extending almost to the tip of gaster ... Legs very long and slender...Body and legs shining. Antennae opaque, coarsely, densely punctured; sparsely pubescent, and having much very long, fine erect hairs, which on the apical joints are shorter and confined to the tips; pubescence of apical joint more dense than the rest. Thorax (=mesosoma) with long silky pubescence, most abundant on the pleurae, and very fine re erect hairs sparsely distributed node without pubescence, but with abundant erect hairs. Gaster with a thick mat of silky pubescence, shorter and finer than that of the thorax (=mesosoma); lateral and apical portions with fine erect hairs... Color rufous, the antennal scape and the first five funicular joints fucous. Wings lightly infuscated, veins and stigma reddish brown. Pubescence yellowish white, exempt the long antennal hairs which are black."

To this Borgmeier (1937) added that the petiole was "rounded on top", "the sting of the pygidium [=pygidial spine] long; subgenital plate with apex slightly concave", and that the wings were 16mm long and "slightly yellowish". Kempf (1971) noted the dorsum of the gaster lacked standing hairs.

**Description of the male genitalia.** Basal ring with wide, thin dorso-anterior loop structures; parameres distinctly long, narrow, rounded end, emarginated ventro-basal edge (Fig. 9A); cuspis volsellaris finger-like with few rounded bumps on medial face, digitus volsellaris broad cusp-like with numerous small circular bumps, 2 teeth at ventro-basal corner of volsella (Fig. 10A); penis valve of aedeagus with lateral arm of apodeme at anterior border, slight ventral concavity under ridge at base of apodeme, distal edge wedge-shaped, proximal ventral edge of penial valve ending in anterior facing tooth, ventral edge with large dorso-laterally curved lip with serrated edge, serrations facing laterally on either side of dorsally curved lip (similar to penis valve in Fig. 8A).

**Distribution.** *Dinoponera quadriceps* is found in the Caatingas, Cerrados, upland humid forest and Atlantic forest (Kempf 1971, Paiva and Brandão 1995) in the north-eastern Brazilian states of Alagoas, Bahia, Ceará, Paraíba, Pernambuco and Rio Grande do Norte (Fig. 13).

**Discussion.** *Dinoponera quadriceps* as characterized by Kempf (1971) is maintained as a valid species by our analysis. *Dinoponera quadriceps* may be confused with *D. mutica*, but has a finely micro-sculptured integument which is not shiny (Fig. 12B), lacks gular striations and has a petiole which bulges on the dorso-anterior edge in contrast to *D. mutica*'s roughly microsculptured integument, striated gula and petiole with even, non-bulging corners (Fig. 1F).

We also agree with the synonymy of *Dinoponera opaca* by Kempf (1975) after examination of the type. *Dinoponera quadriceps* and *D. mutica* differ in micro-sculpturing, gular striations and petiole shape. Distribution records show a distance of over 900 km between the two species, but if specimens are found with an integration of characters in the area of Tocantins and northern Goias than these species should be synonymized.

**Material examined.** BRAZIL, ALAGOAS: Pedra (1 w, viii.1939, A Muller, AMNH); CEARÁ: Tianguá (1 w, 6.iv.1972, JS Bowman, MCZC); PARÁ: Óbidos (1 w, ii.1981, CWEM); Rio Tapajoz region (1 w, viii.1983, CWEM); Santarém (1 w, 20.v.1984, CWEM); PARAIBA: Independencia (1 w, 1 m, Mann and Heath, USNM, 2 w, LACM); João Pessoa (4 w, 21.iv.1975, J Kesselring, CASC, 1 w, i.1976, BA Bkaul, CWEM); João Pessoa forest of Gargau primary forest on ground 45m (1 w, 22.i.1981, G Ekis, MCZC); RIO GRANDE DO NORTE: Baixa Verde (2 w, WM Mann, USNM, 1 w, gift of Wheeler, MCZC); Ceara-Mirim (1 w, 1 m, WM Mann, USNM); Natal (6 w, WM Mann, AMNH, LACM, MCZC, USNM); São José do Bonfim (1 w, 22.iii.1945, HT Dalinat, LACM); state not specified, North Piari (1 w, vi–vii.1944, L Parker, MCZC).

### *Dinoponera snellingi* sp. n.

[url:lsid:zoobank.org:act:791CAB8B-6A94-47FD-B379-5CC85D1A9947](http://www.zoobank.org/act:791CAB8B-6A94-47FD-B379-5CC85D1A9947)

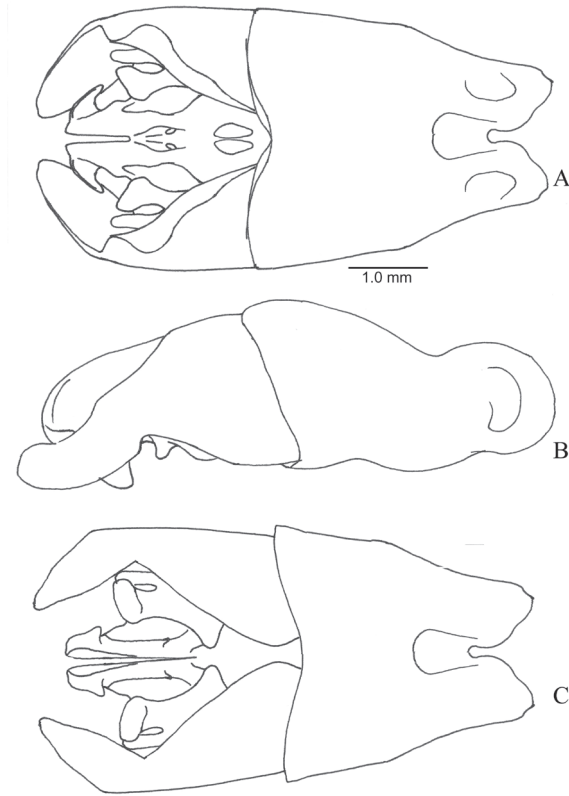
[http://species-id.net/wiki/Dinoponera\\_snellingi](http://species-id.net/wiki/Dinoponera_snellingi)

Figs 4D, 4I, 4N, 5B, 7, 9B, 10B, 11B, 13

**Worker.** Unknown.

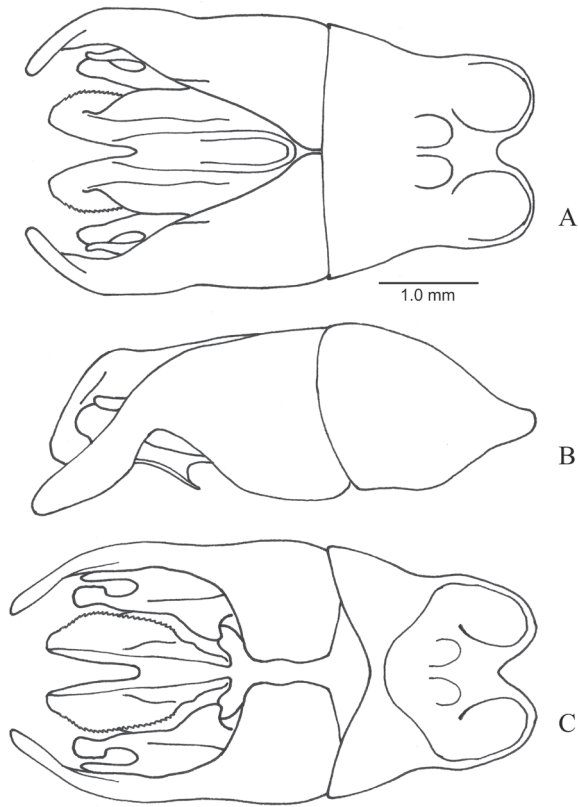
**Male diagnosis.** Specimens of this species are distinct in several respects. The combination of a bicolored body and head possessing bulging compound eyes and ocelli (Fig. 4D) is unique to this species. More definitive is the shape of the aedeagus which possesses a large ventral lobe and finger-like serrated flange (Fig. 11B). The short broad digitus volsellaris with finely toothed basal lobe (Fig. 10B) is distinctive, as well as the paramere shape (Fig. 9B).

**Description of the male.** Measurements (mm) (n=3) TBL: 16.14–17.09 (16.58); HL: 1.90–2.05 (1.98); HW: 2.36–2.51 (2.44); SL: 0.62–0.72 (0.65); EL: 1.23–1.38 (1.32); EW: 0.72–0.82 (0.79); WL: 5.54–6.05 (5.77); FWL: 13.33–13.63 (13.43); HWL: 9.93–10.46 (10.25); PL: 1.44–1.54 (1.49); PH: 1.13–1.23 (1.16); PW: 0.92–1.13 (1.04); GL: 6.66–7.18 (6.94); HFL: 4.20–4.92 (4.54). Integument: smooth and shining; head, mesosoma and petiole dark brown to black; gaster light brown. Head:



**Figure 7.** *Dinoponera snellingi* male genitalia. **A** dorsal view **B** lateral view **C** ventral view.

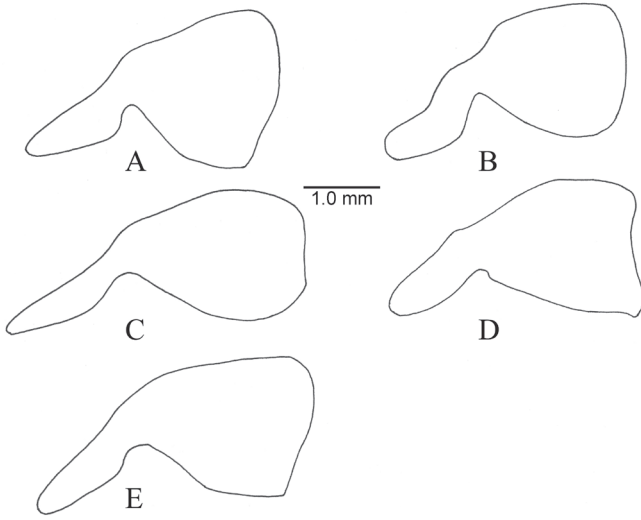
Mandibles reduced, rounded, lacking teeth, rounded lobe on ventro-basal edge, high lateral ridge running along axis; palps elongated; labrum reduced, deeply emarginated on distal margin, covered with setae. Clypeus large, triangular, bulging medially, covered in appressed to subdecumbent setae; anterior tentorial pits large; frontal carinae reduced to slight ridge along antennal socket; antennal sockets close, located at posterior apex of clypeus. Antennae: black; funiculus covered in minute, dense, stiff subdecumbent setae (Fig. 4I); scape shorter than second funicular segment, 1<sup>st</sup> funicular segment reduced. Compound eyes large, along lateral side of head, deeply emarginated border medially. 3 ocelli at posterior margin of head, bulging beyond margin of head, depressed area between posterior ocelli. Entire head covered in short decumbent to erect setae (Fig. 3). Mesosoma: covered in short suberect to decumbent white setae; pronotum triangular, exposed narrowly dorsally anterior to scutum; scutum large, bulging antero-dorsally, with 3 longitudinal carinae; small tegula over insertion of forewing; scutellum domed, with sparse erect setae, sides with vertical carina, dorsal surface smooth; basilar sclerite under hind wing reduced; fused mesopleuron, separated by furrow with mesosternite; metanotum exposed between scutellum and propodeum, reduced; mesoepimera, mesoepisternite and propodeum fused, rounded;



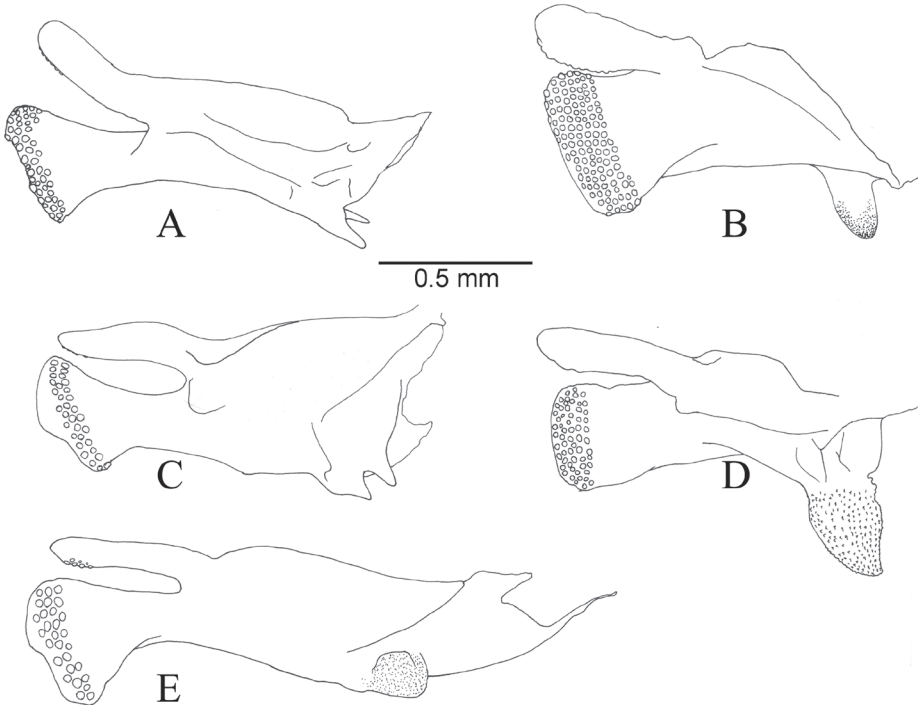
**Figure 8.** *Dinoponera longipes* male genitalia. **A** dorsal view **B** lateral view **C** ventral view.

coxa large, conical, covered in dense subdecumbent to decumbent setae. Wings: covered in dense minute setae, venation as shown in Fig. 5B. Legs: black, covered in minute subdecumbent to decumbent stiff setae; one well-developed, antennae cleaning, pectinate spur on the fore tibia; spine-like and less developed denticular comb on meso-thoracic tibia; spine and comb-like spur on hind tibia; tarsal claws bidentate. Petiole: narrow attachments at base to the propodeum and gaster; petiole humped dorso-posteriorly; subpetiolar process reduced, bulging slightly posteriorly. Gaster: large, cylindrical; covered in fine silvery suberect to subdecumbent setae; first gastric tergite broadly rounded; pygidium terminating in short, broad, triangular, spine (Fig. 4N); cerci short, as long as pygidial spine, covered in erect setae; tabular subgenital plate with posterior end rounded. Genitalia: (Fig. 7) basal ring with thick dorso-anterior loop structures, reduced; parameres short, broad, rounded, large lobe on dorsal edge, emarginated ventro-basal edge (Fig. 9B); volsella with rounded cuspis volsellaris with raised rounded bumps on medial-ventral surface, digitus volsellaris with numerous small circular bumps on lateral distal face, tuft of setae on ventro-distal edge, lobe on basal ventral corner, covered in minute teeth (Fig. 10B); penis valve of aedeagus with

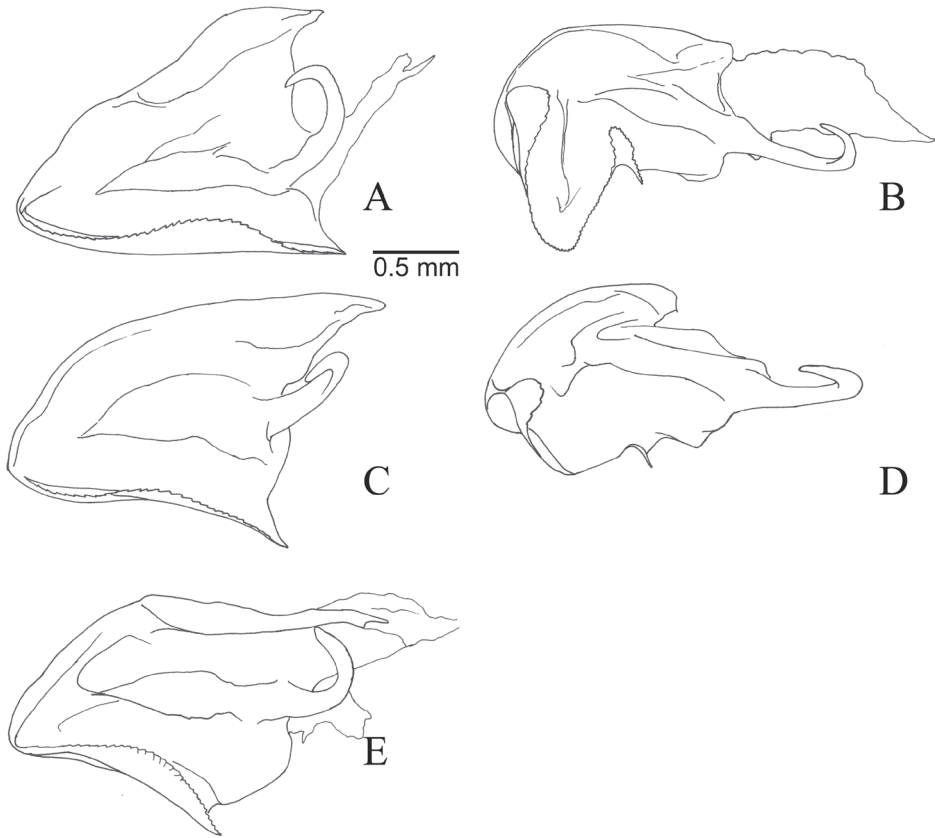




**Figure 9.** *Dinoponera* right basiparamere/paramere of known males, lateral view. **A** *D. quadriceps* **B** *D. snellingi* **C** *D. gigantea* **D** *D. australis* **E** *D. longipes*.



**Figure 10.** *Dinoponera* right volsella of known males, lateral view. **A** *D. quadriceps* **B** *D. snellingi* **C** *D. gigantea* **D** *D. australis* **E** *D. longipes*.

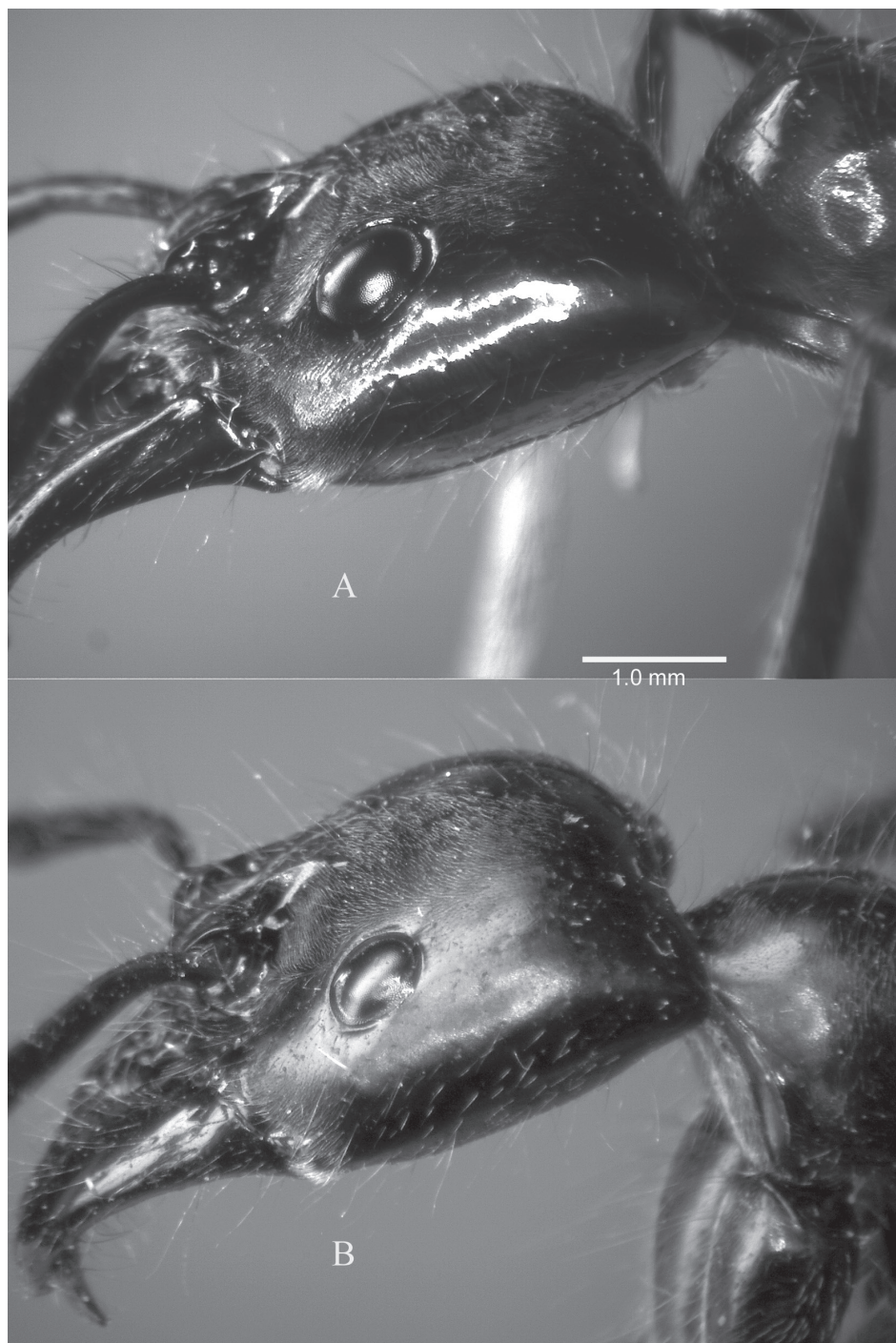


**Figure 11.** *Dinoponera* right penis valves from the aedeagus of known males. **A** *D. quadriceps* **B** *D. snellingi* **C** *D. gigantea* **D** *D. australis* **E** *D. longipes*.

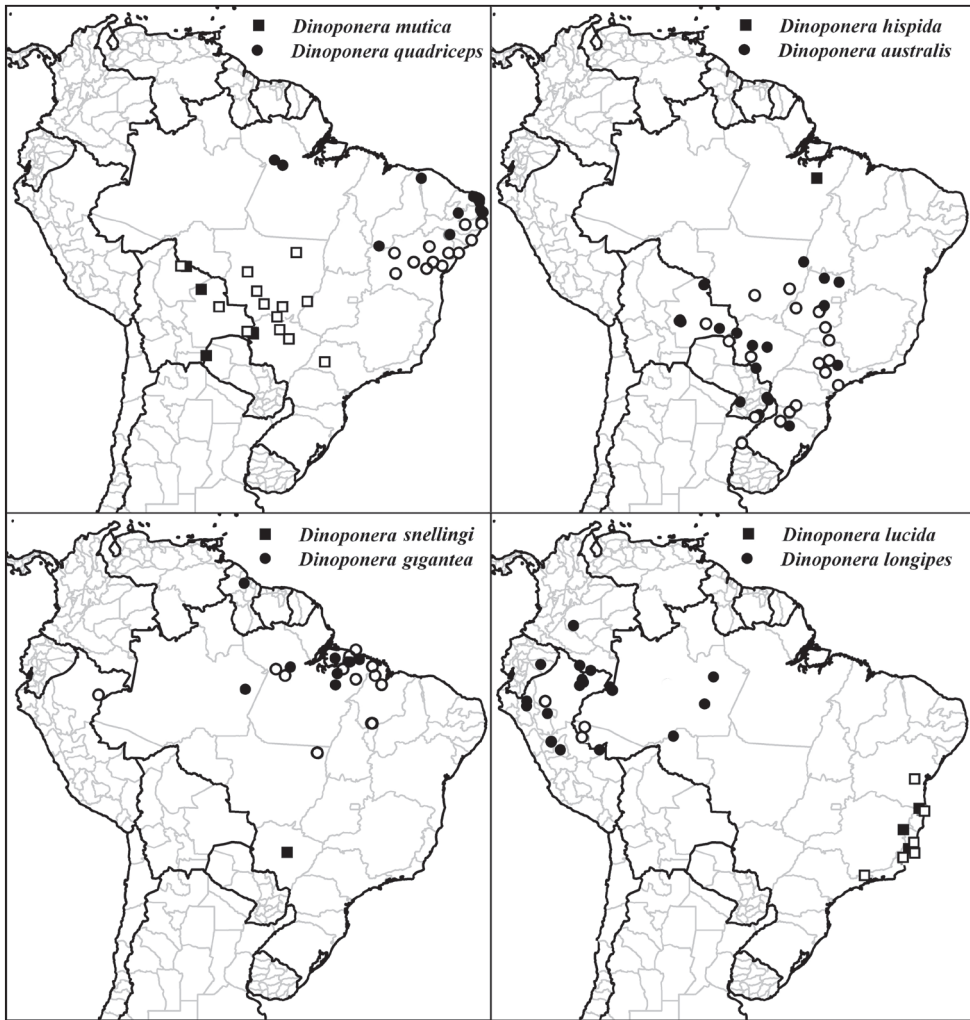
long lateral arm of aedeagal apodeme at anterior border, ventral concavity under ridge at base of apodeme, dorsal edge broadly rounded, ventral tooth projecting into thin anteriorly folded flange with heavy serration, rounded notch at base, large triangular ventral lobe with finely serrated edge and vertical ridge running through middle of lobe, edge of lobe continuing into lateral apical fold with serrated edge (Fig. 11B).

**Distribution.** Known only from type locality; Campo Grande, Brazil (Fig. 13).

**Discussion.** *Dinoponera snellingi* is a new species based on the suite of morphological characters presented in the diagnosis above. Most important are the shape of the aedeagus, volsella and parameres all of which we consider apomorphic characters. The type specimen males were unassociated with workers. Initially *D. snellingi* specimens were considered males of *D. australis*; as workers of this species were collected at the same location and at the same date (see *D. australis* materials examined). Additionally the specimens shared the same character states of bicoloration and short pygidial spine that Kempf (1971) used to designate *D. australis*. However, the size of the compound



**Figure 12.** Worker head, oblique antero-lateral view illustrating microsculpturing difference. **A** *Dinoponera mutica* (this smooth integument type is also found in *D. lucida*, *D. longipes* and *D. hispida*) **B** *D. quadriceps* (this rough integument type is also found in *D. gigantea* and *D. australis*).



**Figure 13.** Distribution map of *Dinoponera* species. Symbols in black are records added by this study; open symbols are from literature sources (Kempf 1971, 1975, Araujo et al. 1990, Peeters et al. 1999, Monnin and Peeters 1999, Fourcassié and Oliveira 2002, Monnin et al. 2003, Mariano et al. 2004, Araújo and Rodrigues 2006, Marques-Silva et al. 2006).

eyes (compare Fig. 4D and 4E), bulging ocelli at the posterior of the head (compare Fig. 4D and 4E), short broad volsella with large tear drop-shaped basal lobe (Fig. 10B) and penis valve of the aedeagus with disto-lateral process, disto-ventral lobe and serrated flange on the ventral edge (Fig. 11B) provide strong evidence supporting that these male specimens represent a novel species.

We have compared male specimens of *D. snellingi* with those of *D. australis* collected in nest series and found they differ in the characters listed above. Campo Grande is within the range of *Dinoponera mutica* and there is a possibility that these specimens represent the currently unknown males of *D. mutica*. However, the males of *D. snellingi*

are closest in character states to the male of *D. australis*, the worker caste of which differs greatly in many characters from the other known *Dinoponera* workers including *D. mutica* (see the *Dinoponera australis* discussion). Therefore we hypothesize that the male of *D. mutica* will most likely be similar to *D. quadriceps* or *D. longipes*, based on the similar worker morphology, and the unknown worker of *D. snellingi* will be similar to the worker of *D. australis*. Species groupings based on worker and male character states overlap; leaving *D. australis* with *D. snellingi* allied and separate from the other *Dinoponera* species. Until associated workers are discovered, we contend that it is better to describe these unique males rather than allow them to remain misidentified and unstudied or describe them as males of *D. mutica* with only anecdotal evidence as justification.

**Etymology.** Named in honor of the late Roy Snelling who made considerable contributions to the field and spirit of myrmecology.

**Type series.** Holotype deposited in MZSP, BRAZIL, Mato Grosso do Sul, Campo Grande, 12 Oct 1989, W.P. Mackay #12404, 2 paratypes, same locality, 8 Oct 1989, #12359 collected at house light (deposited in the CWEM and MCZC).

## Discussion

A synthesis of our understanding of *Dinoponera* morphological characters and geographic distribution supports the six species designations of Kempf (1971, 1975) as well as establishes the two new species *Dinoponera hispida* and *Dinoponera snellingi*. The collection records from material loaned to us, in conjunction with those found in previous works (Kempf 1971, 1975, Araujo et al. 1990, Peeters et al. 1999, Monnin and Peeters 1999, Fourcassié and Oliveira 2002, Monnin et al. 2003, Mariano et al. 2004, Araújo and Rodrigues 2006, Marques-Silva et al. 2006) establishes range overlaps between 7 species, including sympatry between *D. longipes*-*D. gigantea*, *D. gigantea*-*D. quadriceps*-*D. hispida* and *D. australis*-*D. snellingi*-*D. mutica*. *Dinoponera lucida* is the only species which has no sympatric records nevertheless, a record in the state of Bahia, Brazil comes within 62 km of *D. quadriceps*. In all cases there is no perceptible integration of characters.

Worker characters, though seemingly indistinct upon first inspection, allow relatively easy identification of *Dinoponera* species. The most important characters are the tooth on the antero-ventral corner of the pronotum, in conjunction with pilosity, microsculpturing and body size. In males the pilosity of the funiculus, paramere shape, lobes of the volsella and shape of penis lobe of the aedeagus are the differentiating characters.

Kempf (1971) questioned the stability of characters between species' ranges then thought of as being mutually exclusive. The areas between *D. longipes*, *D. mutica*, *D. quadriceps* and *D. gigantea* were specifically questioned. With the exception of *D. mutica*, our study has examined material that shows overlap between these ranges with no integration of characters used to define these species.

Despite the work presented here, many questions still remain in terms of *Dinoponera* taxonomy. The male caste is still undescribed in *D. mutica*, *D. lucida* and *D. hispida* and the worker caste is unknown for *D. snellingi*. These unknown castes likely exist



in the collections of Brazil and elsewhere. Ranges are roughly defined but our study revealed several vast range extensions and country records. As evident in Fig. 13, large areas of South America remain uncollected.

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