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The Baltic amber ant genus *Bradoponera* (Hymenoptera: Formicidae), with description of two new species and a reassessment of the Proceratiini genera

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The Baltic amber ant genus *Bradoponera* (Hymenoptera: Formicidae), with description of two new species and a reassessment of the Proceratiini genera. - Two new species of *Bradoponera* are described from Baltic amber. *B. wunderlichi* sp. n. is described on a single dealate gyne and *B. electrina* sp. n. on a single worker. *B. wunderlichi* resembles in general body shape and sculpture the sole previously known species of the genus, *B. meieri* Mayr. *B. wunderlichi* differs from *meieri* mainly by the antennae, 9-jointed instead of 12-jointed and by its smaller size. *B. electrina* is the most distinctive *Bradoponera* species by possessing at least two autapomorphies, the body with suberect hairs and the petiole narrow and rectangular in profile. *B. electrina* shares with *meieri* the 12-jointed antennae but the two species differ considerably in body shape and size. Description of these new species and re-discovery of the genus *Bradoponera* allow a set of improvements to the classification of the Ponerinae which were needed but impossible before. Among the main taxonomic conclusions made possible by the examination of *Bradoponera* material are, the first definition of a monophyletic ponerine clade corresponding to the "classic" tribe Proceratiini and characterization of its three component genera *Proceratium*, *Discothyrea*, and *Bradoponera* by at least one autapomorphy each.

Key-words: Hymenoptera - Formicidae - ants - *Bradoponera* - new species - Proceratiini - Baltic amber - fossils.

INTRODUCTION

The genus *Bradoponera* Mayr is known from one species only, *B. meieri* Mayr, described from 5 workers from Baltic amber (Mayr,1868). Wheeler (1915) examined 10 additional workers and redescribed the species giving additional details of the sculpture and described for the first time an ergatoid female.

Mayr (1868) considered *Bradoponera* to be close to *Proceratium* and Wheeler (1915) much more closely related to *Discothyrea*. *Proceratium* and *Discothyrea* are the sole two Recent genera constituting the tribe Proceratiini as it is currently understood (see later).

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Brown (1958) synonymized the Proceratiini with the Ectatommini, placing *Proceratium* and *Discothyrea* close to *Heteroponera*. In his conception *Bradoponera* was an intermediate step along this line.

Kugler (1991) by means of a cladistic analysis of six Ectatommini genera (*Paraponera*, *Acanthoponera*, *Gnamptogenys*, *Ectatoma*, *Proceratium* and *Discothyrea*) based on the morphology of the sting apparatus, suggests that *Proceratium* and *Discothyrea* are sister genera. Kugler (l.c.) listed eight synapomorphies linking these two genera together.

Lattke's (1994) phylogenetic study of the ectatommines based on 36 morphological characters, resurrects the tribe Proceratiini including in it *Proceratium* and *Discothyrea* only. On the basis of Mayr's (1868) description and Wheeler's (1915) notes, Lattke (1994) suggests the possibility that *Bradoponera* may represent the ancestral form of *Discothyrea*.

A re-analysis of Lattke's phylogeny by Keller (2000) takes strength from the consideration of 12 additional characters. All these characters, however, are invariant or uninformative within the subset of taxa considered in the present paper.

The crux of the problem, on the other hand, lies on the most probable phylogenetic position of *Bradoponera* and, as a consequence of this, on the possibility to identify two extant and one fossil Proceratiini genera, characterized by at least one clear autapomorphy each.

A concrete difficulty to reach this target is represented by the fact that internal morphological characters (like all those considered by Kugler, 1991) cannot be observed in the fossil *Bradoponera*.

The opportunity to examine five *Bradoponera* specimens, two of which representing two undescribed species, motivated us to attempt the present study.

MATERIAL AND METHODS

The morphological nomenclature, the measurements and their relative acronyms are those already defined by Baroni Urbani & de Andrade (2003) for the closely related genus *Proceratium*.

The following fossil specimens of *Bradoponera* were in 5 samples (4 of which already cut and polished) of Baltic amber. All samples originally belonged to the collection of Jörg Wunderlich, Straubenhardt (Baden-Württemberg, Germany) (JWCS). The holotypes of the two new species described in this paper were subsequently purchased from Dr Wunderlich by the Museo Regionale di Scienze Naturali of Turin (MRSN) in order to allow type deposition in a public collection.

BB-1 (fig. 1). A small, 1.3x0.8x0.3 cm, yellow sample containing a dealate *Bradoponera* gyne and a mite. The preservation condition of the ant is good and is only slightly hindered by a longitudinal fissure filled by whitish impurities.

BB-6 (fig. 2). A opaque-yellow small sample, 0.4x0.7x0.4 cm, containing only a *Bradoponera* worker. The preservation condition of the ant is good and many filaments run it on the left lower side and ventrally. A longitudinal fissure filled with whitish material is also present.

BB-4 (fig. 3). A yellow, slightly opaque sample, 1.2x0.9x0.4 cm, containing a *Bradoponera* worker and many small impurities. The preservation condition of the ant is good and only a few fissures reduce observation.

BB-7 (fig. 4). A transparent yellow sample, 0.8x0.7x0.3 cm, containing a worker of *Bradoponera*, a dipteran and many small impurities. The preservation condition of the ant is good and only a longitudinal fissure filled with whitish material close to the head affects slightly its view.

BB-8 (fig. 5). A large yellow sample, 3.0x1.8x0.7 cm, containing a *Bradoponera* worker, a ponerine male?, a dipteran, many air bubbles and fissures. The preservation condition of the ant worker is good and only a longitudinal fissure runs along its right side, rendering impossible this view.

To assess the distribution of some characters of presumed importance in reconstructing the phylogenetic relationship of *Bradoponera* with its most closely related genera, we examined also Recent material of the other two Proceratiini genera, *Proceratium* and *Discothyrea*, and of the following genera used for the outgroup comparison: *Paraponera*, *Ectatomma*, and *Gnamptogenys*.

Our character coding for the analysis is drawn from examination of the following species:

Bradoponera: three species, i. e. all known ones.

Proceratium: 4 fossil and 73 recent species, i. e. all known species except *longigaster* Karavaiev.

Discothyrea: *Discothyrea* sp. (Darjeeling, India, Naturhistorisches Museum, Basel), *oculata* Emery, *sauteri* Forel, *sculptior* Santschi, *sexarticulata* Borgmeier, *stumperi* Baroni Urbani, †*gigas* de Andrade, i. e. ca. 25% of the known species.

Paraponera: *clavata* (Fabricius) and †*dieteri* Baroni Urbani, i. e. all known species.

Ectatomma: *brunneum* Smith, *edentatum* Roger, *lugens* Emery, *muticum* Mayr, *opaciventre* (Roger), *permagnum* Forel, *ruidum* (Roger), *tuberculatum* (Olivier), i. e. ca. 60% of the known species.

Gnamptogenys: *Gnamptogenys* sp. (two different species, both from Queensland, Australia, both in Naturhistorisches Museum, Basel), *aculeaticoxae* Santschi, *annulata* (Mayr), *arcuata* (Santschi), *bispinosa* (Emery), *bruchi* (Santschi), *continua* (Mayr), *curtula* (Emery), *gracilis* (Santschi), *haenschei* (Emery), *horni* (Santschi), *magnifica* (Santschi), *menozzii* (Borgmeier), *moelleri* (Forel), *mordax* (Smith), *pleurodon* (Emery), *porcata* (Emery), *rustica* (Santschi), *striatula* Mayr, *strigata* (Norton), *teffensis* (Santschi), *tornata* (Roger), *tortuolosa* (Smith), *triangularis* (Mayr), *wasmanni* (Santschi), *wheeleri* (Santschi), i. e. ca. 25% of the known species.

After we submitted our manuscript for publication, an anonymous referee suggested that we should include in our analysis the genus *Heteroponera* according to Brown's (1958) intuitive statement that this is the genus closest to *Proceratium* and *Discothyrea*.

We added it and, of our own initiative, we added also the genus *Acanthoponera*: this genus results regularly as sister genus of *Heteroponera* in both cladistic analyses by Lattke (1994) and by Keller (2000). Of these two genera we examined the following material:

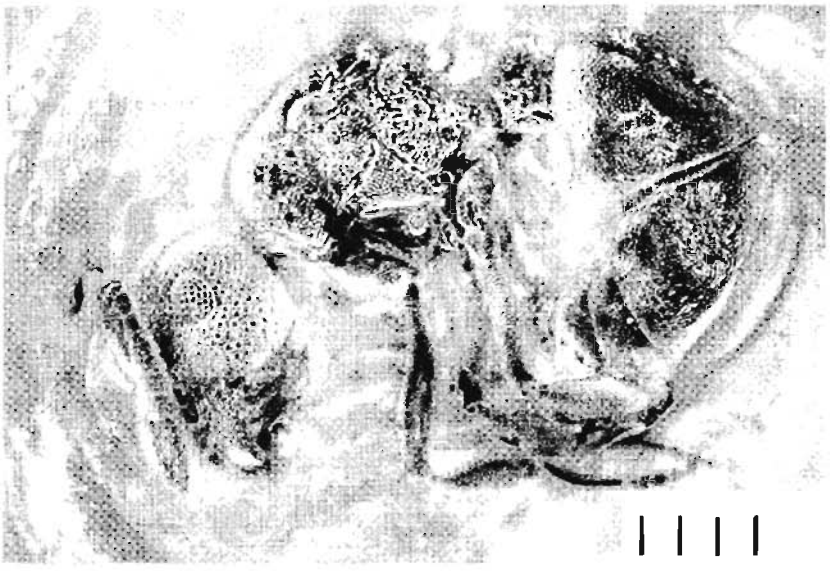


FIG. 1
Baltic amber specimen BB-1, *Bradoponera* sp., dealate gyne, lateral view. Distance between two scale bars 0.1 mm.

Heteroponera: *brounii* (Forel), *carinifrons* Mayr, *dentinodis* (Mayr), *dolo* (Roger), *inermis* (Emery), i. e. ca. 30% of the described species.

Acanthoponera: *Acanthoponera* sp. (S. Paulo, Brazil, Museo Regionale di Scienze Naturali, Turin), *mucronata* (Roger), i. e. ca. 50% of the known species.

Inclusion of these two genera changed our previous conclusions only for the appearance of the two genera in the cladogram among the outgroups (see later, the results of the cladistic analysis).

The following characters were retained as of potential phylogenetic significance (Table 1):

1. Worker and gyne. Anterior clypeal lamella absent (0), or present (1). This is character No. 5 of Lattke (1994). Our coding differs nonetheless from the one of Lattke since we considered the lamella to be polymorphic instead of present in *Ectatomma* (admitted to be polymorphic also in Lattke's text, page 110), *Gnamptogenys* (presence of this structure is equally referred to "most species" by Lattke, page 110, and the lamella is definitely missing in one of our Queensland species), *Heteroponera* (lamella missing at least in *brounii*).

2. Worker and gyne. Antennal insertion separate from clypeus (0), or fused with the clypeus (1).

3. Worker and gyne. Frontal carinae "normally" thin, lamelliform in profile (0), or remarkably thick in profile (1).

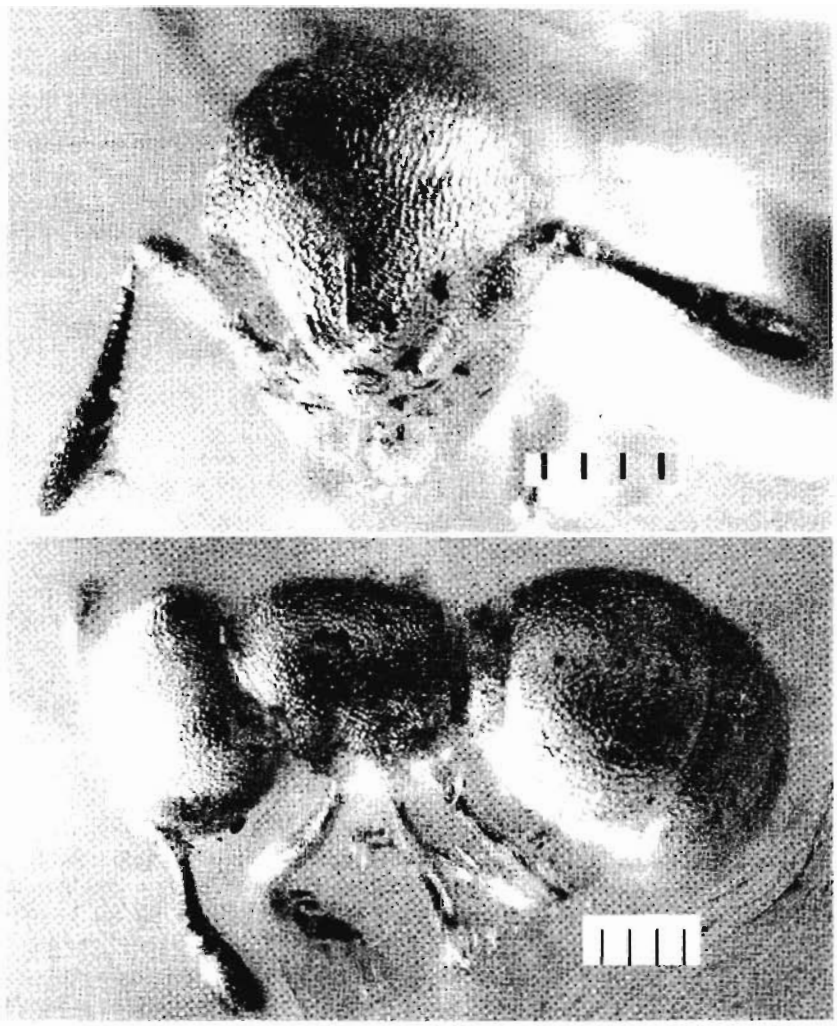
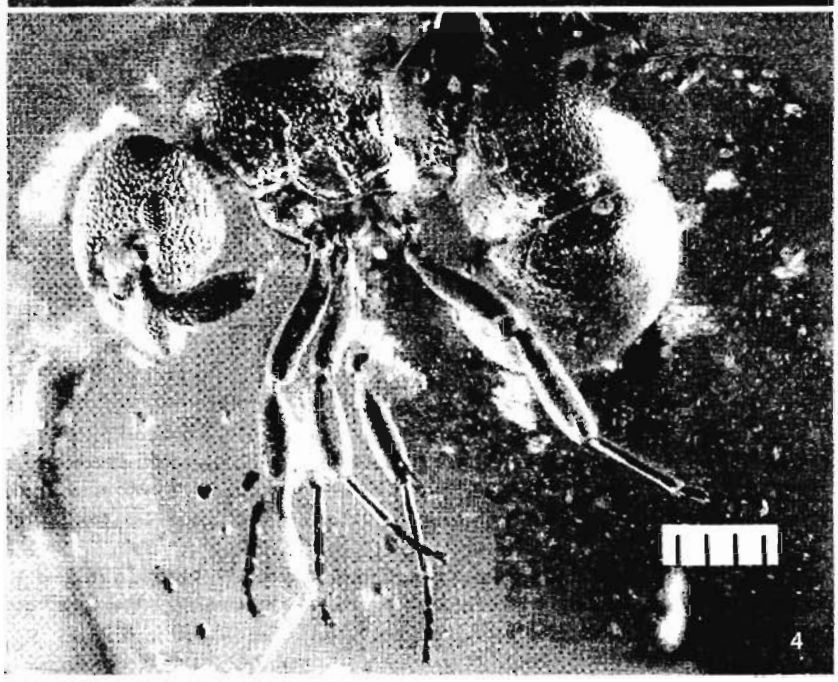


FIG. 2
Baltic amber BB-6, *Bradoponera* sp., worker, head in dorsal view (top) and dorsal view of the whole specimen (bottom). Distance between two scale bars 0.1 mm.

4. Worker and gyne. Funiculus simple (0), or clubbed (1). We find it difficult to make a clear cut between thick and clubbed funiculi. For this reason this is the binary transformation of Lattke's (1994) character No. 7.

5. Worker and gyne. Mandibles toothed (0), or edentate (1).


3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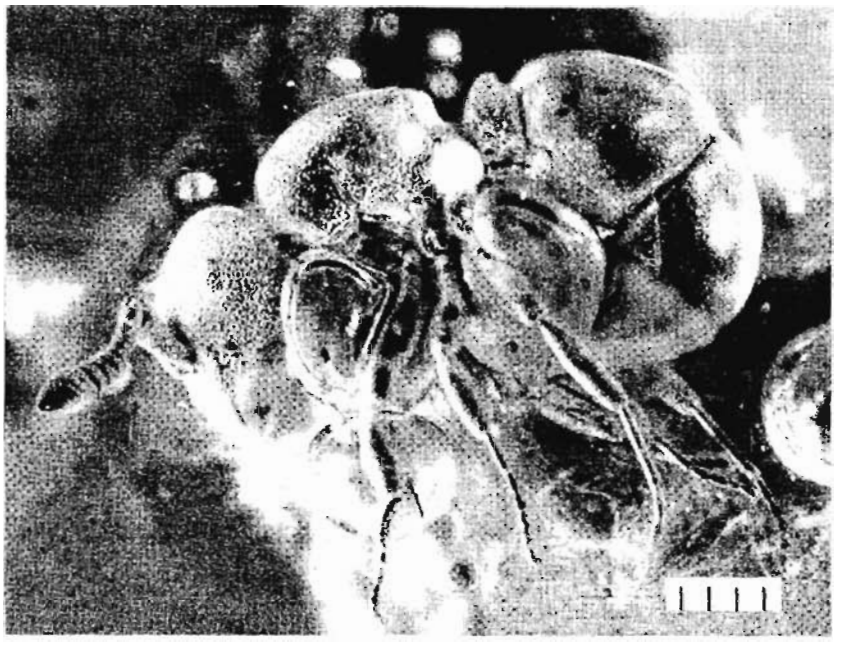

FIG. 5

Baltic amber BB-8, *Bradoponera meieri*, worker, lateral view. Distance between two scale bars 0.1 mm.

6. Worker and gyne. Maxillary palps without remarkable expansions (0), or with the second joint hammer-shaped (1).

7. Worker and gyne. Prosternal process triangular (0), or posteriorly bifurcate (1). This is character No. 9 of Lattke (1994) and it is coded entirely after this work but reduced to binary state for clarity, as already suggested by Keller (2000).

8. Worker. Promesonotal suture movable (0), or fused (1). This is character No. 8 of Lattke (1994)

9. Worker and gyne. Metacoxal cavities open (0), or closed (1). This is character No. 16 of Lattke (1994).

10. Worker and gyne. Number of stout, movable setae on the foretibial apex: one (0), or none (1). This is character No. 10 of Lattke (1994). Our coding differs nonetheless from the one of Lattke since we considered this character to be polymorphic in *Gnamptogenys* (a movable seta is well visible in both Queensland species).

FIGS 3-4

3. Baltic amber BB-4, *Bradoponera meieri*, worker, lateral view. Distance between two scale bars 0.1 mm. – 4. Baltic amber BB-7, *Bradoponera meieri*, worker, lateral view. Distance between two scale bars 0.1 mm.

11. Worker and gyne. Row of foretarsal setae present (0), or absent or at most reduced to a single seta (1). This is character No. 11 of Lattke (1994). Our coding differs nonetheless from the one of Lattke. We considered this character to be polymorphic in *Gnamptogenys* since a row of foretarsal setae is present in both Queensland species and in *haenschei*.

12. Worker and gyne. Prominent seta on the foretarsal base absent (0), or present (1). This is character No. 12 of Lattke (1994).

13. Worker and gyne. Number of mesotibial apical spurs, two (0), one (1), or none (2). This is character No. 13 of Lattke (1994). Our coding differs from the one of Lattke since we have abundant evidence for polymorphism of this character in both *Proceratium* and *Discothyrea*.

14. Worker and gyne. Empodia absent (0), or present (1). We find it difficult to make a clear cut between variable and present empodia. For this reason this is the binary transformation of Lattke's (1994) character No. 15, as already suggested by Keller (2000).

15. Worker and gyne. Claws unidentate (0), or bidentate (1).

16. Worker and gyne. Opening of the metapleural gland directed laterally (0), obliquely or posteriorly (1). This character No. 20 of Lattke (1994).

17. Worker and gyne. Petiole with (0) or without (1) lateral tergite. This is character No. 18 of Lattke (1994).

18. Worker and gyne. Dorsoventral fusion of petiole incomplete (0), or complete (1). This is character 19 of Lattke (1994).

19. Worker and gyne. Edge of posterior petiolar foramen where sternite meets tergite invaginated (0), or straight (1). This is character No. 29 of Lattke (1994).

20. Worker and gyne. Posterior border of petiolar sternite with (0), or without lateral lobes (1). This is character No. 23 of Lattke (1994).

21. Worker and gyne. Dorsal stridulitrum on abdominal segment IV absent (0), or present (1). This is character No. 30 of Lattke (1994).

22. Worker and gyne. Anterior face of third abdominal segment smooth (0), or with a carina or ridge (1). This is character No. 22 of Lattke (1994).

23. Worker (and gyne?). Spiracular plate posterior edge not reduced (0), or abruptly reduced in dorsal half (1). This is character No. 1 of Kugler (1991) and it is coded entirely after this work.

24. Worker (and gyne?). Oblong plate fulcral arm not extending along entire postincision (0), or extending along entire postincision to dorsal ridge of oblong plate (1). This is character No. 2 of Kugler (1991) and it is coded entirely after this work.

25. Worker (and gyne?). Gonostyli two segmented (0), or single segmented (1). This is character No. 3 of Kugler (1991) and it is coded entirely after this work.

26. Worker (and gyne?). Gonostylus pilosity abundant (0), or sparse (1) on distal segment. This is character No. 4 of Kugler (1991) and it is coded entirely after this work.

27. Worker (and gyne?). Furcula dorsal arm large, with lateral flanges (0), a distinct simple shaft without flanges (1), reduced to a small tubercle or absent (2), fused to sting base or entirely lost (3). This is character No. 6 of Kugler (1991) and it is coded entirely after this work.

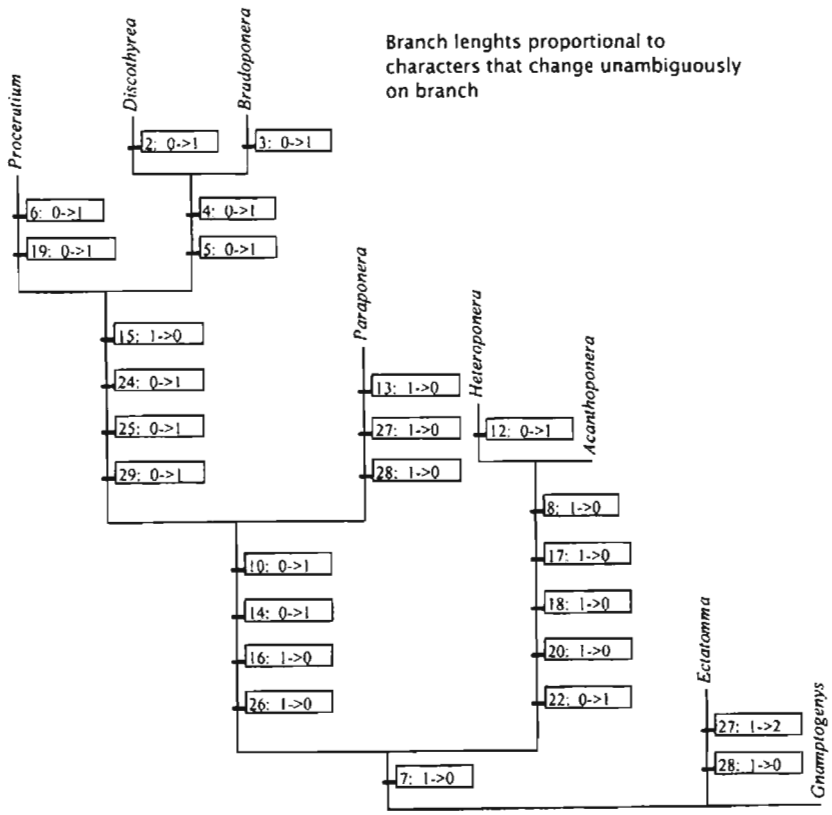

FIG. 6

Phylogram of the three Proceratiini genera and five outgroups. The labels on the branches list the apomorphic characters. See text for further explanations.

28. Gyne (and male?). Jugal lobe of hind wings present (0), or absent (1). This is character No. 34 of Lattke (1994).

29. Larvae. Haired (0), or completely hairless (1). This character is coded according Wheeler & Wheeler (1976, 1985).

Characters employed in other phylogenies and not considered in the present analysis are listed below with their respective justification.

We did not include in our analysis the following characters of Lattke (1994):

For being of difficult appreciation and/or variable in a number of genera (our interpretation would differ from the original one in a number of cases): 1, 24, 33, 35.

For being polymorphic among one or more of the three ingroup taxa considered in the present paper: 3, 4, 6.

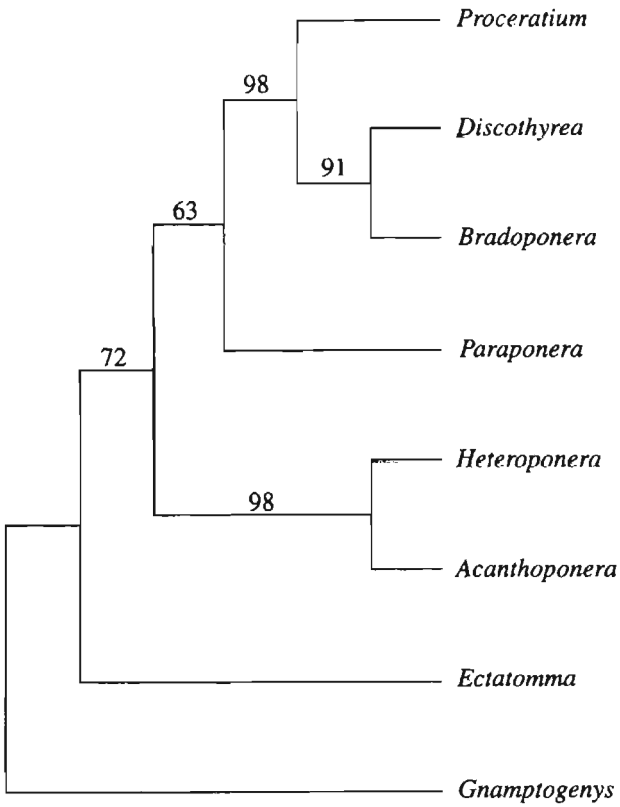

FIG. 7
Same tree as in Fig. 6 obtained as a result of 1,000 bootstrap replicates. The clade including the three Proceratiini genera appears with highly significant frequency.

For being autapomorphic (i. e. uninformative) for an outgroup taxon among those considered in the present paper: 2, 14, 17, 21, 25, 32, 36.

For being invariant among the taxa considered in the present paper: 26, 27, 28, 31.

Character 5 of Kugler (1991) was excluded for being variable according to Kugler's own description and character 7 for being autapomorphic (i. e. uninformative) for an outgroup taxon among those considered in the present paper.

Search for the optimal phylogenetic relationships between the genera considered before was performed by PAUP 4.0b10 (Swofford, 2002). Given the small number of taxa involved, an exhaustive search for the optimal tree(s) was performed.

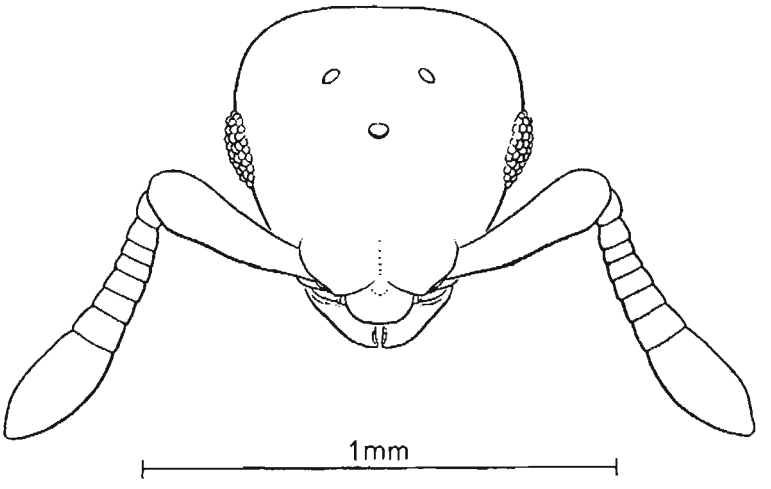

FIG. 8
Bradoponera wunderlichi Baroni Urbani & de Andrade sp. n. dealate gyne, head in dorsal view.

All characters were considered as unordered.

The phylogram with plotted apomorphies over the branches of fig. 6 was obtained by MacClade 3.01 (Maddison & Maddison, 1992).

RESULTS

Searching for the shortest tree(s) for the genera considered on the base of the characters described above results in only one optimal tree of length 51, Consistency index (CI) = 0.9020, Homoplasy index (HI) = 0.3725, CI excluding uninformative characters = 0.8611, HI excluding uninformative characters = 0.1389, Retention index (RI) = 0.8276, and Rescaled consistency index (RC) = 0.7465. This result remains unchanged using as outgroup either all the non-Proceratiini genera or *Gnamptogenys* only. This tree is drawn in form of phylogram at fig. 6.

1,000 bootstrap replicates of the same analysis result in a topologically identical tree where the clade composing the tribe Proceratiini (i. e. ((*Proceratium*, (*Discothyrea*, *Bradoponera*))) has a frequency of 98% (fig. 7).

Rooting the tree by means of all non-Proceratiini genera might imply our forcing the Proceratiini to appear as a monophyletic group. This risk was avoided in our second analysis where the tree was rooted by using *Gnamptogenys* only as outgroup. The use of *Gnamptogenys* as single outgroup appears as the most plausible outgroup choice within our data matrix. In fact, *Gnamptogenys* (and not *Paraponera* as one might have expected) appears as the most distantly related genus to the Proceratiini even in a comprehensive analysis without outgroup definition. This will

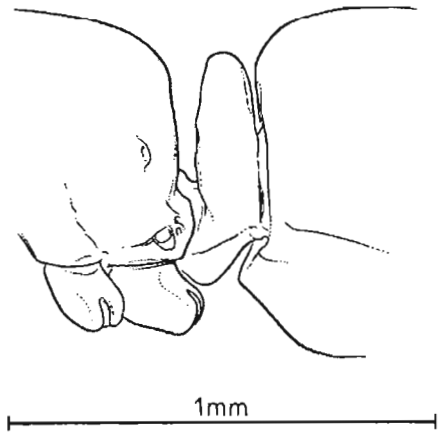

FIG. 9
Bradoponera electrina Baroni Urbani sp. n. worker, petiole in side view.

appear clearly by examination of Table 2 where the patristic distances between the genera considered in such a non-polarized tree are given.

This result could be changed only by changing the data.

One might object, however, that this result was obtained by using a number of characters either unknown in *Bradoponera*, or verified in a small number of species, or both.

But this is not the case.

Performing another exhaustive search after excluding characters 7, 9, and 19, 21, 23-29 results in three trees differing only in the position of *Ectatomma* among the outgroups and with one tree perfectly identical to the one of figs 6 and 7. These trees have a length of 33, Consistency index (CI) = 0.9394, Homoplasy index (HI) = 0.4242, CI excluding uninformative characters = 0.9091, HI excluding uninformative characters = 0.0909, Retention index (RI) = 0.8889, Rescaled consistency index (RC) = 0.8350.

A bootstrap analysis of these data results in a tree with a minority clade (29%) where *Ectatomma* appears as sister group of the clade containing (*Paraponera*, (*Proceratium*, (*Discothyrea*, *Bradoponera*))), but -understandably- the clade comprising the Proceratiini and the one comprising *Discothyrea* and *Bradoponera* appear at lower frequencies (71% and 87% respectively).

We consider as Proceratiini all ponerine ants corresponding to the description following the tribal synonymy.

PROCERATIINI Emery

Proceratii Emery, 1895: 765. Type genus: *Proceratium* (by root homonymy). Valid genera included: *Proceratium*, *Discothyrea*.

Proceratiini Emery, Ashmead, 1905: 382. Valid genera included: *Proceratium*, *Discothyrea*.
Proceratiini, Emery, 1911: 49. Valid genera included: *Proceratium*, *Discothyrea*, *Probolomyrmex*.
Proceratiini Emery, Wheeler, 1922: 644. Valid genera included: *Proceratium*, *Discothyrea*, *Probolomyrmex*.
Ectatommini Emery (partim), Brown, 1958. Senior synonym of Proceratiini.
Proceratiini Emery, Wheeler & Wheeler, 1985: 256. Tribal status justified. Valid genera included: *Proceratium*, *Discothyrea*.
Discothyrinae Clark, 1951: 15. Type genus *Discothyrea* (by root homonymy). Implicit synonym of Proceratiini, Wheeler & Wheeler, 1985: 256. Synonym of Ectatommini, Bolton, 1994: 264.
Proceratiini Emery, Lattke, 1994: 112. Valid genera included: *Proceratium*, *Discothyrea*.
Proceratiini Emery, Bolton, 1995: 15. Valid genera included: *Proceratium*, *Discothyrea*, *Bradoponera*.

There seems to be broad but not unequivocal consensus on the genera to be included in the tribe. Former attributions of *Probolomyrmex* to the Proceratiini were shown to be improbable by means of non-phylogenetic, but morphologically plausible arguments by Brown (1952). A recent paper by Perrault (2000) suggests that *Probolomyrmex* should represent a separate, monotypic subfamily within the Formicidae. If, on one hand, we are rather sceptic on this conclusion and on the rationale from which it was drawn, we take advantage of it at least as a further argument for the exclusion of *Probolomyrmex* from the Proceratiini.

PROCERATIINI: DIAGNOSIS AND DESCRIPTION

Worker. Monomorphic but variable in size. Head subglobose, generally longer than broad, rarely as long as broad or broader than long, variable in shape, i. e. with sides convex, subparallel, diverging posteriorly or converging anteriorly. Clypeus well developed, rectangular or subround, rarely triangular, largely or partially overhanging the mandibles, or medially armed with an anterior projection of variable size, convex, rectangular or triangular, or unarmed (truncate). Frontal carinae apart from each other with thin, rarely thick lateral expansions, diverging backwards, gently convex or straight, or attached to form a vertical plate of variable shape and size. Lateral expansions of the frontal carinae never or only partially covering the antennal insertions. Genal carina absent or present; in this case variably marked and generally delimiting a sulcus of changeable depth. Gular area impressed or not. Eyes absent or present; when present represented by small pigmented dots, or by a clear convex facet, or by an agglomeration of salient ommatidia generally with interommatidial pilosity and placed approximately below or over the mid line of the head. Ocelli absent, rarely only the anterior ocellus vestigial or as developed as in the gyne. Antennal insertions entirely or partially surpassing, or on the same line as, or behind the anterior margin of the head. Antennae 6-12-jointed. Scapes surpassing, reaching or much shorter than the vertexal margin, gently or strongly incrassate apically. First funicular joint about as long as broad, broader than long or longer than broad. Funicular joints 2-10 generally broader than long, or about as broad as long, or slightly longer than broad. Last funicular joint slightly inflated or strongly globular, about as long as the sum of joints 2-7, 3-10, 6-10, 7-10, or 8-10, or as long as or longer than the remaining joints. Mandibles subtriangular. Basal margin of the mandibles straight or convex distally.

Mandibles always with a pointed apical tooth. Masticatory margin of the mandibles edentate or with 2-13 denticles of variable size. Palp formula (basal condyle included, when present) 1,3, 2,2, 3,2, 3,3, 4,3, 4,4, 5,3, or 5,4. Second maxillary palp joint hammer-shaped or not.

Mesosoma short to elongate. Dorsum of the mesosoma sloping posteriorly or variably convex dorsally. Promesonotal and propodeal sutures generally absent, rarely superficially impressed. Promesopleural and meso-metapleural sutures more impressed ventrally. Propodeum unarmed, simply angulate or denticulate or toothed, rarely with a pair of spines. Area between basal and declivous faces of the propodeum variably concave medially and with or without carina. Each side of the declivous face of the propodeum with a variably marked margin, carina or lamella. Propodeal lobes simply convex or truncate, with or without a pointed or rounded dorsal tooth. Propodeal spiracle round or tubuliform and at mid propodeal height in lateral view. Petiole variable in size, width and height. Petiolar node loaf-shaped, or scale-like, variable in width and thickness, rarely dorsally compressed or pointed. Ventral petiolar process small or large, truncate, triangular, subround or spiniform. Postpetiole (abdominal segment III) anteriorly as broad as or broader than petiole. Postpetiole in dorsal view antero-laterally with sides diverging, convex or angulate. Postpetiolar sternite antero-medially with a variably marked subtriangular margin bearing or not a longitudinal carina prolonged posteriorly. Constriction between postpetiole and gastral segment I present, more or less impressed. Gastral tergum I (abdominal tergum IV) of variable length, convex, continuously curved ventrally or at least with a posterior half clearly separated by a curve from the dorsal one. Sides of the gastral sternite I diversely projecting anteriorly. Remaining gastral tergites and sternites curved ventrally. Sting developed, curved downwards. Legs short or variably elongate. Tibiae of fore and hind legs with a large, pectinate spur. Mid tibiae with or without a pectinate spur variably developed. Spurs of fore legs with or without a basal spine. Mid basitarsi generally shorter or at most as long as the fore ones. Second tarsomere of all legs about as long as, slightly or much longer than the third and fourth tarsomeres. Pretarsal claws simple. Arolia reduced or well developed. Head, mesosoma, petiole, postpetiole and gastral tergum I variably reticulate and/or punctate-granulate; this sculpture superimposed or not by irregular rugosities or by foveae. Remaining gastral tergites variably smooth, reticulate-punctate, punctate, or punctate-foveolate. Legs variably smooth, with superficial or deep punctuation-granulation. Body covered by at least two types of hairs: (1) short and often dense, erect, suberect or subdecumbent on the whole body, rarely sparse and appressed, (2) very short, decumbent or appressed on the funicular joints only. A third hair type may be present or absent: (3) long erect or suberect on the whole body, sometimes subdecumbent, dense or sparse; in some cases this pilosity is restricted to the apex of the gaster only. Colour yellowish light brown, reddish-brown, dark brown or black. Legs concolorous with or lighter than the body.

Gyne. Similar to the worker but slightly differing from it in the usual caste-dependent characters. The most salient of these characters are the following: size generally larger; compound eyes larger and with apparently widespread ocular pilosity; ocelli always present; mesosoma robust; promesonotal and propodeal sutures impressed; metanotum sometimes spiniform. Basal face of the propodeum very short or slightly prolonged backwards.

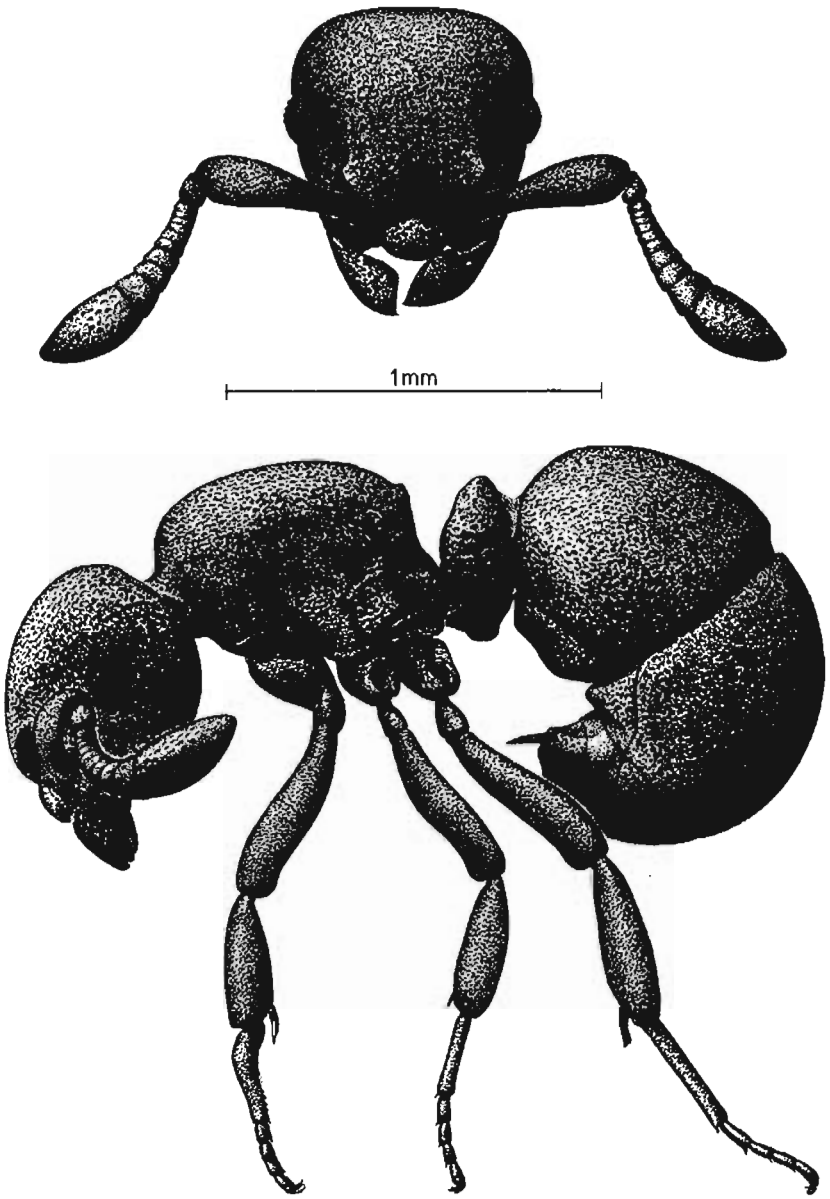

FIG. 10
Bradoponera meieri Mayr, worker, head in dorsal view (top) and entire profile (bottom).

Wings. Fore wings variably pigmented, in some species infuscate, brown or whitish-yellow to hyaline. The wing venation appears to follow six distinct patterns as follows (*Bradoponera* wings are unknown):

1. *m-cu* marked and *Rsf3* not reaching *Rsf1*. *2r, Rsf4, Rsf5, r-m, Mf4* marked. *Rsf5* reaching the Costa.

2. *m-cu* marked, *Rsf3* and *Rsf4* missing. *2r, Rsf5, r-m* marked. *Rsf5* not reaching the Costa.

3. *m-cu* marked, *Rsf3, Rsf4, r-m* and *Mf4* missing. *2r, Rsf5* marked. *Rsf5* not reaching the Costa.

4. *m-cu, Rsf3* and *Rsf4* missing. *2r* very long, *Rsf5, r-m,* and *Mf4* of variable length. *Rsf5* not reaching the Costa.

5. *m-cu Rsf3, Rsf4, r-m* and *Mf4* missing. *2r* very long, *Rsf5* of variable length. *Rsf5* not reaching the Costa.

6. *m-cu Rsf3, Rsf4,* and *Mf4* missing. *2r* short, *Rsf5* and *r-m* absent to long. *Rsf5* approaching or reaching the Costa. According to the material available to us this type seems to be the characteristic *Discothyrea* wing.

Hind wings pigmented as the fore wings and showing three venation patterns (we were unable to examine *Discothyrea* hind wings):

1. *r-m* distinct and *R* reaching the anterior margin. *M* and *CuA* variably marked.

2. *r-m* distinct and *R* not reaching the anterior margin. *M* and *CuA* variably marked.

3. *r-m* missing. *M* and *CuA* variably marked.

Male. Size variable, generally smaller than or nearly as large as the gyne. Head about as broad as long, broader than long or longer than broad. Vertex variably convex. Clypeus antero-medially variably projecting; simply straight, slightly convex, subrectangular or subtriangular. Frontal carinae reduced, never hiding the antennal socket and generally separate, rarely close to each other. Sides of the frontal carinae subparallel, or slightly diverging posteriorly. Antennae 13-segmented. Ocelli large. Compound eyes very large and mostly on the anterior half of the head sides. Scapes variable in size, not reaching or surpassing the unpaired ocellus or slightly surpassing the vertexal margin. First funicular joint shorter than or as long as the second; distal joint as long as the sum of joints 10-11 or 9-11. Mandibles slender, edentate or minutely and irregularly denticulate, and with a visible apical, pointed tooth. Palp formula (basal condyle included) 3,2 4,3, 5,2 or 5,3. Second maxillary palp joint with or without hammer-shape. Mesosoma robust. Mesonotum and scutellum convex. Propodeum with or without differentiated basal and declivous faces. Sides between basal and declivous faces of the propodeum separate by similar projections as in the worker and gyne but sometimes more reduced. Metanotum spiniform or not. Propodeal lobes similar to those of the worker and gyne. Petiole variably convex, rarely scale-like, lower and narrower than in the female castes. Subpetiolar process and postpetiolar sternite with structures resembling those of the female but usually much more reduced. Postpetiole broader than the petiole. Gastral segments generally less curved than in the worker and gyne. Legs long and slender. Sculpture similar to the one of the worker and gyne but generally more superficial; few species with the sculpture on the first gastric tergite more impressed than in the worker and gyne. Pilosity resembling the one of the worker and gyne but slightly less dense.

Wings. Gynes and males have similar fore and hind wings. Male wings are usually smaller than those of the gynes but their venation follows the same patterns.

Colour generally darker than the worker and the gyne. Some species black with lighter legs.

Members of the tribe Proceratiini are often easy to distinguish from their general appearance. At least the combination of a short cephalic capsule coupled with exposed antennal insertions and the curved gaster should allow an easy separation of these ants from the remaining ponerines in most instances.

According to Wheeler & Wheeler (1976, 1985) the Proceratiini larvae are highly characteristic by being entirely hairless. This conclusion is based on examination of three *Proceratium* and two *Discothyrea* species.

In our cladistic framework, the following characters result synapomorphic for the tribe:

Claws unidentate.

Oblong plate extending along entire postincision of plate.

Unisegmented gonostyli.

Hairless larvae.

There are at least three additional characters shared by the Proceratiini genera and not by what results as their sister genus in our study, i. e. closed metacoxal cavities, loss of foretarsal setae and loss of the dorsal stridulitrum. These characters can not be interpreted as Proceratiini synapomorphies in our analytical framework since they are present also in *Acanthoponera* and *Heteroponera*.

We are aware that the previous synapomorphy list is likely to undergo modifications if the analysis would be extended to a broader array of ponerine genera.

The following genera are included in the tribe: *Proceratium*, *Discothyrea* and †*Bradoponera*.

Proceratium Roger

Proceratium Roger, 1863: 171. Type species *Proceratium silaceum* Roger, 1863, by monotypy.
Proceratium Roger, Baroni Urbani & de Andrade, 2003: 40 ff. World revision.

Undoubted autapomorphy of the genus: worker, gyne and male with hammer-shaped maxillary palps.

Discothyrea Roger

Discothyrea Roger, 1863: 171. Type species *Discothyrea testacea* Roger, 1863, by monotypy.

Undoubted autapomorphy of the genus: worker and gyne antennal insertion fused with the clypeus. This character is actually present in one *Proceratium* species as well: *P. microsculptum* de Andrade. Our phylogenetic analysis (Baroni Urbani & de Andrade, 2003) shows that its appearance in this species is homoplastic. *P. microsculptum*, however, has the characteristic hammer-shaped maxillary palps missing in *Discothyrea*.

†***Bradoponera*** Mayr

Bradoponera Mayr, 1868: 73. Type species: *Bradoponera meieri* Mayr, 1868, by monotypy.

Undoubted autapomorphy of the genus: worker and gyne frontal carinae thick (not lamelliform) in profile.

Table 3 summarizes the main characters distinguishing *Proceratium*, *Discothyrea* and *Bradoponera*.

For the genus *Bradoponera* we propose the following detailed diagnosis and description:

†***Bradoponera*** Mayr

Worker. Monomorphic and little variable in size. Head subglobose, slightly longer than broad, with sides convex or diverging posteriorly. Clypeus medially armed with a slightly developed anterior projection, convex in shape. Frontal carinae separate from each other with narrow, thick lateral expansions diverging backwards. Lateral expansions of the frontal carinae only partially covering the antennal insertions. Genal carina absent or superficially marked posteriorly only and delimiting a shallow sulcus. Gular area not impressed. Eyes small, flat and represented by few inconspicuous ommatidia with ocular pilosity, or large, convex and composed by an agglomeration of salient ommatidia, generally with ocular pilosity and approximately over the mid line of the head. Antennal insertions at the same level of the anterior margin of the head. Antennae 9 or 12-jointed. Scapes shorter than the vertexal margin, gently incrassate apically. First funicular joint about as long as broad or slightly longer than broad. Second funicular joint broader than long or about as long as broad. Joints 3-7 or 3-10 broader than longer. Last funicular joint about as long as the sum of joints 3-10 or slightly shorter than the sum of joints 2-7.

Mandibles subtriangular. Basal margin of the mandibles gently convex distally, with a pointed apical tooth. Masticatory margin edentate. Palp formula 5,4. Second maxillary palp joint apparently not hammer-shaped.

Mesosoma short and robust, its dorsum gently convex. Promesonotal suture superficially impressed (see e. g. fig. 3). Propodeal suture superficially impressed or not. Promesopleural and meso-metapleural sutures more impressed ventrally. Propodeum unarmed, or with a pair of small subround teeth. Area between the basal and declivous faces of the propodeum weakly concave medially. Sides of the declivous face of the propodeum with a variably marked margin. Propodeal lobes gently convex. Propodeal spiracle round and placed at mid height in profile. Petiole in side view with cuneiform apex, or scale-like. Ventral petiolar process subround. Postpetiole (abdominal segment III) anteriorly broader than the petiole. Postpetiole in dorsal view antero-laterally with variably convex sides. Postpetiolar sternite antero-medially with a marked subtriangular margin. Constriction between postpetiole and gastral segment I impressed. Gastral tergum I convex, continuously curved dorsoventrally. Sides of the gastral sternite I projecting or not anteriorly. Remaining gastral tergites and sternites curved ventrally. Sting developed. Legs little elongate with slightly incrassate tibiae. Tibiae of fore and hind legs with a large, pectinate spur. Mid tibiae with a small pectinate spur. Spurs of fore legs without basal spine. Mid basitarsi shorter than the fore ones. Second tarsomere of the three pairs of legs about as long as or slightly longer than each third and fourth tarsomeres. Pretarsal claws simple. Arolia strongly developed.

Head, mesosoma, petiole and postpetiole punctate-granulate or variably punctate-foveolate. Gastral tergum I superficially punctate and with traces of small foveae or superficially granulate. Legs punctate.

Body covered by short, appressed hairs with or without additional, short, sparse, suberect and subdecumbent hairs.

Colour apparently dark brown.

Gyne. Similar to the worker and differing from it only by the presence of ocelli and by the stouter mesosoma with wing sclerites.

Wings unknown.

Male unknown.

Species Descriptions

Bradoponera wunderlichi Baroni Urbani & de Andrade sp. n. Figs 1, 8

Type material: holotype, unique, dealate gyne in Baltic amber, labelled: BB-1, in the MRSN.

Derivatio nominis: this species is named after Dr J. Wunderlich who sent us several important Baltic amber samples to study.

Diagnosis. A *Bradoponera* species, known from the gyne only, similar to *meieri* but differing from it, by the antennae 9 segmented instead of 12 segmented, by the integumental sculpture more superficial and by its smaller size (TL = 2.53 mm instead of TL = 3.25 mm).

Gyne. Head slightly longer than broad with the sides diverging posteriorly. Vertex convex. Frontal carinae stout, partially covering the antennal insertions. Lateral expansions of the frontal carinae narrow, very thick, diverging anteriorly and gently convex posteriorly. Frontal carinae dorso-medially with a superficial sulcus starting from a small, subround anterior denticle and reaching the median ocellus posteriorly. Clypeus strongly convex, protruding anteriorly, slightly narrower than the frontal carinae anteriorly and clearly separated from them by a superficial suture. Antennal sockets about as long as the antero-lateral clypeal margin. Scapes stout, surpassing the posterior border of the eyes. First and second funicular joints subequal in size, about as long as broad. Joints 3-7 broader than long. Last funicular joint slightly shorter than the sum of joints 2-7. Eyes slightly longer than 1/5 of the head length (mandibles excluded). Interocellar pilosity, if present, indistinguishable in the sole specimen available. Mandibles triangular, edentate and dorsally convex.

Mesosoma robust, about as long as the head (mandibles included). Mesonotum and scutellum gently convex. Propodeum with distinct basal and declivous faces. Basal face short, weakly depressed medially. Sides between the basal and declivous faces with a stout angle. Declivous face flat. Propodeal lobes subround.

Petiole twice broader than long, with the apex of the node angled in profile. Anterior face truncate to gently declivous anteriorly in side view. Petiolar sides subparallel. Ventral process of the petiole subround and developed. Postpetiole about as long as the first gastric tergite. Anterior face of the postpetiole gently concave and about as high as the apex of the petiolar node. First gastral tergite gently curved ventrally. First gastral sternite triangular in lateral view and very narrow medially. Remaining gastral tergites and sternites curved ventrally.

TABLE 1: Distribution of characters of presumed phylogenetic value among a sample of ponerine genera. Further explanations in the text.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Proceratium	0	01	0	0	0	1	0	1	1	1	1	0	12	01	0	0	1	1	1	1	0	0	1	1	1	0	1	1	1
Discothyrea	0	1	0	1	1	0	0	1	1	1	1	0	12	1	0	0	1	1	0	1	0	0	1	1	1	0	3	1	1
Bradoponera	0	0	1	1	1	0	?	1	?	1	1	0	1	1	0	0	1	1	?	1	?	0	?	?	?	?	?	?	?
Gnamptogenys	01	0	0	0	01	0	1	1	0	01	01	1	1	0	01	1	1	1	0	1	01	0	0	0	0	1	1	1	0
Ectatomma	01	0	0	0	01	0	1	1	0	0	0	0	1	0	1	1	1	1	0	1	1	0	0	0	0	1	2	0	0
Paraponera	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0
Heteroponera	01	0	0	0	0	0	01	0	1	0	1	1	1	0	01	1	0	0	0	0	0	1	?	?	?	?	?	1	0
Acanthoponera	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	1	?	0	0	1	?	1	0

TABLE 2: Patristic distances among the genera considered in the present paper in the unique most parsimonious unrooted tree.

Below diagonal: adjusted character distances. Above diagonal: patristic distances.	*Proceratium*	*Discothyrea*	*Bradoponera*	*Gnamptogenys*	*Ectatomma*	*Paraponera*	*Heteroponera*	*Acanthoponera*
Proceratium		5	5	17	17	10	24	23
Discothyrea	4		2	18	18	11	25	24
Bradoponera	4	2		18	18	11	25	24
Gnamptogenys	11	12	5		2	9	11	10
Ectatomma	15	16	7	2		9	11	10
Paraponera	10	11	5	7	6		16	15
Heteroponera	11	13	12	6	10	13		1
Acanthoponera	15	17	13	8	10	14	1	

TABLE 3: Synopsis of some significant characters distinguishing the three Proceratiini genera: *Proceratium*, *Discothyrea* and *Bradoponera*.

	Proceratium	*Discothyrea*	*Bradoponera*
Clypeus anteriorly	protruding or not	protruding	protruding
Antennal insertions on a clypeal prominence	on or out	on	out
Number of antennal joints	12	6 to 12	9 or 12
Last funicular joint	at most as long as joint 6 up to penultimate	at least as long as joint 2 up to penultimate	about as long as joint 2 up to penultimate
Mandibles	dentale	edentate	edentate
Palp formula	2,2; 3,2; 3,3; 4,3	1,3; 4,3; 4,4; 5,3	5,4
Second maxillary palp	Hammer-shaped	at most slightly curved	apparently curved only
Petiolar peduncle	present or absent	absent	absent
Fore tibiae basal seta	present or absent	absent	absent
Empodia	developed or not	developed	developed

Femora slightly elongate. Tibiae inflated. Each tibia with a pectinate spur; spurs of mid legs small. Hind tibiae about 1/6 shorter than the hind femora. Hind basitarsi slightly shorter than the hind tibiae. Arolia strongly developed.

Sculpture. Head, mesosoma and petiole densely and minutely punctate-foveolate, the foveae slightly deeper and larger on the head sides, variably clumped on the mesosoma and missing on the declivous face of the propodeum. Postpetiole super-

ficially punctate-foveolate, the foveae very small and denser antero-laterally. First gastral tergite minutely and superficially punctate and with traces of foveae on the sides only. Legs punctate.

Pilosity. Body covered by minute, appressed hairs.

Colour. Dark brown-black.

Measurements in mm and Indices: TL 2.53; HL 0.67; HW 0.61; EL 0.14; SL 0.41; WL 0.73; PeL 0.16; PeW 0.32; HFeL 0.39; HTiL 0.33; HBaL 0.31; LS4 0.16; LT4 0.47; CI 91.0; SI 61.2; IGR 0.34.

Bradoponera electrina Baroni Urbani sp. n. Figs 2, 9

Type material: holotype, unique, worker in Baltic amber, labelled: BB-6, in the MRSN.
Derivatio nominis: From the Latin *electrinus* (= made of amber).

Diagnosis. A *Bradoponera* species the worker of which differs from the worker of *meieri* and from the gyne of *wunderlichi* by its larger size (TL = 3.49 mm instead of TL $\leq$ 2.85 mm), by the petiole almost four times broader than long instead of only twice broader than long and by the body with suberect hairs (missing in *meieri* and *wunderlichi*).

Worker. Head stout, slightly longer than broad, with convex sides. Vertex weakly convex. Frontal carinae narrower and less raised than in *meieri* and *wunderlichi*, leaving completely exposed the antennal insertions. Sides of the frontal carinae diverging posteriorly. Frontal carinae dorso-medially with a longitudinal ruga prolonging posteriorly. Clypeus less developed than in *meieri* and *wunderlichi*, convex, protruding anteriorly, about as broad as the frontal carinae anteriorly and clearly separated from them by an impressed suture. Antennal sockets about as long as the antero-lateral clypeal margin. Scapes less stout than in *meieri* and *wunderlichi*, surpassing the posterior border of the eyes. First funicular joint about 1/4 longer than broad. Joints 2-10 broader than long. Last funicular joint slightly shorter than the sum of joints 2-10. Eyes small, composed by a flat agglomeration of inconspicuous ommatidia with inter-ocellar pilosity. Mandibles triangular, edentate and dorsally convex.

Mesosoma stout, 1/5 shorter than head length (mandibles included). Mesosoma in profile weakly convex. Pronotal suture superficially impressed. Propodeum with separate basal and declivous faces. Basal face not distinctly differentiated from the mesonotum and slightly sloping posteriorly, close to the declivous face. Basal and declivous propodeal faces separated dorsally and laterally by a superficial margin only. Declivous face of the propodeum flat. Propodeal lobes reduced and subround.

Petiole almost four times broader than long. Petiole in profile scale-like, weakly narrowing apically and with gently convex apex. Anterior and posterior faces of the petiole in side view truncate. Ventral process of the petiole subround and developed. Postpetiole slightly longer than the first gastric tergite. Anterior face of the postpetiole straight and about as high as the apex of the petiolar node. First gastral tergite gently curved ventrally, less triangular than in *meieri* and *wunderlichi* in profile, and narrow medially. Remaining gastral tergites and sternites curved ventrally.

Femora slightly elongate. Mid and hind tibiae less inflated than in *meieri* and *wunderlichi*. Fore tibiae moderately inflated. Each tibiae with a pectinate spur; spurs of fore legs small. Hind tibiae about 1/10 shorter than the hind femora. Hind basitarsi about 1/3 shorter than the hind tibiae. Arolia well developed.

Sculpture. Head, mesosoma and petiole densely punctate-granulate. Postpetiole and gaster superficially granulate and with minute piligerous punctures. Legs punctate.

Pilosity. Body covered by dense, short, appressed hairs and by sparser suberect and subdecumbent hairs longer than the appressed ones, slightly shorter and sparser on the funicular joints.

Colour. Dark brown-black.

Measurements in mm and Indices: TL 3.49; HL 0.91; HW 0.86; EL 0.07; SL 0.51; WL 0.86; PeL 0.15; PeW 0.55; HFeL 0.49; HTiL 0.45; HBaL 0.31; LS4 0.26; LT4 0.68; CI 94.5; SI 56.0; IGR 0.38.

Bradoponera meieri Mayr Figs 3-5, 10

Material examined: BALTIC AMBER: 3 workers, BB-4, BB-7, BB-8 [all JWCS].

Diagnosis. A *Bradoponera* species the gyne of which is similar to the one of *wunderlichi*, but differs from it by the antennae 12 instead of 9 segmented, by the sculpture more impressed, and by the larger size (TL = 3.25 mm instead of 2.53 mm).

Worker. Vertex gently convex. Frontal carinae stout, reaching the internal border of the antennal insertions. Lateral expansions of the frontal carinae narrow, very thick, anteriorly diverging and posteriorly gently convex. Frontal carinae dorso-medially with a superficial sulcus originating from a small, subtriangular anterior denticle and prolonging posteriorly.

Clypeus strongly convex, protruding anteriorly, about as broad as the frontal carinae anteriorly and clearly separated from them by an impressed suture. Antennal sockets about as long as the antero-lateral clypeal margin. Scapes stout, surpassing the posterior border of the eyes. First funicular joint about as long as broad. Joints 2-10 broader than long. Last funicular joint as long as the sum of joints 3-10. Eyes about 1/5 of the head length (mandibles excluded) with minute interocellar pilosity. Mandibles triangular, edentate and dorsally convex.

Mesosoma robust, about as long as the head (mandibles included), dorsally convex in profile. Pronotal and propodeal sutures superficially impressed. Propodeum with distinct basal and declivous faces. Basal face very short and gently sloping posteriorly. Basal and declivous faces separated by a superficial margin dorsally and by a marked angle resembling a small, subround tooth laterally. Declivous face of the propodeum flat. Propodeal lobes subround.

Petiole twice broader than long. Petiole in side view with the apex of the node angle-shaped. Anterior face of the petiole in profile truncate to gently declivous. Petiolar sides subparallel. Ventral process of the petiole subround and developed. Postpetiole subequal in length to the first gastric tergite. Anterior face of the postpetiole about as high as the apex of the petiole. First gastral tergite gently curved ventrally. First gastral sternite triangular in lateral view and very narrow medially. Remaining gastral tergites and sternites curved ventrally.

Femora moderately elongate. Tibiae inflated. Each tibia with a pectinate spur; spurs of mid legs small. Hind tibiae slightly shorter than or about as long as the hind femora. Hind basitarsi about 1/5 shorter than the hind tibiae. Arolia well developed.

Sculpture. Head, mesosoma and petiole densely and minutely punctate-foveolate and minutely rugulose, the foveae slightly deeper and larger on the head sides,

sparser on the pleurae and on the petiole, missing on the declivous face of the propodeum, and the rugosities rare on the petiole. Postpetiole punctate-foveolate, the foveae smaller and denser antero-laterally. First gastral tergite superficially punctate and with very sparse foveae, more superficial than those on the postpetiole. Legs punctate.

Pilosity. Body covered by minute, appressed hairs.

Colour. Dark brown-black.

Measurements in mm and Indices: TL 2.70-2.85; HL 0.68-0.70; HW 0.60-0.63; EL 0.14; SL 0.45; WL 0.76-0.78; PeL 0.17-0.19; PeW 0.34-0.38; HFeL 0.44-0.45; HTiL 0.42-0.44; HBaL 0.33-0.35; LS4 0.19-0.20; LT4 0.52-0.56; CI 88.2-90.0; SI 64.3; IGR 0.34-0.38.

CONCLUDING REMARKS

Since the original description of Mayr (1868) the genus *Bradoponera* was never fully justified to belong to the Proceratiini. The main reason for such ambiguity is the fact that *Bradoponera* was known from a single fossil species from Baltic amber and the sole specimens representing it were deposited in the Koenigsberg amber collection, a collection partly lost or destroyed during Second World War. Placement within the Proceratiini, however, appears likely and is fully confirmed by the rediscovery of the genus reported in this paper. The Proceratiini, hence, result as a rather homogeneous tribe of Ponerinae containing three genera, *Proceratium*, *Discothyrea* and *Bradoponera*, all represented in the fossil record (de Andrade, 1998, Baroni Urbani & de Andrade, 2003, and present contribution). The first two genera have a broad tropical and subtropical distribution with deep penetrations into the temperate zones today, while the third one appears to be extinct, although the three species described from Baltic amber in this paper demonstrate a previously unsuspected species diversity in Europe during Palaeogene.

We show for the first time that each Proceratiini genus is characterized by a clear, significant autapomorphy. The sole known exception (the fusion of the clypeus with the antennal insertions characteristic of *Discothyrea* and appearing occasionally also in *Proceratium microsculptum*) is interpreted as due to homoplasy. This interpretation is confirmed by the internal phylogeny of the genus *Proceratium* proposed by Baroni Urbani & de Andrade (2003) where *P. microsculptum* occupies a rather terminal position.

The Proceratiini as a whole appear as a fairly homogeneous tribe whose members are easy to recognize by a combination of characters ranging from their bauplan to the clypeal and antennal morphology.

We suggest a set of four synapomorphies for the tribe after a cladistic analysis of their genera comprising five plausible, potential outgroups. We are aware, however, that a broader analysis considering the whole subfamily Ponerinae or the discovery of new characters might modify at least partially our results.

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