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PHYLOGENY AND BIOGEOGRAPHY
OF THE ANT SUBFAMILY PRIONOMYRMECINAE

(HYMENOPTERA, FORMICIDAE)

INTRODUCTION

WARD & BRADY (2003) propose a number of novelties concerning the systematic rank and the relative assignment of one extant and three fossil ant taxa without examining any of the fossils in question.

The paper by WARD & BRADY (l. c.) is supported by a formidable analytical framework applied to four data sets, two morphological, one of ribosomal RNA, and one combination of morphological data and rRNA sequences which are supposed to support the authors' conclusions.

In the following I will show that 1) the target of the paper by WARD & BRADY is essentially the same as the one of BARONI URBANI (2000), 2) in spite of considerable changes to the data on which BARONI URBANI (2000) drew his deductions, WARD & BRADY (2003) reach exactly the same conclusion, 3) WARD & BRADY insist nonetheless that these conclusions must be interpreted in a different way without providing valid reasons for it.

As a matter of fact WARD & BRADY (2003) re-propose precisely the same phylogeny already published by BARONI URBANI (2000) but suggest that it should be interpreted in a different way. Ward and Brady's conclusions are drawn from the consideration of a few characters not considered by BARONI URBANI (2000). The phylogenetic meaning and the validity of these characters will be discussed in the following.

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MATERIALS AND METHODS

The following discussion is largely restricted to the information contained in WARD & BRADY's MORPH1 data matrix (their Appendix 1), since that is the sole data set including the fossil taxa whose rank and assignment is focused in their paper. WARD & BRADY's phylogeny of Fig. 21 is the sole phylogenetic reconstruction containing the three fossil genera considered by these authors. The other phylogenetic tree where all taxa involved appear (their Fig. 22) is unresolved and drawn by hand, i.e. it is not the result of parsimony, distance, or other analysis. A re-examination of WARD & BRADY (2003) data by the same software that they used (PAUP 4; SWOFFORD 2002) gives the same results but allows insights into some partial output that receives insufficient attention in their paper or is completely omitted from it. Apomorphy tracing, some character analysis, and graphic display of these same data was performed by means of MacClade 4.03 (MADDISON & MADDISON 2001).

BROWN & TAYLOR (1970), SNELLING (1981) and PETRULEVICIUS (1999) already included in the subfamily Myrmeciinae the two South American fossil genera *Ameghinoia* Viana & Haedo Rossi and *Polanskiella* Rossi de García as proposed by WARD & BRADY (2003). In addition, DLUSSKY & PERFILIEVA (2003) consider both names to be junior synonyms of *Archimyrmex* Cockerell, 1923, a genus that DLUSSKY & PERFILIEVA (l. c.) place equally in the subfamily Myrmeciinae considered separate from the Prionomyrmecinae. In the following pages *Archimyrmex* is regarded accordingly as the oldest available name for all the New World fossils as already done also by BOLTON (2003). Using the name *Archimyrmex* instead of *Ameghinoia*/*Polanskiella* is the sole difference between the data used for the present paper and those of WARD & BRADY (2003).

RESULTS

Under the title "Reclassification of the Myrmeciinae" WARD & BRADY (2003: p. 375) state: "The results given here establish with high certainty the monophyly of a group containing *Myrmecia*, *Nothomyrmecia* and *Prionomyrmex*". I can hardly disagree with this statement; in fact this discovery is precisely the same result obtained by BARONI URBANI (2000, see e. g. his Fig. 7 and WARD & BRADY's

Fig. 16). These figures are identical except for the separation of the two Baltic Eocene species visible only in WARD & BRADY (2003), a separation imposed *a priori* by WARD & BRADY (l. c.).

The taxonomic and nomenclatorial changes proposed by WARD & BRADY have nothing to do with it and are justified by the authors (page 375) "in the interests of informativeness and utility". I suppose it signifies that the number of synapomorphies for *Prionomyrmex* and "*Nothomyrmecia*" treated separately is greater than the number of synapomorphies unifying them. If my understanding is correct, this same idea is expressed again in the same page as "we provide strong evidence for the monophyly of *Prionomyrmex* (94% bootstrap support), even stronger than indicating a sister-group relationship between *Prionomyrmex* and *Nothomyrmecia* (85%)". Translated into simple English, this means that the two Baltic Eocene species are more closely related to each other than to the extant Australian representative, another fact never doubted by anybody. While describing the second Eocene species (*P. janzeni*), I stressed that it differs from the first (*P. longiceps*) only by the pilosity of the first antennal segment... Nonetheless, a bootstrap analysis of the same data including the American fossils of the genus *Archimyrmex* as suggested by WARD & BRADY (2003) implies placement of the three generic names (*Archimyrmex*, *Nothomyrmecia*, and *Prionomyrmex*) in a unique clade whose oldest available name remains *Prionomyrmex* (see later, my Fig. 4). This may explain why WARD & BRADY (2003) added the New World fossils to their data matrix of Appendix 1 and cleared them from its relevant output in their Fig. 16.

WARD & BRADY (2003:376) support generic separation between *Nothomyrmecia* and *Prionomyrmex* by means of a list of six apomorphies for the first and four for the second. Both the count and the list are erroneous. Since the monophyly of *Prionomyrmex* (which was treated as paraphyletic to *Nothomyrmecia* by BARONI URBANI 2000) seems to be the major result of WARD & BRADY (2003) it becomes necessary to critically examine the new synapomorphies discovered by WARD & BRADY.

Fig. 1 gives the MacClade tracing of all apomorphies for the taxa under discussion and on the same tree as the one of Fig. 16 of WARD & BRADY (2003). In it three (not four) synapomorphic characters should characterize the fossil *Prionomyrmex*. All these characters

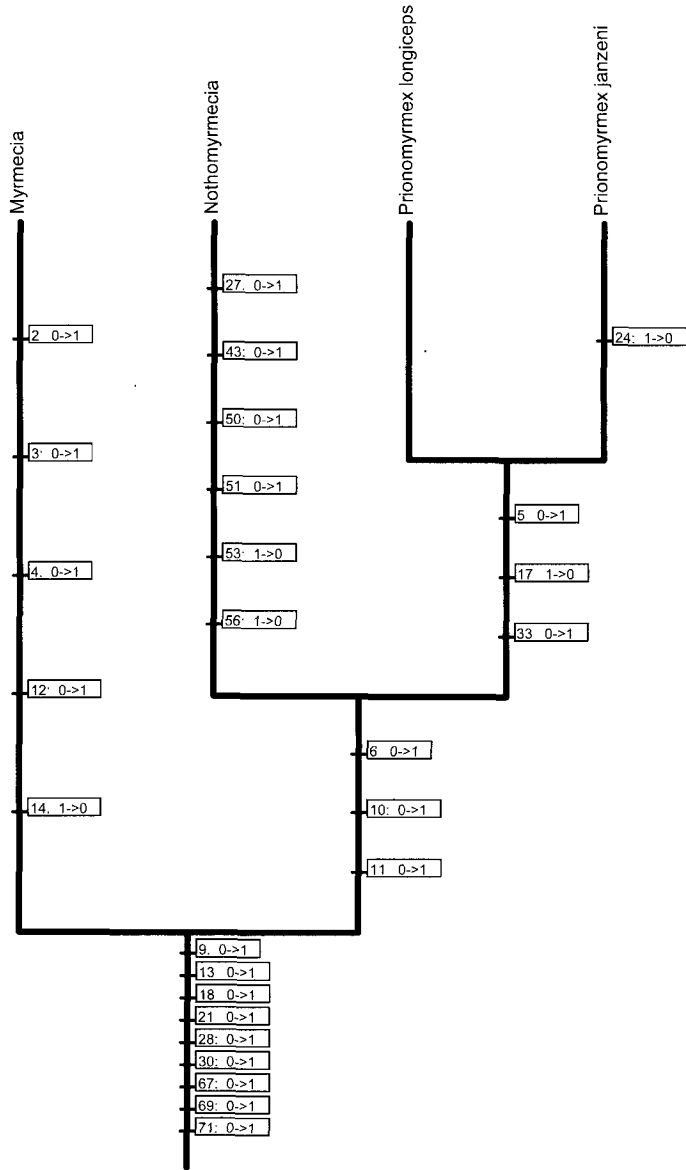


Fig. 1 - Phylogeny of the ingroup species considered by WARD & BRADY (2003) according to BARONI URBANI (2000, Fig. 7) and WARD & BRADY (2003, Fig. 16), drawn from the data of WARD & BRADY (2003). The boxes show synapomorphic character changes on each branch. Character numbering and coding from WARD & BRADY (2003).

are introduced by WARD & BRADY (2003) and were not considered by BARONI URBANI (2000). These are the following:

1. Anterior clypeal margin acuminate instead of rounded. Fig. 2 shows the clypeal morphology in *Myrmecia pyriformis* (A), a representative of the undoubted sister group of both “*Nothomyrmecia*” and *Prionomyrmex*, in *Prionomyrmex* (= *Nothomyrmecia*) *macrops* (B) and in *P. janzeni* (C). WARD & BRADY claim that A and B share the same character state and C is apomorphic for *Prionomyrmex*. I regard Fig. 2 as an ample demonstration of the fallacy of this contention.

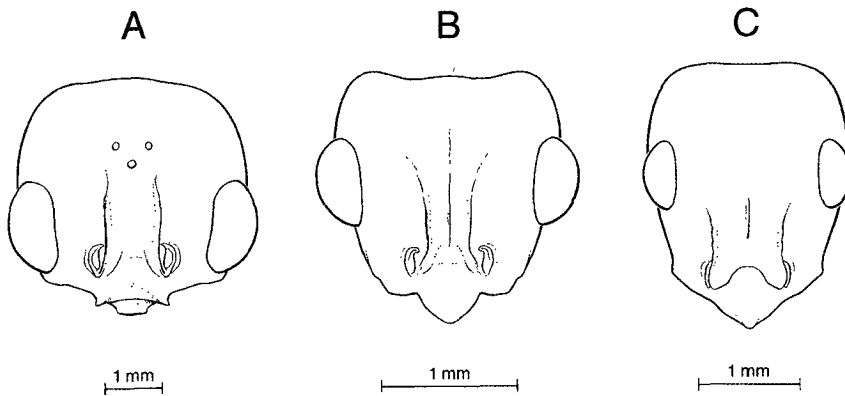


Fig. 2 - Clypei of *Myrmecia pyriformis* Smith (A), *Prionomyrmex macrops* (Clark) (B), and *Prionomyrmex janzeni* Baroni Urbani (C). In order to revive the genus *Nothomyrmecia*, WARD & BRADY (2003, Appendix 1, character # 5) code A and B as sharing the same character state and C as genus-level apomorphy for the fossil *Prionomyrmex* only.

2. First funicular segment shorter (instead of longer) than the third. This character is erroneously given as apomorphic for “*Nothomyrmecia*” in WARD & BRADY’s (2003: tab. 5). It is particularly surprising since WARD & BRADY (2003, Appendix 1) code it *a priori* as unique (i. e. apomorphic) for the Baltic fossils as opposed to all the Recent Australian ingroup species. Both, coding and inter-

pretation of this character are wrong since there are no remarkable differences between the Baltic species and e. g. *Myrmecia gulosa* (see OGATA 1991: fig. 365). I see no distinction between the fallacy of this and the one of the former "synapomorphy".

3. Presence of minuscule propodeal spines. Anyone with the slightest acquaintance with ant systematics is aware of the risk of separating species by means of this character. In the few instances in which propodeal spines are used as a generic character, they are of a much greater order of magnitude. The use of propodeal spines of this order of magnitude as a genus-level apomorphy by WARD & BRADY remains unprecedented.

WARD & BRADY's Tab. 5 also records as apomorphy for the fossils a character not appearing in the list of characters used to draw their phylogeny, the ratio scape length/head width. According to WARD & BRADY (l. c.) this ratio should be ~ 1.10 in "*Nothomyrmecia*" and ~ 1.25 in *Prionomyrmex*. Within the undoubted sister group of this clade, i. e. among *Myrmecia*, this same ratio varies between 0.72 and 1.36 (OGATA 1991, tab.2).

I think it unnecessary to analyse in detail also the six pretended apomorphies of "*Nothomyrmecia*". Lack of convincing apomorphies for *Prionomyrmex* renders it automatically paraphyletic to *Nothomyrmecia* and the oldest available name for both. This argument is a principle of phylogenetic systematics accepted also by WARD & BRADY (p. 375). WARD & BRADY warn nonetheless that "the 'paraphyly argument' can be turned on its head: there is a possibility that a taxon formed by the union of *Prionomyrmex* and *Nothomyrmecia* would itself be paraphyletic since there are South American fossil taxa to which *Nothomyrmecia* may be closely related".

If it were so, however, *Prionomyrmex* remains the oldest available name for all these ants. Surprisingly, except for conversational allusions, the paper by WARD & BRADY contains no phylogenetic reconstructions showing this possibility.

I obviate this need of inclusion by re-computing a majority-rule tree after 10,000 bootstrap replicates of WARD & BRADY's MORPH1 data using the Vespidae as outgroup. The resulting tree (Fig. 3) is identical to the one of WARD & BRADY's Fig 21, except for the name of the American fossils, called in my figure *Archimyrmex* according to DLUSSKY & PERFILIEVA (2003). *Archimyrmex*'s inclu-

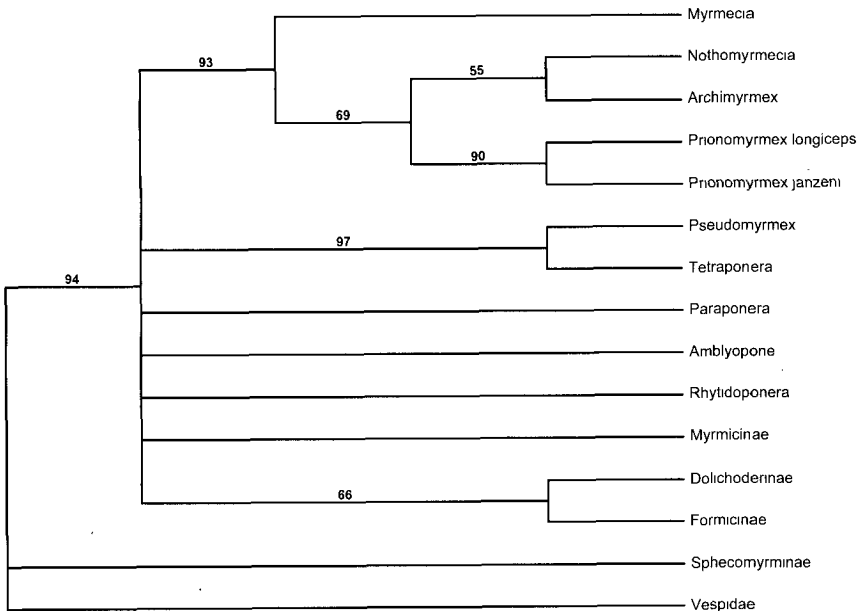


Fig. 3 - 50% majority-rule consensus tree resulting from 10,000 bootstrap replicates of WARD & BRADY's MORPH1 data using the Vespidae as outgroup. The tree is identical to the one of WARD & BRADY's Fig 16, except for the omission in the latter of the two South American fossils that these authors added to their data matrix and cleared from their figure. These fossils, called by WARD & BRADY's *Ameghinoia* and *Polanskiella*, are called *Archimyrmex* here, as suggested by DLUSSKY & PERFILIEVA (2003).

sion shows that, if the paraphyly argument should be applied to it, *Archimyrmex* Cockerell, 1923 becomes the senior synonym of WARD & BRADY's revived name *Nothomyrmecia* Clark, 1934 and *Prionomyrmex* Wheeler, 1915 will either not be affected by it, or it will become the oldest available name for the whole clade as already suggested by BARONI URBANI (2000).

This conclusion is reinforced by the apomorphy listing of Fig. 4. In it the sole synapomorphy of *Nothomyrmecia*+*Archimyrmex* is WARD & BRADY's character No. 43, presence of a pedunculate petiole. Fig. 5 shows the variation of the petiolar pedunculation among a sample of the better observable species discussed here and should justify my reluctance to consider it as phylogenetically significant at genus level.

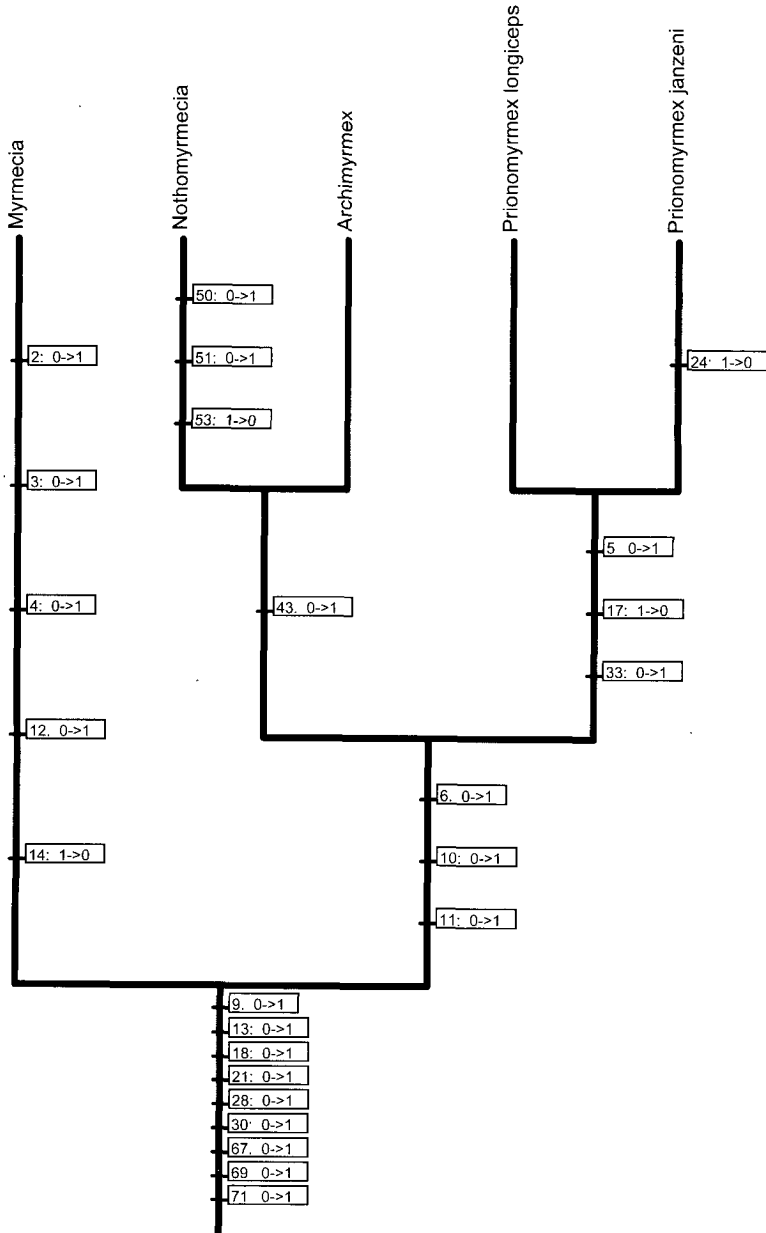


Fig. 4 - Detail of the same tree of Fig. 3 including only the taxa under discussion. Data and character numbering after WARD & BRADY (2003). Synapomorphy list drawn by MacClade 4.3 (MADDISON & MADDISON 1992).

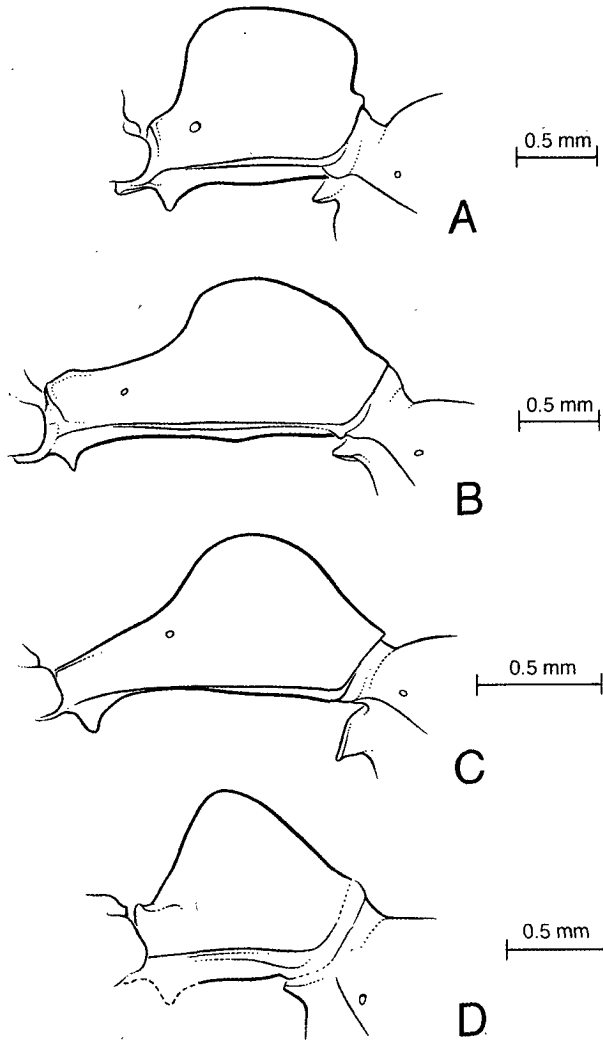


Fig. 5 - Comparable species-level variation in the morphology of the postpetiole among the two sister subfamilies and genera, i. e. Myrmeciinae (genus *Myrmecia*, figures A and B) and Prionomyrmecinae (genus *Prionomyrmex*, figures C and D). A) *Myrmecia gilberti* Forel, B) *Myrmecia nigriceps* Mayr, C) *Prionomyrmex macrops* (Clark), D) *Prionomyrmex janzeni* Baroni Urbani. According to WARD & BRADY'S (2003) coding, the pedunculate condition (here visible in *Myrmecia nigriceps* and *Prionomyrmex macrops*) is the sole "synapomorphy" joining unequivocally the Australian *Prionomyrmex* (C) and the poorly known fossil *Archimyrmex* in a genus-level clade separate from the fossil *Prionomyrmex*.

DISCUSSION

I regard the explanations and the details given above as largely sufficient to revive the nomenclature already proposed by BARONI URBANI (2000), i. e.

Subfamily Prionomyrmecinae Wheeler, 1915. Status revived.

= Tribe Prionomyrmecini Wheeler; WARD & BRADY 2003.

= Subfam. Myrmeciinae Emery, 1877; WARD & BRADY 2003, in part.

Notice that BARONI URBANI (2000) changed only the nomenclature resulting from the literature: the underlying classification already existed, was originally proposed by CLARK (1951), revived by TAYLOR (1978) and since then universally accepted. The subfamily Prionomyrmecinae is characterized by the following worker (and probably gyne) apomorphies: 1) presence of the lateral clypeal carina, 2) masticatory margins of the mandibles in opposition (instead of crossing), 3) presence of the setiform cuticular projection on the masticatory margin of the mandibles, 4) presence of the ventral stridulitrum.

The Prionomyrmecinae (under the name Nothomyrmeciinae) were first proposed subfamilial status by CLARK (1951) in a frequently blamed book where 15 ant subfamilies instead of 9 as in the previous literature are recognized. CLARK's proposal is rather eccentric for having been made succinctly in an identification key to the Australian ant subfamilies. It has, however, the advantage of offering an immediate comparability term with other, established ant subfamilies. The curious taxonomic history of this subfamily continues with BROWN (1954: 22) reaction stating, "such immoderate and arbitrary subfamily revisions as CLARK's are not likely to gain the support of many myrmecologists". A few years later, rediscovery of *Nothomyrmecia* by R. W. TAYLOR (1978) seemed to render inevitable resurrection of CLARK's subfamily Nothomyrmeciinae, an achievement supported by a broad array of subsequent papers and different scientists. BOLTON (2003) recognizes 25 ant subfamilies including 11 of those recognized by CLARK (1951) but not CLARK's broadly supported Nothomyrmeciinae. The contradiction of this way of thinking is that, in this same work, BROWN's (1954) paper criticizing so severely CLARK's classification is cited as "this famous paper [that] marked the beginning of modern investigations on ant classification and phylogeny". Nonetheless, in BOLTON (l. c.) *Priono-*

myrmex, is denied subfamilial rank by simply referring to WARD & BRADY's paper still in press and without adding additional evidence or corroboration.

I have no strong opinion about the subfamilial status of the Prionomyrmecinae but a conservative attitude is compulsory considering the weakness or lack of arguments brought by WARD & BRADY (2003) and by BOLTON (2003) against the uncontested opinion available in the last 25 years of myrmecological literature.

Only one genus can be attributed with certainty to this subfamily:

Genus *Prionomyrmex* Mayr, 1868
= *Nothomyrmecia* Clark, 1934. Synonymy by BARONI URBANI 2000 revived here.

From all the most significant data sets for these ants, i.e. BARONI URBANI et al. (1992), BARONI URBANI (2000) and WARD & BRADY (2003), the sister group of the Prionomyrmecinae results the subsequent:

Subfamily Myrmeciinae Emery, 1877
Myrmeciinae Emery; WARD & BRADY, 2003, in part.

The following worker and, where it applies, gyne apomorphies, characterize this subfamily: 1) presence of the labial protrusion, 2) clypeo-labral connection exposed, 3) presence of an anteromedian clypeal depression, 4) reduction of the malar area, 5) presence of worker ocelli, 6) mid and hind metatarsi with sulcus, 7) fusion of the presclerites of abdominal segment 4.

The sole genus that can be included with certainty in this subfamily is *Myrmecia* Fabricius, 1804.

WARD & BRADY's (2003) original result restricts to the suggested divergence times between a sample of ant taxa based on Bayesian analysis. Their estimate of 74 million years divergence between the subfamilies Myrmeciinae and Prionomyrmeciinae and 99 million years between the latter and the Dolichoderinae is perfectly consistent with their understood morphological divergence and classification in three separate subfamilies as it is established in the literature.

Inclusion of the two South American fossil genera *Ameghinoia* and *Polanskiella* and/or of their senior synonym *Archimyrmex* in one or the other of these subfamilies remains an interesting con-

ture difficult to justify or to refute on the base of unequivocal data. None of the true or presumed subfamilial synapomorphies listed by WARD & BRADY (2003) and by myself (2000 and present paper) can be examined with confidence in them.

I have neither strong opinions on the subject nor objections to accepting one or the other of these judgements. In WARD & BRADY's MORPH1 matrix these ants are scored for 17 characters out of 74 considered. I would recommend omitting these names from future cladistic analyses to avoid discussion about too weakly supported trees and proliferation of non-data supported phylogenetic reconstructions.

Consideration of the Eocene Colorado fossil genus *Archimyrmex* as belonging to either of the *Myrmecia* and *Prionomyrmex* clades, however, reverses WARD & BRADY's (2003: 378) conclusion about a "southern origin" of the "myrmeciines": the oldest known fossils of both subfamilies discussed in the present paper are from the northern hemisphere.

OVERVIEW

The current trend in taxonomy is to focus on phylogenetic relationships between organisms and to leave nomenclatorial issues to taxonomy users needing a name for the objects of their attentions.

A positive aspect of the present situation is that WARD & BRADY (2003) perfectly agree with BARONI URBANI (2000) on all phylogenetic reconstructions. The differences are restricted to subjective aspects of taxonomic rank and the resulting nomenclature.

In this case users of these results are not only museum curators reluctant to change again the labels under their specimens, but, at least in the case of *Prionomyrmex*, several scientists who investigated various aspects of physiology, ecology, behaviour, genetics, etc. of the famous "dinosaur ant".

Accepting WARD & BRADY's (2003) opinions will render the "dinosaur ant" paraphyletic to the fossil *Archimyrmex* and, since the latter is the oldest available name, the "dinosaur ant" should be called "*Archimyrmex macrops*".

This is definitely not "in the interest of informativeness and utility" as stated by WARD & BRADY (2003: 375).

Moreover, negating to *Prionomyrmex* a subfamilial rank separate from *Myrmecia* would greatly diminish its interest as presumed archetypal living ant, which received the names of living fossil, and "dinosaur ant". This will reduce also the relevance of all the published papers already devoted to it and referring to it in this sense.

The latter, of course, is not a scientific argument. It is just a remark.

In the present paper I blame the speciousness of the arguments developed by WARD & BRADY (2003) with the sole intent of refusing a nomenclature recently supported and only partly proposed in one of my previous papers (BARONI URBANI 2000).

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ABSTRACT

The phylogenetic relationships between the Recent Australian and the Baltic Eocene ant genera *Myrmecia*, *Nothomyrmecia* and *Prionomyrmex* are investigated again by means of the same data used by WARD & BRADY (2003). These data, derived from BARONI URBANI (2000) after considerable changes and additions of characters and inclusion of new taxa, regularly allow construction of the same phylogeny proposed by BARONI URBANI (2000) with simple addition of the poorly known genus *Archimyrmex* not considered by BARONI URBANI (2000).

Inclusion by WARD & BRADY (l. c.) of the fossil genus *Archimyrmex* in their data and in their discussion (under the names of its junior synonyms *Ameghinoia* and *Polanskiella*) contrasts with its exclusion from most of their outputs. Blind acceptance of WARD & BRADY (2003) character interpretation would force recognition of three genera, i. e. *Myrmecia* (Recent Australian), *Archimyrmex* (= *Nothomyrmecia*), including three New World fossils and one extant Australian species, and *Prionomyrmex*, including two Baltic Eocene species. It is suggested to exclude *Archimyrmex* from future phylogenetic analyses until its fragmentary knowledge will be not improved.

Critical examination of dubious generic characters introduced by WARD & BRADY (2003), discussed in this paper and entirely supported by the last 25 years of publications-rich ant literature maintains the presence of two ant subfamilies, Myrmeciinae and Prionomyrmecinae including one genus each, *Myrmecia* and *Prionomyrmex*. Merging the two subfamilies into one remains an opinion expressed by WARD & BRADY (2003) without support of new data or significant facts. WARD & BRADY's (2003: 378) conclusion that the ants considered in this paper should have a "southern origin" is rejected: all the oldest known true or presumably related fossils, i. e. the Baltic Oligocene *Prionomyrmex* and the Eocene Colorado *Archimyrmex* are from the northern hemisphere.

RIASSUNTO

Filogenesi e biogeografia della sottofamiglia di formiche Prionomyrmecinae (Hymenoptera, Formicidae).

Si riesaminano i rapporti filogenetici tra i generi di formiche *Myrmecia* (recente australiano), *Nothomyrmecia* (recente australiano) e *Prionomyrmex* (oligocenico dell'ambra baltica) sulla base della matrice di dati usata da WARD & BRADY (2003). Questi dati, ripresi da BARONI URBANI (2000), nonostante notevoli modifiche ed aggiunte di caratteri e di taxa, conducono inevitabilmente alla stessa ricostruzione filogenetica proposta da BARONI URBANI (2000) con la sola aggiunta del genere fossile *Archimyrmex*, escluso da BARONI URBANI (2000) perché a morfologia quasi sconosciuta. L'inclusione da parte di WARD & BRADY (2003) di *Archimyrmex* (sotto il nome dei due suoi sinonimi, *Ameghinoia* e *Polanskiella*) contrasta con la sua esclusione dalla maggior parte delle figure e dei risultati.

L'accettazione incondizionata dei caratteri di WARD & BRADY (2003) implica il riconoscimento di tre generi, *Myrmecia* (recente australiano), *Archimyrmex* (= *Nothomyrmecia*) (con tre specie fossili americane ed una specie recente australiana) e *Prionomyrmex* (due specie oligoceniche del Baltico). Si suggerisce inoltre di escludere da successive analisi filogenetiche il genere fossile americano *Archimyrmex* fino a quando se ne avranno conoscenze meno frammentarie.

Un'analisi critica dei caratteri introdotti da WARD & BRADY (2003) interamente sostenuta dagli ultimi, ricchi 25 anni di bibliografia mirmecologica, conferma la classificazione tradizionale con due sottofamiglie Myrmeciinae e Prionomyrmecinae comprendenti un genere ciascuna, *Myrmecia* e *Prionomyrmex*. La loro fusione in una sola sottofamiglia non risulta dai dati forniti da WARD & BRADY (2003). La deduzione biogeografica di WARD & BRADY (l. c.) secondo cui tutte le formiche qui discusse avrebbero "un'origine meridionale" è invalidata dal fatto che tutti i più antichi fossili appartenenti o simili a questo clade provengono dall'emisfero settentrionale.

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