

Rediscovery of the Baltic amber ant genus *Prionomyrmex* (Hymenoptera, Formicidae) and its taxonomic consequences

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ABSTRACT

Two specimens of the Baltic amber monotypic ant genus *Prionomyrmex*, known only on a few specimens supposed to have been destroyed during the Second World War, are described as a new species, *P. janzeni*. *P. janzeni* shows remarkable similarities with the Recent Australian genus *Nothomyrmecia*. A parsimony analysis of the relationships between the three most closely related genera, i. e. *Myrmecia* (Recent Australian), *Nothomyrmecia* (Recent Australian), and *Prionomyrmex* (Baltic Eocene) based on 34 morphological characters, suggests the following phylogeny: (*Myrmecia*, (*Nothomyrmecia*, *Prionomyrmex*)). In this reconstruction, however, *Nothomyrmecia* is characterised by only two, doubtful, apomorphies and *Prionomyrmex* is paraphyletic to it. As a consequence of this, the following nomenclature changes are proposed:

1. The genus *Nothomyrmecia* Clark, 1934 is a junior synonym of *Prionomyrmex* Mayr, 1868.
2. *Prionomyrmex macrops* (Clark) is a new combination (from *Nothomyrmecia*).
3. The subfamily Nothomyrmecinae Clark, 1951 is a junior synonym of the tribe Prionomyrmecini Wheeler, 1915.
4. The tribe Prionomyrmecini Wheeler, 1915 is raised to subfamilial status (Prionomyrmecinae, new status).

In this classification the Myrmecinae result characterised by four apomorphies and the Prionomyrmecinae by three: one undoubted, the appearance of a lateral clypeal carina, and two verified in the Recent species only and assumed by extrapolation from similarity in "Bauplan" to be present in the fossils as well, presence of a ventral stridulitrum and of a biaculeate subgenital plate.

It is stressed that a hypothetical future demonstration of absence of the last two characters in the fossil species will not affect the classification proposed in this paper. This hypothetical discovery, in fact, would render again *Prionomyrmex* paraphyletic to *Nothomyrmecia* and hence its senior synonym.

Introduction

The fossil ant genus *Prionomyrmex* was destined by Mayr (1868) to include the new species *longiceps* based on a single, badly preserved, worker in Baltic amber. In spite of the diffi-

ZUSAMMENFASSUNG

Zwei neue Exemplare der monotypischen Ameisengattung *Prionomyrmex* aus Baltischem Bernstein, bisher nur von wenigen Exemplaren bekannt, die seit dem zweiten Weltkrieg verschollen sind, werden als neue Art *P. janzeni* n.sp. beschrieben. *P. janzeni* zeigt bemerkenswerte Ähnlichkeiten mit der rezenten australischen Gattung *Nothomyrmecia*. Eine auf 34 Merkmalen basierende cladistische Analyse der drei nächstverwandten Gattungen, i.e. *Myrmecia* (rezent, Australien), *Nothomyrmecia* (rezent, Australien) und *Prionomyrmex* (baltisches Eozän) legt folgende Verwandtschaftsbeziehungen nahe: (*Myrmecia*, (*Nothomyrmecia*, *Prionomyrmex*)). Bei dieser Gruppierung ist *Nothomyrmecia* allerdings nur durch zwei zweifelhafte Apomorphien gegenüber *Prionomyrmex* ausgezeichnet; *Prionomyrmex* nimmt gegenüber *Nothomyrmecia* eine paraphyletische Stellung ein. Deshalb werden folgende nomenklatorische Änderungen vorgeschlagen:

1. Die Gattung *Nothomyrmecia* Clark, 1934 ist ein Juniorsynonym von *Prionomyrmex* Mayr, 1868.
2. *Prionomyrmex macrops* (Clark), nov. comb. (von *Nothomyrmecia*).
3. Die Tribus Prionomyrmecini Wheeler, 1915 wird auf Unterfamilienrang erhoben (Prionomyrmecinae, nov. stat.).
4. Die Unterfamilie Nothomyrmecinae Clark, 1951 ist ein Juniorsynonym von Prionomyrmecini Wheeler, 1915.

In dieser Klassifikation sind die Myrmecinae durch vier und die Prionomyrmecinae durch folgende drei Apomorphien gekennzeichnet:

Die erste, das Vorhandensein eines lateralen clypealen Kiels wurde bei allen Taxa festgestellt. Die zwei weiteren, ein ventrales Stridulationsorgan und eine zweispitzige Subgenitalplatte, konnte nur bei den rezenten Arten verifiziert werden; ihr Vorhandensein bei den fossilen Taxa kann nur durch Extrapolation angesichts der hohen Ähnlichkeit im "Bauplan" vermutet werden.

Sollte in Zukunft nachgewiesen werden, dass die beiden letztgenannten Merkmale bei den fossilen Arten fehlen, so würde dies nicht die hier vorgeschlagene Klassifikation berühren. Die hypothetische Entdeckung würde wiederum in einer paraphyletischen Stellung von *Prionomyrmex* gegenüber *Nothomyrmecia* resultieren, wodurch *Prionomyrmex* als älteres Synonym Priorität erhält.

culty of observation of this single specimen, Mayr noticed accurately its close relationships with the Recent Australian genus *Myrmecia*. A record of a second, petrified, probable

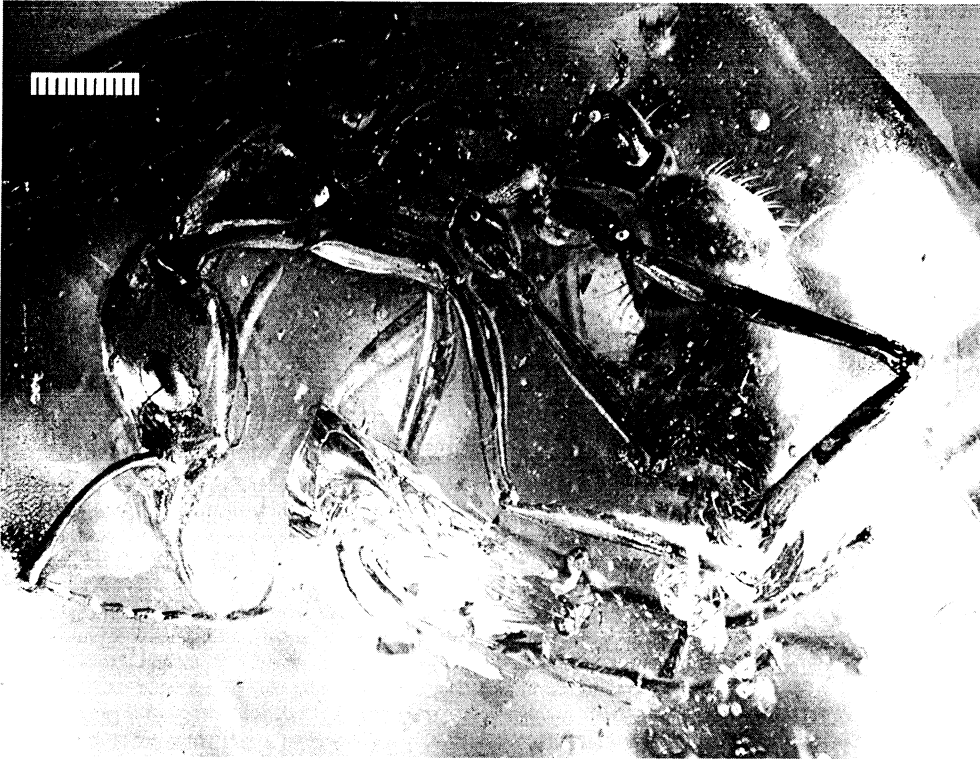


Fig. 1. Amber specimen No. 1, lateral view. Distance between the scale bars 0.1 mm.

Prionomyrmex species from the Upper Miocene of Baden (Scudder, 1895) needs confirmation and seems to have been ignored by all subsequent ant specialists.

Nearly half a century after Mayr, Wheeler (1915) re-described *P. longiceps* on seven workers in different preservation conditions and on a male without gaster. His description can be regarded as exhaustive even for modern standards and is complemented by a reasonable figure of a worker in the position in which it is embedded in amber, i. e. without stretching or orienting some body parts to allow optimal view of the morphology. Wheeler emphasised again the close relationship of *Prionomyrmex* with the Recent Australian *Myrmecia*, a genus constituting alone what was at that time the monotypic tribe Myrmeciini (today subfamily Myrmeciinae), considered until recently as the less specialised of all known ants. Wheeler (l. c.) went even farther in stressing the systematic position of *Prionomyrmex* by creating for it the new tribe Prionomyrmicini (sic), related to the Australian Myrmeciini. The interest of this ant was immediately clear to all myrmecologists, although it is very likely that nobody ever examined a specimen of *Prionomyrmex* since Wheeler's time. The concern for *Prionomyrmex* had a last peak when Clark (1934) described another new genus of extant Australian ants close to *Myrmecia*: *Nothomyrmecia*. In the original description Clark (l. c.) wrote correctly that the new genus appears 'somewhat similar' to the Baltic amber fossil *Prionomyrmex* (unknown to him) 'but the nodes are different'. Rumours of complete destruction during the Second World War of the Königsberg amber collection

where the *Prionomyrmex* material was preserved probably also contributed to decrease the popularity and the number of literature citations of this genus.

This was not the case for *Nothomyrmecia*, judged to represent a subfamily of its own by Clark (1951) and object of a paper appealing to its further collection by Brown & Wilson (1959).

Nothomyrmecia was eventually collected again (Taylor, 1978) and this finding persuaded previously dissenter ant specialists that the genus was worth of separate subfamilial status within the Formicidae as already suggested by Clark (1951). This was destined to become one of the most famous ant records of the century.

The relationships between *Nothomyrmecia* and *Prionomyrmex* are often mentioned in the paper by Taylor (l. c.) and in other papers as well but without adding to the scanty remarks already made by Clark (1934) new information on the relationships between the Australian species and the Baltic amber fossil.

On the other hand, the renown of *Prionomyrmex* had its finishing stroke when Grimaldi et al. (1998) excluded it from their phylogeny of the Formicidae on the basis of a rule (invented by themselves) banning from consideration taxa scored for less than 30% of the characters they employed.

Information on *Nothomyrmecia* is easily available to anyone today. There are representative specimens in different collections and a set of published drawings of dorsal and lateral view of the worker (Clark, 1934), of the mandibular dentition

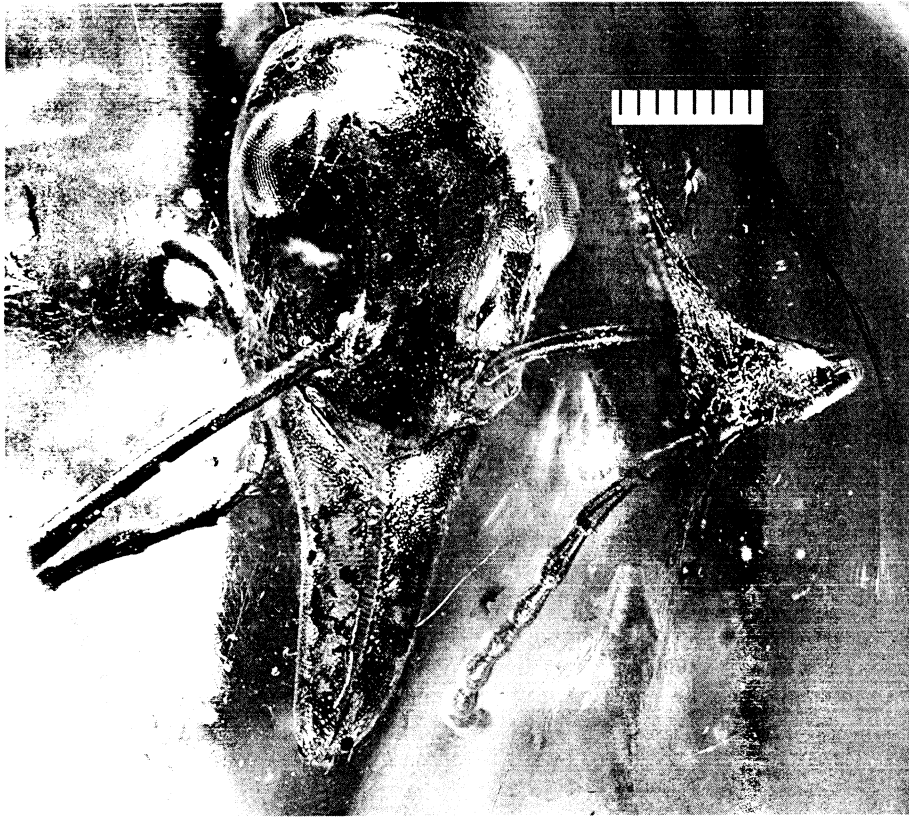


Fig. 2. Amber specimen No. 1, dorsal-oblique view of the head showing the eyes and the mandibles. Distance between the scale bars 0.1 mm.

(Brown & Wilson, 1959) and of the male and gyne wings (Taylor 1978). SEM photographs of the worker and gyne and details thereof have been also published by Taylor (1978) and by Bolton (1994). Wheeler et al. (1980) published drawings and SEM photographs of the preimaginal stages. In addition, a set of behavioural papers contain superb examples of black and white and colour photographs and drawings of workers, gynes and larvae in different body postures.

The current fame of *Nothomyrmecia*, however, implies two contradictory attitudes: on one hand the interest for *Nothomyrmecia* derives essentially from its similarity with *Prionomyrmex*, and, on the other, it overrules the attention for *Prionomyrmex*, i. e. of the main justification for its own celebrity.

The fact that the old, less glamorous figure of *Prionomyrmex* by Wheeler (1915) appeared in a journal of difficult access may explain in part the unequal attention received by the two genera.

The opportunity to examine two perfectly preserved specimens of *Prionomyrmex* representing a still undescribed species justifies the publication of the present report.

Material and Methods

I received the two Baltic amber specimens described in the present paper respectively by Dr. Hans Pohl of the Depart-

ment of Zoology, Hessisches Landesmuseum, Darmstadt and by Dr. Wolfgang Weitschat of the Geological-Palaeontological Institute and Museum Seevetal, University of Hamburg. The first specimen originally belonged to the collection of Mr. Jens-Wilhelm Janzen, Hamburg and the second to the collection Jonas Damzen, Vilnius. Mr. Janzen, however, donated his specimen to the Geological-Palaeontological Institute and Museum Seevetal of the University of Hamburg. This same Museum acquired the second specimen as well.

A short description of the two amber samples is as follows:

Specimen No. 1 (ex coll. Janzen) (Figs. 1, 2 & 3). Half-oval very transparent amber sample cut straight on one side. Approx. 19x15x7 mm. The ant is intact except for the right side of the first gastral segment, slightly affected by polishing. The vision of the specimen, otherwise perfect or only slightly hindered by few fissures and air bubbles, is reduced by the presence of whitish impurities on some body parts. The impurities do not prevent examination of the external morphology but mask at different extents the microsculpture and the pilosity.

Specimen No. 2 (ex coll. Damzen, No. 103) (Fig. 4). Semi-rectangular, very transparent amber sample of ca. 50x31x8 mm. The ant, virtually intact, lies in one corner of the amber sample and only the claws of the left hindleg have been damaged during polishing. A milky covering prevent the observation at a lesser extent and only on the gaster and part of the petiole.



Fig. 3. Amber specimen No. 1, dorsal view of the anterior clypeal border and of the mandibles showing the characteristic denticulation and the seta-like cuticular projections. Distance between the scale bars 0.1 mm.

Given the excellent preservation conditions and the facility of examination of both specimens no further cutting or polishing of the amber was necessary. Observation, measurements and drawings were the standard ones with the specimens immersed in 66% sucrose solution to avoid deformation due to the curved amber surfaces as in previous works on amber (e. g. Baroni Urbani, 1994).

Specimen No. 2 is larger and better visible than No. 1 but it is probably an intercaste bearing some worker and some gyne characters. For this reason the drawings are based on specimen No. 1, presumably a typical worker.

The drawings, executed by Armin Coray, are the result of partial reconstruction since the ant was drawn in the standard posture as usual for Recent ants to allow better comparison of its morphology. In addition to this "artificial mounting", the

dorsal view of the ant needed no particular attention except trivial symmetric copying of some details better visible on one side onto the other, less visible side.

Drawing the left profile of the ant needed some additional care as follows:

Head drawn from the left side. Microscopic uncertainties on the distal half of the mandibles and weak milky covering over the eye corrected by symmetric drawing of the right side.

On the mesosoma the metapleural gland and small covered areas are drawn from the right side.

Petiole and gaster drawn essentially from the right side, only the intersegmental articulations and the apex drawn from the left side.

Left metacoxa visible only at base. Reconstructed in part from view in a different perspective and in part from the right one.

The photographs illustrating this paper are all a patchwork of several different pictures. They result from the combination of the sharpest area of each individual picture. Merging together of the best areas of different pictures is performed automatically by the software Montage Explorer, Version 1.01.003 (© Synoptics Ltd., 1998, 1999).

The cladistic analysis was performed by means of PAUP 4.0b2 (Swofford, 1998). Some graphic display of the results was obtained by means of MacClade 3.01 (Maddison & Maddison, 1992).

Description

Prionomyrmex janzeni n.sp.
(Figs 1–6)

Diagnosis: a *Prionomyrmex* species differing from the sole previously known species, *longiceps*, by the absence of pubescence at least on the scapes.

Derivatio nominis: the species is named after the enthusiastic palaeoentomologist Jens-Wilhelm Janzen who first identified the ant at generic level and generously donated the holotype to the Hamburg Museum.

Type material: holotype worker and paratype ergatogyne respectively in the amber samples No. 1 and No. 2 described in the Material Chapter and deposited in the Geological-Palaeontological Institute and Museum, University of Hamburg.

Worker description: Head elongate, with weakly convex sides and straight vertexal border. Frontal carinae moderately curved and protruding over the cephalic capsule anteriorly. Clypeus markedly angulate anteriorly and with a weak median carina. Genae bordered, antero-dorsally, by a longitudinal carina arising from the clypeus and visible on the head in full frontal view. Eyes oval, large and slightly behind the median cephalic line. Antennae slender, 12-jointed, the scape, bent backwards, trespasses the vertexal border more than twice its maximum diameter. First funicular joint shorter, second to tenth joints decreasing distally in length, the last (11th) slightly longer than the penultimate. Mandibles long, nearly 3/4 of the



Fig. 4. Amber specimen No. 2, lateral view. Distance between the scale bars 0.1 mm.

maximum head length, remarkably curved downwards; masticatory border straight, except a strong apical incurvation, and armed with a regular row of minute denticles. Palpal formula apparently 5,2. This figure can be taken with a reasonable degree of confidence, though the presence of additional, short, basal joints invisible in the amber specimens can not be categorically excluded.

Mesosoma slender; pronotal and propodeal sutures deeply impressed; the pronotal suture presumably movable; propodeum continuously curved in profile, without distinction between basal and declivous faces; a pair of minute propodeal spines; propodeal spiracle protruding and slit-shaped; metapleural gland present. Legs long and slender; mid- and hind-tibiae with two spurs, one of which pectinate; mid- and hind-metatarsi with longitudinal sulcus; claws dentate.

Petiole high, dome-shaped, with distinct, flat anterior and posterior faces.

Postpetiole strongly constricted anteriorly and weakly posteriorly, bell-shaped and distally curved in dorsal view; its articulation with the gaster broad but marked by a deep constriction. Presence or absence of a stridulitrum either ventral or dorsal impossible to ascertain in both specimens.

Gaster moderately elongate and with round sides, with 5 segments visible in dorsal view; the first segment (abdominal IV) as long as the remaining ones.

Pilosity: the whole body and legs up to the tibiae sparsely covered by weakly curved, acuminate hairs, erect or suberect, shorter on the dorsal surface and much shorter on the ventral part of the head, on the mandibles and of the mesosoma; tarsi with even shorter, subdecumbent hairs; a pair of very long ventrally protruding setae arise from the mouthparts; antennae with hairless scapes and very few, minute hairs on the funiculi.

Sculpture: most of the integument shining and very superficially punctate; a few longitudinal striae on the sides of the mesonotum and of the propodeum.

Colour apparently brown in the holotype and black in the paratype.

Measurements in mm and indices: Total Length 13.62; Head Length (maximum) (HL) 2.48; Head Width (maximum) (HW) 1.72; Scape Length (SL) 2.30; Petiole Length (maximum) (PL) 1.12; Petiole Width (maximum) (PW) 0.76; Petiole Height (maximum) (PH) 1.00; Postpetiole Length (maximum) (PpL) 1.36; Postpetiole Width (maximum) (PpW) 1.48; Gaster Width (maximum) (GW) 1.88; Cephalic Index (= $HW \times 100 / HL$) 69.35; Petiolar Index ($PW \times 100 / PL$) 67.86; Petiole and Postpetiole Index ($PW \times 100 / PpW$) 51.35; Postpetiole Gastral Index ($PpW \times 100 / GW$) 78.72.

TL of the paratype ergatogyne ~15.5.

Note: the description above is based essentially on the holotype worker and integrated, when necessary, with details better visible in the paratype ergatogyne. The measurements refer

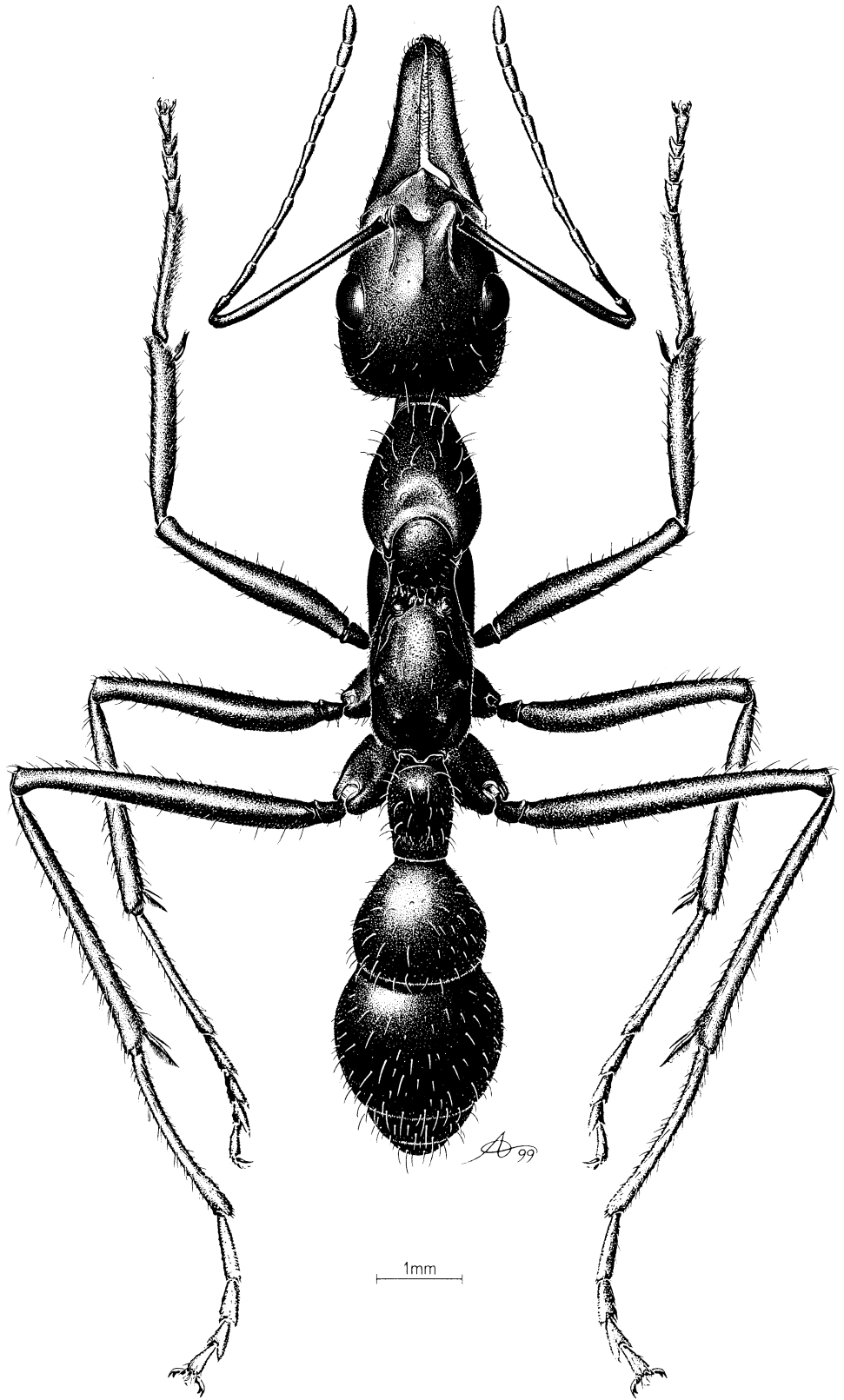


Fig. 5. *Prionomyrmex janzeni* n. sp. from Baltic amber. Holotype worker in dorsal view. The specimen is drawn as artificially re-mounted to allow optimal view of all body parts and better comparison with extant related taxa. Drawing by Armin Coray.

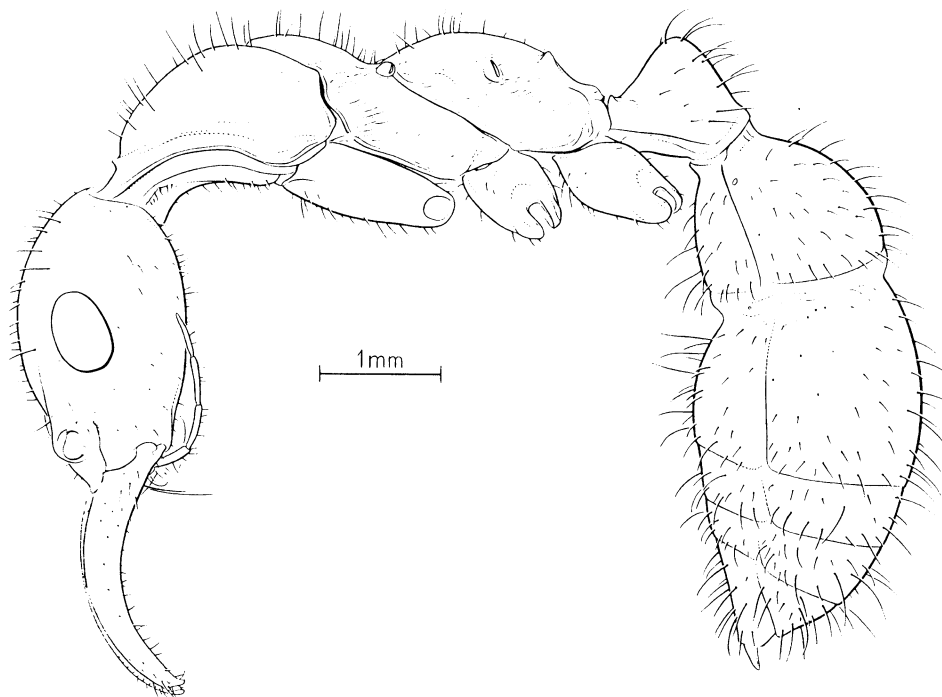


Fig. 6. *Prionomyrmex janzeni* n. sp. from Baltic amber. Schematic drawing of the holotype worker in lateral view. Legs and antennae omitted. Parts not visible on the left profile symmetrically reproduced from the right side. Drawing by Armin Coray.

exclusively to the worker for the double reason that the paratype is likely to be an abnormal individual and that, in spite of its superb preservation conditions, its posture in amber prevents orientation of several body parts on a perfectly horizontal plane as needed for a correct measurement.

Discussion

Since no specimens of the sole previously described *Prionomyrmex* species (*longiceps*) were available for the present study, comparison between the latter and *janzeni* is derived essentially from the drawing of Wheeler (1915). Several minor differences in shape and pilosity result from the comparison between the specimens described above and this drawing but, due to the diversity of the objects compared, it is difficult to evaluate their taxonomic significance. The drawing of Wheeler (1915) differs in important details (e. g. the anterior clypeal border) also from the one accompanying the original description of Mayr (1868). These differences are likely to be explained by the bad preservation conditions and by the consequent difficulty of observation of the original specimen studied by Mayr.

The material available for the present study reveal, however, at least one character of undoubted specific value resulting clearly different from all specimens previously identified as *longiceps*: both specimens of *janzeni* have perfectly hairless scapes. Wheeler's (1915) drawing of *longiceps* shows the scapes covered by dense, minute, standing hairs. This trait is equally focused in the accompanying text where it is stated that the hairs are "moderately abundant, erect or suberect,

short on the head, thorax, legs and scapes...". In a similar manner, the original description of *longiceps* by Mayr (1868) stresses the presence of a "spärlichen abstehenden Behaarung" over the whole body. Considering the material described in the present paper as closely related to but specifically distinct from *longiceps* seems, hence, the most reasonable course of action.

Rediscovery of the European Eocene *Prionomyrmex* urges reconsideration of its relationships with the extant Australian genera *Myrmecia* and *Nothomyrmecia*. The three genera are very similar to each other in habitus and share some unusual traits of presumable phylogenetic significance. Since each one of these three genera was assumed to represent a monotypic suprageneric taxon, for the purpose of the present analysis, initially, they have been all regarded as simple genera in order to assess their most probable taxonomic rank as a result of the analysis.

Table 1 gives a list of the characters potentially useful to ascertain the phylogenetic relationships between these genera coded also for their sister ant subfamilies Myrmicinae + Pseudomyrmecinae and for an undoubted common outgroup: the wasps. The close relationship between the three genera discussed here and the two subfamilies mentioned above as well as most of their respective character states are derived from Baroni Urbani et al. (1992).

One potentially meaningful character, namely the palpal formula, was not considered. The palpal formula is 6,4 in both *Myrmecia* and *Nothomyrmecia* and appears to be 5,2 in *P. janzeni*. If confirmed, the *P. janzeni* condition should be the apomorphic and the *Myrmecia*+*Nothomyrmecia* the ple-

Table 1.

Matrix of the presence (1) or absence (0) of 34 potentially significant characters among the three genera discussed in the text, two closely related ant subfamilies, and the Vespidae, included in the analysis as outgroup. Character description 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	30	31	32	33	34	
Myrmecia	1	0	0	1	0	1	1	1	0	0	1	1	0	1	1	0	0	1	0	0	1	1	1	0	1	1	0/1	0	0	1	1	0	1	0	
Myrmicinae	1	1	0	0/1	1	0	0/1	1	1	1	1	0	1	0	0	1	1	1	0/1	0	1	0/1	0	1	0	1	0	1	1	1	0/1	0/1	0/1	1	
Nothomyrmecia	1	1	1	1	?	0	1	1	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	1	0	1	0
Pseudomyrmecinae	1	1	0	0	0	0	1	1	1	0	1	1	1	0/1	0	0	0	1	1	0	1	0	0	0	1	0	1	0	0	1	1	1	1	0	
†Prionomyrmex	1	1	1	1	?	0	1	1	0	?	1	?	?	1	1	?	?	1	?	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	
Vespidae	0	1	0	0	0	0/1	0	0	0/1	0	0	0	0/1	0	0	0/1	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1

siomorphic condition. The reasons for the exclusion of this character from the analysis are twofold: 1) the proximal articulation of both, labial and maxillary palps, due to the milky covering, is not clearly visible in both amber specimens, a fact which could increase the number of segments I was able to count, and, 2) there are examples of intra-generic and of intercaste variation of the palpal formula in ants. The palpal formula may be specifically reduced as a consequence of relatively simple behavioural shifts (Gotwald, 1969). It is usually regarded as an interesting evidence for potential relationships and not as a genus-level discriminating character.

The following characters, tabulated in Table 1, are considered:

1. Worker and gyne, head position: hypognathous (0), or prognathous (1). Natural orientation of the head is particularly difficult to assess among fossils. In *Prionomyrmex* the prognathous condition is inferred from two sources: a) by homology with the known condition of *Myrmecia* and *Nothomyrmecia* with which it shares all most significant cephalic morphological traits, and b) functionally, since its long mandibles, in hypognathous position, would inevitably hit the ground during locomotion.
2. Worker and gyne, clypeus: anteriorly compressed and/or reduced (0), or protruding (1).
3. Worker and gyne, lateral clypeal carina: absent (0), or present (1).
4. Worker and gyne, mandibles: short (0), or elongate (1).
5. Worker and gyne, labial pegs: present (0), or absent (1).
6. Worker and gyne, malar area: developed (0), or reduced (1).
7. Worker, gyne and male, antennal socket: exposed (0), or not exposed (1).
8. Worker and gyne, antennal scape: short (0), or elongate (1).
9. Worker and gyne, 2nd funicular joint: elongate (0), or short (1).
10. Worker, promesonotal suture: mobile (0), or fused (1).
11. Worker and gyne, metapleural gland: absent (0), or present (1).
12. Worker and gyne, metapleural gland: without (0), or with flange (1).
13. Worker, gyne and male, metacoxal cavities: open (0), or closed (1).
14. Worker and gyne, mid and hind metatarsi: without (0), or with (1) sulcus.
15. Worker and gyne, claws: simple (0), or dentate (1).
16. Worker and gyne, A II dorsoventrally: not fused (0), or fused (1).
17. Worker and gyne, A III presternite: overlapped (0) or not overlapped (1) by pretergite.
18. Worker, A III: subequal to (0), or smaller than (1) A IV.
19. Worker, dorsal stridulitrum: absent (0), or present (1).
20. Worker, ventral stridulitrum: absent (0), or present (1).
21. Worker and gyne, A IV presclerites: absent (0), or present (1).
22. Worker and gyne, A IV presclerites: not fused (0), or fused (1).
23. Worker and gyne, A IV presclerites: short (0), or long (1).
24. Worker and gyne, A IV presternite: shorter (0), or longer (1) than pretergite.
25. Worker and gyne, sting bulb gland: absent (0), or present (1).

26. Gyne, A III: undifferentiated (0), or forming a petiole (1).
27. Male, basal hamuli: present (0), or absent (1). Taylor (1978) states basal hamuli to be present in *Nothomyrmecia* and produces a drawing (his Fig. 2A) where two sets of hamuli, one basal and one distal are visible. Grimaldi et al. (1998) assert that basal hamuli "have not been seen... in *Nothomyrmecia*". I never saw a *Nothomyrmecia* male. Presence or absence of this character in *Nothomyrmecia* does not change the topology of the unique most parsimonious tree resulting from the data. I coded the character as present, as asserted first by Taylor (l. c.) just because either coding seems to have 50% probability of being correct. I prefer leaving the truth flowing from a direct confrontation between the involved scientists.
28. Male, jugal lobe: present (0), or absent (1).
29. Male, propodeal spiracle: slit-shaped (0), or round (1).
30. Male, A IV presclerites: absent, (0), or present (1).
31. Male, cerci: absent (0), or present (1).
32. Male, subgenital plate: round (0), or biaculate (1).
33. Male genitalia: retractile (0), or not retractile (1).
34. Pupa: with cocoon (0), or naked (1).

These data allow the construction of only one most parsimonious tree of length 37 as in Fig. 7 (Consistency Index = 0.92; Retention Index = 0.80; Rescaled Consistency Index = 0.73).

From the figure one can see that *Prionomyrmex* results paraphyletic to *Nothomyrmecia*. The latter, in turn, appears to be characterised only by two, naturally correlated, putative apomorphies: character 18, secondary loss of the worker postpetiole, and character 26, secondary loss of the gyne postpetiole. I consider both these presumed apomorphies as implausible and interpret them as artefacts of character optimisation. The evolutionary sequence they imply is improbable and the lack of postpetiole in both female castes is likely to be the pleisiomorphic state under any imaginable evolutionary scenario.

Former studies not applying the cladistic principles already stressed the odd status of *Nothomyrmecia* for its lack of a differentiated postpetiole (as opposed to its presence in *Myrmecia* and, subordinately, in *Prionomyrmex*). Even accepting their point of view and the character reconstruction resulted from the previous analysis (i. e. the apomorphic status of the reduced postpetiole by interpreting it as a secondary loss), one should not overemphasise the importance of this character. Analogous different degrees of constriction between A III and A IV are known in other genera of ants, like *Proceratium* (see e. g. the species *tio* Snelling & Cover and *pergandei*

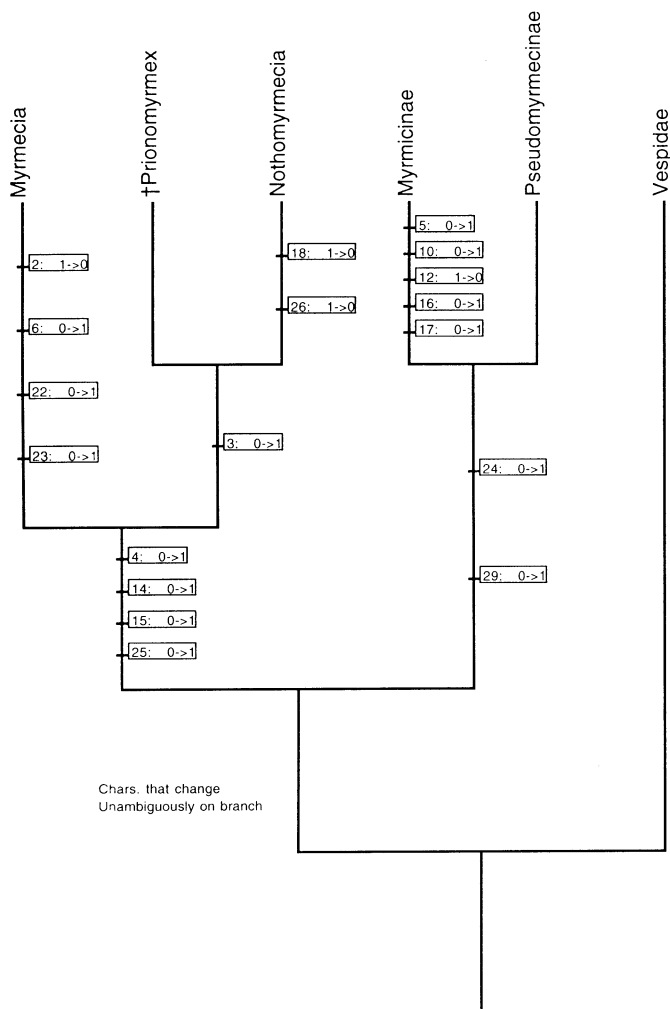


Fig. 7. Unique most parsimonious phylogeny for the taxa considered and drawn from the characters listed in Table 1. The boxes on branches indicate character changes assumed to be apomorphic. A number of undoubted apomorphies for the Pseudomyrmecinae are omitted from the data since they are irrelevant in this context.

(Emery)). In the case of the two *Proceratium* species, due to their great similarity in "Bauplan", nobody ever thought to a generic separation between the two. This great structural similarity is precisely the case of *Prionomyrmex* and *Nothomyrmecia* as well.

If *Prionomyrmex* and *Nothomyrmecia* belonged to the same fauna, extant or fossil, their generic separation would have no chance of acceptance. The sole chronological (39–50 millions of years according to Weitschat & Wichard, 1998) or continental gaps between the Baltic amber and the Recent Australian genus are a meagre argument: 26 out of 43 ant genera recorded from Baltic amber are still to be found in contemporary tropical faunas.

As far as I can imagine, only an eventual rediscovery of the *Prionomyrmex* male (already described by Wheeler, 1915, on a

damaged specimen presumably lost or destroyed during World War II) may represent a small chance of separating *Prionomyrmex* from *Nothomyrmecia*.

Until this exceptional find and the even more improbable consequent discovery of new genus-level male apomorphies for *Prionomyrmex* will occur, we are forced to conclude the following genus-level synonymy:

Genus *Prionomyrmex* Mayr

Prionomyrmex Mayr, 1868: 77. Type species: *Prionomyrmex longiceps* Mayr, by monotypy.

Nothomyrmecia Clark, 1934: 17. Type species: *Nothomyrmecia macrops* Clark, by original designation. *New synonymy*.

Included species:

Prionomyrmex longiceps Mayr, Baltic amber.

Prionomyrmex janzeni Baroni Urbani, Baltic amber.

Prionomyrmex macrops (Clark), Australia. *New combination*.

From all this it follows that the classification of the two genera in two different ant subfamilies results untenable.

The following family-group list of synonyms appears hence appropriate:

Subfam. Prionomyrmecinae Wheeler, new status

Prionomyrmecini Wheeler, 1915: 25. Type genus: *Prionomyrmex* (by monotypy). Tribe of Ponerinae.

Prionomyrmecini Brown, 1954: 22. Tribe of Myrmeciinae.

Prionomyrmecini, Baroni Urbani et al., 1992: 303. Emended spelling.

Nothomyrmecinae Clark, 1951: 16. Type genus *Nothomyrmecia* (by inference). Subfamily of Formicidae. *New Synonymy*.

Nothomyrmeciini. Brown, 1953: 1. Tribe of Myrmeciinae.

Nothomyrmecinae. Taylor, 1978: 982. Subfamily of Formicidae.

The sole genus included in the subfamily Prionomyrmecinae is *Prionomyrmex* Mayr.

I tested by means of a new parsimony analysis the apomorphy status of the newly named and newly defined subfamily Prionomyrmecinae versus its sister subfamily, Myrmeciinae, after merging the two genera *Prionomyrmex* and *Nothomyrmecia*. The results are displayed graphically in Fig. 8 and can be summarised as follows:

1. The Myrmeciinae and Prionomyrmecinae share four apomorphies, namely, i) female mandibles elongate, ii) female mid and hind metatarsi with dorsal sulcus, iii) female claws dentate, iv) sting bulb gland present (presence in the fossils inferred by parsimony character reconstruction).
2. The Myrmeciinae are characterised by the following four apomorphies. i) reduction of the female clypeus, ii) reduction of the female malar area, iii) fusion of the A IV presclerites in the female, iv) elongation of the female A IV presclerites.
3. The Prionomyrmecinae also result slightly better defined, although three out of four synapomorphies are attributed to the fossils by simple inference. These true or presumed synapomorphies are, i) presence of a lateral clypeal carina in the female castes, ii) presence of a ventral stridulitrum,

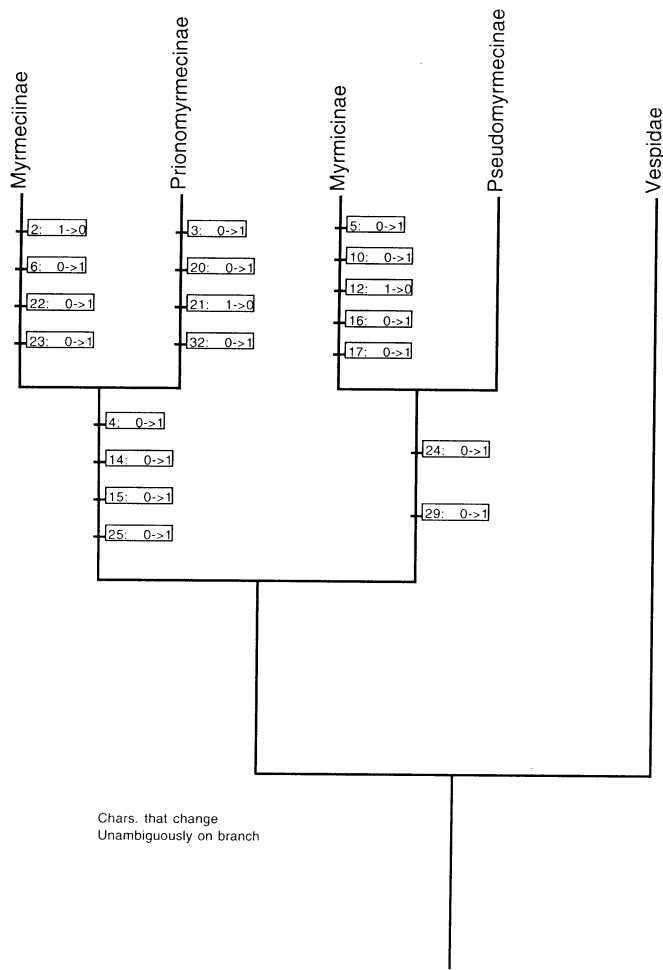


Fig. 8. Unique most parsimonious phylogeny for the taxa considered and drawn from the characters listed in Table 1 after re-attributing subfamilial status to the Myrmeciinae and after merging *Nothomyrmecia* with *Prionomyrmex* into the subfamily Prionomyrmecinae. The boxes on branches indicate character changes assumed to be apomorphic. A number of undoubted apomorphies for the Pseudomyrmecinae are omitted from the data since they are irrelevant in this context.

iii) secondary loss of the female A IV presclerites, and, iv) subgenital plate biaculate.

I must acknowledge the obvious: only the common presence of the clypeal carina appears to be a fully documented and plausible synapomorphy. The secondary loss of the A IV presclerites appears improbable. This is more likely to be a plesiomorphic character. In addition, attribution to the fossil species of the ventral stridulitrum and of the biaculate subgenital plate is due to simple parsimonious extrapolation and may result true or false.

If the above hypothetical attribution of these characters of the extant species to the two fossils will prove to be false, how-

ever, the classification presented in this paper is not destined to change. The fossil species would result paraphyletic to the Recent one and, as such, *Prionomyrmex* will equally be a senior synonym of *Nothomyrmecia*.

Taylor's (1978) definition of *Prionomyrmex macrops* as a "living-fossil" results even more pertinent.

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