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 *Notomyrmecia*. A parsimony analysis of the relationships between the three most closely related genera, i.e. *Myrmecia* (Recent Australian), *Notomyrmecia* (Recent Australian), and *Prionomyrmex* ( Baltic Eocene) based on 34 morphological characters, suggests the following phylogeny: (Myrmecia, (Notomyrmecia, Prionomyrmex)). In this reconstruction, however, *Notomyrmecia* is characterised by only two, doubtful, apomorphies and *Prionomyrmex* is paraplectic to it. As a consequence of this, the following nomenclature changes are proposed:

1. The genus *Notomyrmecia* Clark, 1934 is a junior synonym of *Prionomyrmex* Mayr, 1868.
2. *Prionomyrmex macrops* (Clark) is a new combination (from *Notomyrmecia*).
3. The subfamily Notomyrmecinae 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 eyepear 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 baculature 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* paraplectic to *Notomyrmecia* and hence its senior synonym.

**ZUSAMMENFASSUNG**


2. *Prionomyrmex macrops* (Clark), nov. comb. (von Notomyrmecia).
3. Die Tribus Prionomyrmecini Wheeler, 1915 wird auf Unterfamilienrang erhoben (Prionomyrmecinae, nov. stat.).

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

Die erste, das Vorhandensein eines lateralen eypenalen 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.


**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 difficulty 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

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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) redescribed 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 Myrmecciini (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 Myrmecini. 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...
(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, gyne 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 Department 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.
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 palaeontologist 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...
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 cannot 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 stridultrum 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 scape 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) (PpPL) 1.36; Postpetiole Width (maximum) (PpPW) 1.48; Gaster Width (maximum) (GW) 1.88; Cephalic Index (= HWx100/HL) 69.35; Petiolar Index (PWx100/PL) 67.86; Petiole and Postpetiole Index (PWx100/PpPW) 51.35; Postpetiole Gastral Index (PpPWx100/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. *Prionomyrmmm junzeni* 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.
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 reveals, 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-
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 1 was able to count, and, 2) there are examples of intra-generic and of inter-caste 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 gynae, 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 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 gynae, elytrum: anteriorly compressed and/or reduced (0), or protruding (1).

3. Worker and gynae, lateral elytral carina: absent (0), or present (1).

4. Worker and gynae, mandibles: short (0), or elongate (1).

5. Worker and gynae, labial pegs: present (0), or absent (1).

6. Worker and gynae, malar area: developed (0), or reduced (1).

7. Worker, gynae and male, antennal socket: exposed (0), or not exposed (1).

8. Worker and gynae, antennal scape: short (0), or elongate (1).

9. Worker and gynae, 2nd funicular joint: elongate (0), or short (1).

10. Worker, promesonal suture: mobile (0), or fused (1).

11. Worker and gynae, metaleptal gland: absent (0), or present (1).

12. Worker and gynae, metaleptal gland: without (0), or with flange (1).

13. Worker and gynae, male metacoxal cavities: open (0), or closed (1).

14. Worker and gynae, mid and hind metatarsi: without (0), or with (1) sulcus.

15. Worker and gynae, claws: simple (0), or dentate (1).

16. Worker and gynae, A II dorsoventrally: not fused (0), or fused (1).

17. Worker and gynae, 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 striae: absent (0), or present (1).

20. Worker, ventral striae: absent (0), or present (1).

21. Worker and gynae, A IV prescereites: absent (0), or present (1).

22. Worker and gynae, A IV prescereites: not fused (0), or fused (1).

23. Worker and gynae, A IV prescereites: short (0), or long (1).

24. Worker and gynae, A IV presternite: shorter (0), or longer (1) than pretergite.

25. Worker and gynae, sting bulb gland: absent (0), or present (1).

26. Gynae, 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 (i.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 spiral: slit-shaped (0), or round (1).

30. Male, A IV prescereites: absent (0), or present (1).

31. Male, cerci: absent (0), or present (1).

32. Male, subgenital plate: round (0), or biuncate (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 gynae 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 pliosiomorphic 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 Proceratum (see e.g. the species tio Snelling & Cover and pergandei.
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


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, Myrmecinae, after merging the two genera *Prionomyrmex* and *Nothomyrmecia*. The results are displayed graphically in Fig. 8 and can be summarised as follows:

1. The Myrmecinae 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 Myrmecinae 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,
never, 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 *Nothomyrmex*.

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

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Without the talent and the patience of Armin Coray who executed the drawings, this paper would have transmitted more cryptic information and would have had a much diller look.

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

I must acknowledge the obvious: only the common presence of the eycleal 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 stridilum and of the biauculate subgenital plate is due to simple parsimomous 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-