

DORIANA

Supplemento agli
ANNALI DEL MUSEO CIVICO DI STORIA NATURALE "G. DORIA"
GENOVA

Vol. VIII - N. 358

30.IV.2008

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ORTHOTAXONOMY AND PARATAXONOMY OF TRUE AND PRESUMED BULLDOG ANTS

(HYMENOPTERA, FORMICIDAE)

In a recent paper by ARCHIBALD *et al.* (2006) several new genera of Eocene compression fossil "bulldog ants" were described in the subfamily Myrmeciinae. However, it was not possible for the authors to determine by normal standards whether these fossils belonged to the Myrmeciinae or the Prionomyrmecinae, since the characters used to separate these two subfamilies (four synapomorphies for Prionomyrmecinae and seven synapomorphies for Myrmeciinae; BARONI URBANI 2005) were not visible. The same problem exists for the Eocene compression fossil genus *Archimyrmex* Cockerell, 1923, a potential senior synonym of *Nothomyrmecia* if it would be also considered as an orthotaxon. It is symptomatic that ARCHIBALD *et al.* (2006) did not discuss the status of the two subfamilies, which have been maintained separate since the erection of Prionomyrmecinae (under the relative junior synonym Nothomyrmecinae) by TAYLOR in 1978. All the material referred to the above nominal genera share the impossibility to observe synapomorphic characters decisive for their higher assignment, as it will be further documented below. For this reason, in the present paper, all these poorly supported generic names will be treated as parataxa.

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SUBFAMILIAL CLASSIFICATION

The need for establishing a separate taxonomic unit for the Baltic amber *Prionomyrmex longiceps* Mayr, 1868 was first discussed by WHEELER (1915) who erected the tribe Prionomyrmecini. CLARK (1934) first proposed that the Australian closest recent relative of the fossil belonged to a separate subfamily and TAYLOR (1978) agreed and reinstated the Prionomyrmecinae when he re-described the extant *Prionomyrmex macrops* (under its relative junior synonym Nothomyrmecinae and *Nothomyrmecia*). A third species of the genus, *P. janzeni* Baroni Urbani, 2000, was described from Baltic amber and its placement in the Prionomyrmecinae confirmed (BARONI URBANI 2003).

A subsequent distinction between the Myrmeciinae (including the fossil *Prionomyrmex*) and Nothomyrmeciinae (including *Nothomyrmecia* only) was proposed by DLUSSKY & PERFILEVA (2003) on insecure grounds and abandoned in the successive literature. After WARD & BRADY (2003) merged the Prionomyrmecinae with the Myrmeciinae, diagnostic characters separating the two subfamilies were presented by BARONI URBANI (2005). The characters uniquely derived among workers and probably gynes of the subfamily Prionomyrmecinae (dinosaur ants) are: 1) a lateral clypeal carina, 2) masticatory margins of the mandibles in opposition (as opposed to crossing), 3) a setiform cuticular projection on the masticatory margin of the mandibles and 4) a ventral stridulitrum. The Myrmeciinae (bulldog ants) are characterized by: 1) a labial protrusion, 2) an exposed clypeo-labral junction, 3) an anteromedial clypeal depression, 4) reduction of the malar area, 5) ocelli in the workers, 6) mid and hind metatarsi with sulcus, and 7) fusion of the presclerites of abdominal segment IV. Partly identical and additional, undisputed apomorphies for the two subfamilies already resulting from the previous literature are: for the Myrmeciinae the reduction of the malar area, and for the Prionomyrmecinae the presence of a ventral stridulitrum and of the biaculeate subgenital plate (BARONI URBANI *et al.* 1992). While a few other recent papers have adopted Ward and Brady's classification, none of these considered the above morphological characters that clearly separate these two subfamilies. Attributing a hierarchic position whatever to a set of species often implies a subjective judgment. In this case, on the contrary, there are concrete arguments suggesting that the Myrmeciinae and

the Prionomyrmecinae are much more worth of subfamilial separation than other commonly recognized pairs of ant subfamilies. The five and seven apomorphies listed above respectively for the Prionomyrmecinae alone and for the Myrmeciinae after exclusion of the Prionomyrmecinae, largely outnumber the few apomorphies characterizing all the other ant subfamilies morphologically recognized either analytically (BARONI URBANI *et al.* 1992), or intuitively (BOLTON 2003).

If, on one hand, there is no serious doubt about the monophyly of the Myrmeciinae and Prionomyrmecinae (exactly as it is the case e.g. for the Formicinae and Dolichoderinae) there is a patent unfairness of judgment when, without justification and in the same paper, the Prionomyrmecinae are considered as a synonym of Myrmeciinae and subfamilial status is granted to the Aneuretinae without valid justification (e.g. BOLTON 2003; ARCHIBALD *et al.* 2006; MOREAU *et al.* 2006; BRADY *et al.* 2006). BARONI URBANI *et al.* (1992) and BARONI URBANI (2004) showed that Aneuretinae are an *a priori* imposed taxon without known apomorphies, a still unchallenged conclusion.

From the above, it follows that the Myrmeciinae and Prionomyrmecinae taken separately are among the most characteristic and apomorphies-rich (i.e. dissimilar) ant subfamilies, a reality further demonstrated by the fact that Myrmeciinae (bulldog ants) and Prionomyrmecinae (dinosaur ants) are the sole two ant subfamilies bearing, in addition to their respective Latin names, also a universally used and universally understood English vernacular name each.

METHODS OF TAXONOMIC ASSIGNMENT

None of the 12 subfamilial characters listed above is unmistakably visible among the compression fossils described by ARCHIBALD *et al.* (2006); on the contrary, the sole potentially observable myrmecine synapomorphy (worker and gyne reduction of the malar area) is clearly absent from most drawings of the compression fossils presented by these authors.

In addition, it should be noted that classification of these 'genera' among the Formicidae, while plausible on the basis of generic body shape traits, cannot be an absolute certainty. The reason for this is that there are other Hymenoptera with similar body shapes and

the diagnostic characters for family definition as described e. g. by BARONI URBANI *et al.* (1992) and by BOLTON (2003) are not visible in a number of species. This fact is implicitly acknowledged by ARCHIBALD *et al.* (2006) who start discussing subfamilial attributions without explaining their rationale for assigning the fossils in question to the Formicidae.

The criterion for assigning fossils to higher taxa used by ARCHIBALD *et al.* (2006) can be exemplified by their sentence (p. 506): “plesiomorphic character states... have been included in its diagnosis to distinguish these ants in combination with other traits (Bolton 2003, Ward and Brady 2003)”. This novel taxonomic philosophy conflicts with universally accepted procedures on theoretical and practical grounds. In fact plesiomorphic characters must be ignored in drawing classifications (e.g. HENNIG 1950; WILEY 1981; etc.), and the pretended uniqueness of combination of the plesiomorphic traits used by ARCHIBALD *et al.* (2006) is far from being unique, as these same authors admit in part.

In the present paper, according to common phylogenetic theory (see references above), full systematic position of a taxon will be inferred exclusively by means of shared derived characters. Assignment of a fossil genus either to the Myrmeciinae or to the Prionomyrmecinae will be retained on the basis of the following trivial requirements: possession of at least one, observable, unequivocal subfamilial synapomorphy as listed above, or, when the subfamilial synapomorphy in question may be equivocal, a second subfamilial or a general formicid familial synapomorphy will be also requested. Among the formicid synapomorphies generally recognized, only one, the relative length of the female antennal scape (DLUSSKY 1983; BARONI URBANI *et al.* 1992; BOLTON 2003; a. o.) is likely to be easily observable in compression fossils. Consequently, according to the above references, possession of “wasp-like antennae” is regarded as a reason for exclusion of a taxon from the Formicidae. The term “wasp-like antennae”, meaning “non-ant” morphology, was coined by WILSON *et al.* 1967, for insects with short scape in opposition to “ant-like” traits, i.e. typical ant characters. As a matter of fact WILSON *et al.* 1967, after correctly emphasizing the presence of this (and another) non-ant trait, decided for the ant nature of *Sphecomyrma* because of the presence of a “typical” (not synapomorphic) ant character, i.e. presence of a metapleural gland. I disagree with

this choice for obvious cladistic arguments (i.e. lack of formicid synapomorphies) and for a simple numerical reason: two typical non-ant traits (wasp-like antennae and wasp-like mandibles) should have more weight than the single ant trait (metapleural gland). This same reasoning, of course, applies also to other presumed fossil Formicidae with wasp-like mandibles and antennae described more recently.

In the following, and according to the character evaluation of the above literature, presence of elongate scapes in the female castes will be used to assign genera to the Formicidae and their absence for their exclusion. For those considering the metapleural gland as an additional, stronger formicid synapomorphy, one must remember that the gland does not result as synapomorphic from parsimony analyses (BARONI URBANI *et al.* 1992) because it is absent in two phylogenetically basal and species-rich formicid genera, *Camponotus* and *Polyrhachis*. Advocates of the phylogenetic value of the metapleural gland ignore this analytic result and argue that *Camponotus* and *Polyrhachis* might have secondarily lost their gland because they live on trees. This explanation was first hesitantly formulated by HÖLLDOBLER & ENGEL-SIEGEL (1984) and it is now smuggled as a logical reason in some publications (HÖLLDOBLER & WILSON 1990: 30; GRIMALDI *et al.* 1998). As a matter of fact, this explanation does not account for the hundreds of terrestrial *Camponotus* and *Polyrhachis* species without the gland and for the dozens of arboreal ant genera regularly equipped with a metapleural gland.

TAXONOMIC CONSEQUENCES

1. Parataxa transferred from the subfamily Myrmeciinae to Formicidae *incertae sedis*.

Archimyrmex Cockerell, 1923 (type species *A. rostratus* Cockerell) assigned to Formicidae *incertae sedis*.

Justification: Repeated attributions of *Archimyrmex* or of one of its synonyms to the Myrmeciinae s. l. are essentially due to the relative proportions of its abdominal segments III and IV, a presumed characteristic Prionomyrmeciinae trait clearly visible also e.g. in the Brazilian Lower Cretaceous *Cariridris*, which was also originally considered as a Myrmeciinae (BRANDÃO *et al.* 1989). However, a similar structure appears in at least seven different, major ant clades and in other Hymenoptera as well (BARONI URBANI *et al.* 1992: Table 2, char. 21). As a consequence of this and of other insecurity factors, later, *Cariridris* was either assigned to the Sphecidae (VERHAAGH 1996), or to the Ampulicidae (RASNITSYN & QUICKE 2002), or generically excluded from the Formicidae (several references). I see little

reason for a much different treatment of *Archimyrmex*: none of the species assigned to *Archimyrmex* allows observation of Myrmeciinae or Prionomyrmecinae synapomorphies as described above. Retention of *Archimyrmex* within the Formicidae is extrapolated from the inclusion in *Archimyrmex* by DLUSSKY & PERFILEVA (2003) of at least two species (out of three) based on gynes with elongate scape, an important formicid synapomorphy as repeated above.

Ypresiomyrma Archibald, Cover & Moreau, 2006 (type species *Y. orbiculata* Archibald, Cover & Moreau) assigned to Formicidae *incertae sedis*.

Justification: All the species assigned to this genus must be excluded from the Myrmeciinae by showing a normal development of the malar area contrasting with the synapomorphic reduction of the area of the Myrmeciinae. In addition ARCHIBALD *et al.* (2006: 492) state that the type species of the genus has an “antenna not determinable” rendering indeterminable in this way also its assignment to the Formicidae. Retention of *Ypresiomyrma* within the Formicidae in the present paper is extrapolated from the inclusion in *Ypresiomyrma* of *Pachycondyla rebekkae* Rust & Anderson, 1999 as suggested by ARCHIBALD *et al.* (2006: 493) and, as a consequence of this, it is maintained under their entire responsibility for the generic transfer of *rebekkae*. In fact, *Y. rebekkae* is the sole *Ypresiomyrma* species clearly showing antennae with an elongate scape, a formicid synapomorphy forcing to consider this genus as an ant.

2. Parataxa transferred from the subfamily Myrmeciinae to Hymenoptera *incertae sedis*.

Avitomyrmex Archibald, Cover & Moreau, 2006 (type species *A. mastax* Archibald, Cover & Moreau) assigned to Hymenoptera *incertae sedis*.

Justification: None of the specimens attributed to this genus allows examination of critical subfamilial or familial apomorphies as discussed above for *Ypresiomyrma*. The morphology and number of wings, of course, leave no doubt about the hymenopteran nature of *Avitomyrmex*.

Macabeemyrma Archibald, Cover & Moreau, 2006 (type species *M. ovata* Archibald, Cover & Moreau) assigned to Hymenoptera *incertae sedis*.

Justification: The unique known specimen of this genus was figured by ARCHIBALD *et al.* (2006: fig. 11B) with an extreme reduction of the malar area, area occupied by the eyes as in *Myrmecia*. However, the description (p. 498) warns that the eyes are “possibly preserved”, and (p. 500) explains: “the eyes seem to be preserved, but faintly”.

As already stated, reduction of the malar area is synapomorphic among Myrmeciinae but it re-appears homoplastically in *Harpegnathos* within the Formicidae, and in a number of wasps. The mandibles of *Macabeemyrma* are said (p. 498) to have “exact shape not determined” but are drawn in Fig. 11B as linear and curved

upwards on their sagittal plane as in *Harpegnathos*. Due to the resulting insecurity of classification within the Formicidae and to the lack of formicid synapomorphies, *Macabeemyrma* must be considered as a hymenopteron *incertae sedis*.

Myrmeciites Archibald, Cover & Moreau, 2006 (collective generic name without diagnosis and type species) assigned to Hymenoptera *incertae sedis*.

Justification: *Myrmeciites* is stated by ARCHIBALD *et al.* (2006: 500) to be destined to include “all fossil ant species referable to the subfamily Myrmeciinae, yet whose orthotaxonomic generic position is unclear by the poor or incomplete preservation”. The flaws of the criteria used by ARCHIBALD *et al.* (2006) to attribute their genera to the subfamily Myrmeciinae are already discussed above and affect even more seriously the familial assignment of this name.

3. Orthotaxa included in the formicid subfamilies Myrmeciinae and Prionomyrmecinae.

From the above, it results that

- a) the subfamily Myrmeciinae Emery, 1877 contains only one genus, the Recent *Myrmecia* Fabricius, 1804, distributed in New Caledonia, Australia and Tasmania; and
- b) the subfamily Prionomyrmecinae Wheeler, 1915 comprises only one genus, *Prionomyrmex* Mayr, 1868 (= *Nothomyrmecia* Clark, 1934), recorded fossil in Baltic amber (Eocene) and Recent in South and Western Australia.

ADDITIONAL REMARKS

The cladistic analysis by ARCHIBALD *et al.* (2006: fig. 18D) resulted in clustering together undisputed bulldog ants, dinosaur ants, and compression fossils in 53% of the bootstrap trees. However, the compression fossils are extraneous to the undisputed bulldog ants in 47% of the bootstrap trees (a nearly random score), even when using the data presented by ARCHIBALD *et al.* (l.c.). The low number of characters in the compression fossils producing “noise” when treated together with completely known taxa can explain this situation. Another problem with combining compression fossils that lack many characters with more adequately described taxa can be shown by the treatment of the two Baltic *Prionomyrmex* sister species, *P. longiceps* Mayr and *P. janzeni* Baroni Urbani, which differ only in the pilosity of the antennal scape (BARONI URBANI 2003).

According to ARCHIBALD *et al.* (2006: fig. 18D) these two species cluster together only in 91% of the bootstrap trees (i.e. less than the usual statistical significance threshold). This points out the problem of combining extant and amber specimens with compression fossils, which is why BARONI URBANI (2005: 592) suggested omitting poorly preserved compression fossils from cladistic analyses involving taxa with well-defined characters.

The present note calls attention to one of the problems with systematics, namely that following the most practical course of action often results in not seriously considering relevant information present in previous work.

ACKNOWLEDGEMENTS

Special thanks are due to Dr. George O. Poinar, Jr. of the Oregon State University, Corvallis, Oregon, for his patience and competence in carefully reading, criticizing and concretely improving an earlier draft in its substance and in its shape by pruning the irony transpiring from some of my sentences. My gratitude goes also to Dr. Roberto Poggi and to Dr. Fabio Penati for a deep, careful analysis of the manuscript that greatly benefited of it.

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ABSTRACT

Three compression fossil genera, i.e., *Avitomyrmex*, *Macabeemyrma*, and *Myrmeciites* recently described in the ant subfamily Myrmeciinae by ARCHIBALD *et al.* (2006), are transferred to the Hymenoptera *incertae sedis* since none of the critical characters currently used to define either one of the two sister subfamilies Myrmeciinae and Prionomyrmecinae or the Formicidae can be observed with confidence in these fossils. Another two compression fossil genera, *Archimyrmex* Cockerell, 1923 and *Ypresiomyrma* Archibald *et al.*, 2006, equally attributed to the Myrmeciinae, are retained as members of the Formicidae, but show morphological evidence adequate to be excluded from the Myrmeciinae.

RIASSUNTO

Ortotassonomia e paratassonomia in formiche bulldog vere e presunte (Hymenoptera, Formicidae).

Tre generi di fossili su lastra, *Avitomyrmex*, *Macabeemyrma*, *Myrmeciites*, recentemente descritti come Myrmeciinae da ARCHIBALD *et al.* (2006) sono trasferiti tra gli Imenotteri *incertae sedis*. Infatti, nessuna delle apomorfie caratteristiche delle sottofamiglie gemelle Myrmeciinae e Prionomyrmecinae o della famiglia dei Formicidae è riconoscibile nei fossili in questione. Altri due generi di fossili su lastra attribuiti alle Myrmeciinae, *Archimyrmex* Cockerell, 1923 ed *Ypresiomyrma* Archibald *et al.*, 2006, vengono considerati come Formicidi *incertae sedis* dato che gli esemplari finora noti mostrano una buona evidenza morfologica per la loro esclusione dai Myrmeciinae unita ad un carattere sinapomorfico dei Formicidi.

