

Molecular taxonomy and phylogenetic relationships among Australian *Nasutitermes* and *Tumulitermes* genera (Isoptera, Nasutitermitinae) inferred from mitochondrial COII and 16S sequences

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Abstract

The subfamily Nasutitermitinae Hare (1937) is a tropical and subtropical group, generally considered as the most specialised subfamily of Termitidae. To highlight some taxonomic inconsistencies, the phylogenetic relationships among seven Australian species, morphologically ascribed to the genera *Nasutitermes* and *Tumulitermes*, were studied through the analyses of the mitochondrial markers cytochrome oxidase II and 16S ribosomal RNA genes. In our trees, *N. longipennis* samples clearly pertain to two different specific entities with an apparently parapatric distribution. Further, the phylogenetic analysis performed on separated and combined data sets shows the placement of *Tumulitermes* species within a clade grouping *Nasutitermes* ones, and vice versa. Tests for alternative topologies do not support the monophyly of the genera *Nasutitermes* and *Tumulitermes*. Our results confirm the hypothesis that the morphological features used to establish relationships among these species are not phylogenetically decisive.

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1. Introduction

Termitidae is the most species-rich family of Isoptera. Its representatives are mainly distributed in the tropics with very few species found in the temperate regions. The subfamily Termitinae is at the apex of the Isoptera phylogenetic tree (Miura et al., 1998; Donovan et al., 2000; Eggleton, 2001), with the subfamily Nasutitermitinae as sister group. The latter, with 93 genera, is the second largest subfamily of Termitidae. The genera of Nasutitermitinae are traditionally divided into two sections. The first comprises a Neotropical group whose soldiers have mandibles with a biting function. The second section embodies termites in which the soldier mandibles are greatly reduced

and the frontal area is always elongated into a sharply pointed nasus or rostrum, through which the secretion of the frontal gland can be squirted at a considerable distance (Ahamad, 1950). All the Australian genera belong to the latter section which is on the whole represented by 42 described species in six genera (Miller, 1997). Among these genera, *Nasutitermes* (the type-genus of Nasutitermitinae) and *Tumulitermes* are of particular interest owing to their dubious taxonomy and mutual phylogenetic relationships. It must be noted that the current distinction between *Nasutitermes* and *Tumulitermes* was not present in Hill's work (1942), where the species presently distributed between the two genera were all ascribed to the genus *Eutermes* Heer.

At present, the genus *Nasutitermes* represent a heterogeneous assemblage of full nasute termites (Miura et al., 2000), being, with more than 240 species, the largest genus

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of wood-feeding Isoptera. Owing to its huge distribution, it is ecologically dominant in the tropics throughout the world. Australian *Nasutitermes* taxa comprise termites that construct strikingly different nest structures and feed on different cellulosic material: there are wood-feeding arboreal and epigeous nester species and a large number of grass feeders, some of these building typical huge mounds in open woodland and savannas. The nomenclature of this genus is very tangled and well depicted in a recent review made by Constantino (2002). Many species now placed in *Nasutitermes* were originally included in *Eutermes* Heer, 1849. In 1890 Dudley described a new genus *Nasutitermes* (“soldier with beak”), without indicating any type species. Holmgren, in 1912, and later Banks (1918) included in *Eutermes* = *Nasutitermes* several species, and among them, Emerson (1925) designated *Nasutitermes* (*Eutermes*) *costalis* Holmgren as the type-species. This constitutes a valid designation following Constantino (2002). Recently, Engel and Krishna (2005) proposed to the Bulletin of Zoological Nomenclature the suppression of *Eutermes* Heer and the conservation of the generic names *Nasutitermes* Dudley (1890) and *Microcerotermes* Silvestri (1901). Adverse comments were made about this proposal (Roisin, 2005) and the question remains open.

At variance of the genus *Nasutitermes*, *Tumulitermes* is endemic of the Australian region, with 17 accepted species. Several surveys, particularly in Western and Central Australia, have disclosed a substantial undescribed fauna, primarily composed by soil-dwelling detritivores or harvesters (Watson and Abbey, 1993). It now appears that *Tumulitermes* may be a generic complex including more than 50 species of major ecological significance in the arid and semi-arid parts of Australia (Watson and Abbey, 1993). The name *Tumulitermes* was used for the first time by Holmgren (1912), as a subgenus of *Eutermes*. The same author introduced *Eutermes tumuli* Froggatt (1898) as the nominal species. Later, Snyder (1949) raised the Holmgren’s subgenera to a generic rank.

As far as the relationships between *Nasutitermes* and *Tumulitermes* have been investigated, the CSIRO’s Report of Research (Lenz et al., 1997) about “Biology and Taxonomy of Termites” stated: “The examination of the phylogeny of the Australian Nasutitermitinae shows that criteria currently used to define genera are inadequate. These criteria allow species to be assigned to more than one genus when characters of different castes are used. Further, morphological analysis shows that some species currently assigned to *Nasutitermes* and *Tumulitermes* belong to different undescribed genera”. The characters upon which the Australian genera were established are inadequate from a taxonomic point of view and this had obviously an impact on the clarification of their phyletic relationships. Most of the apparently anomalous placements lies within the genera *Nasutitermes* and *Tumulitermes*. Other works highlight this point: the phylogeny of Nasutitermitinae based on morphological characters (Miller, 1997) supports the placement of *T. pastinator* within the *Nasutitermes*

genus. Moreover, Bulmer and Crozier (2004) showed that the relationship among *T. pastinator* and several Australian species of *Nasutitermes*, cannot be resolved by the phylogeny constructed on the mRNA sequences of termicine, an antifungal peptide. They observed that *T. pastinator* samples pertained to different clusters of *Nasutitermes*, suggesting a polyphyletic origin of the two genera. As far as the genus *Nasutitermes* is concerned, Miller’s morphological analysis (1997) highlighted that Australian *Nasutitermes* should be separated from other neotropical congeners and placed in a distinct genus. A different position emerged in Miura and co-workers phylogenetic analysis inferred from sequences of COII and 16S mitochondrial genes (2000): this study revealed a strongly supported clade including species from south-eastern Asia, New Guinea and Australian/American tropics. To complete the picture, Emerson (1941) suggested on morphological characters the evolution of fully nasute soldiers from different mandibulate stems, i.e. a diphyletism in the Nasutitermitinae lineage. Morphological evidence about frontal gland secretion (Prestwich and Collins, 1981) and differences in gut structure (Miller, 1986) do not correlate with the diphyletic theory of the subfamily, and led Miller (1986) to suggest a monophyletic phylogeny. On the other hand, Ohkuma et al. (2004), on mitochondrial COII gene, postulate that the subfamily Nasutitermitinae is polyphyletic, although the polyphyly was not well supported statistically.

In the present work, we give the results of the phylogenetic analysis performed on samples from the Northern Territory region in Australia. These specimens have been morphologically attributed to seven species. The Indonesian long-legged species *Longipeditermes longipes* and *Hospitalitermes medioflavus* were included as representative of other full nasute termites, even more specialized than *Nasutitermes* (Miura et al., 2000). In order to better understand the phylogenetic relationship among these groups, other *Nasutitermes* species from Neotropical and Indonesian regions were drawn from GenBank and included in the analysis.

The mitochondrial genes encoding for cytochrome oxidase II (COII) and large ribosomal subunit (16S) were considered to probe taxonomy and phylogenetic relationships among the analyzed samples. Previous works (Marini and Mantovani, 2002; Luchetti et al., 2004) showed a higher resolution power of the COII gene in comparison with the 16S gene, but also that the analyses of the combined dataset gave a better supported picture.

2. Material and methods

Samples were collected in the Australian Northern Territory region, in March–May 2003 and September–December 2005 (Fig. 1; Table 1) and preserved in absolute ethanol until DNA extraction. From 2 to 10 colonies were analyzed for each species.

Termites were identified using the morphological keys by Hill (1942) and Miller (1991), and also using the CSIRO

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