Oldest known ant fossils discovered

Here we report fossil ants, including a new genus of Ponerinae, about 50 million years (Myr) older than the previous oldest specimens. These discoveries in amber from the Turonian stage (92 Myr ago) of New Jersey in the United States have important implications for estimates dating the origin of ants, and extend the age of an extant ant subfamily back about 50 Myr.

Until now, a specimen of *Sphecomyrma freyi* in a piece of amber from Cliffwood Beach, New Jersey, was one of the few non-compression fossil ants from the Cretaceous period showing most morphological details[1]. The metapleural gland is the only morphological trait unique within the Hymenoptera that distinguishes ants, and can be seen in most ants embedded in amber. This gland produces antibiotic-like substances[2], necessary to maintain nests underground or in humid pieces of wood, where bacteria and fungi would otherwise invade immobile broods. The gland is seen in modern species, opening above the hind coxae. Development of the gland and eusociality were probably correlated and are involved in the great ecological success of the ants. In an Amazonian rainforest, for example, ants make up more than 25% of the total animal biomass[3].

Wilson *et al.*[1] described an almost perfectly preserved worker of *S. freyi*, but the debate remained whether this fossil is an ant because the presence of the metapleural gland was uncertain. *Sphecomyrma* was thus excluded from a recent phylogenetic analysis of the Formicidae[4], and its relatively short first antennal segment in workers was assumed to prevent the basic social behaviour of trophallaxis[5].

Our new specimens include three worker and four male ants. One complete, well-preserved worker was the second discovery of *S. freyi*. Among other well-preserved traits in this specimen are the external and even part of the internal anatomy of the metapleural gland. The gland has a circular opening and a very large subcuticular atrium (Fig. 1a). *Sphecomyrma* is thus an ant.

Two of the males are a new species of the Cretaceous genus *Baikuris*, known previously only from Upper Cretaceous (Santonian) amber from Taymyr, northern Siberia. The third male belongs to a genus as yet undetermined. The fourth male is tentatively assigned to *Sphecomyrma* and would be the first known male of that genus.

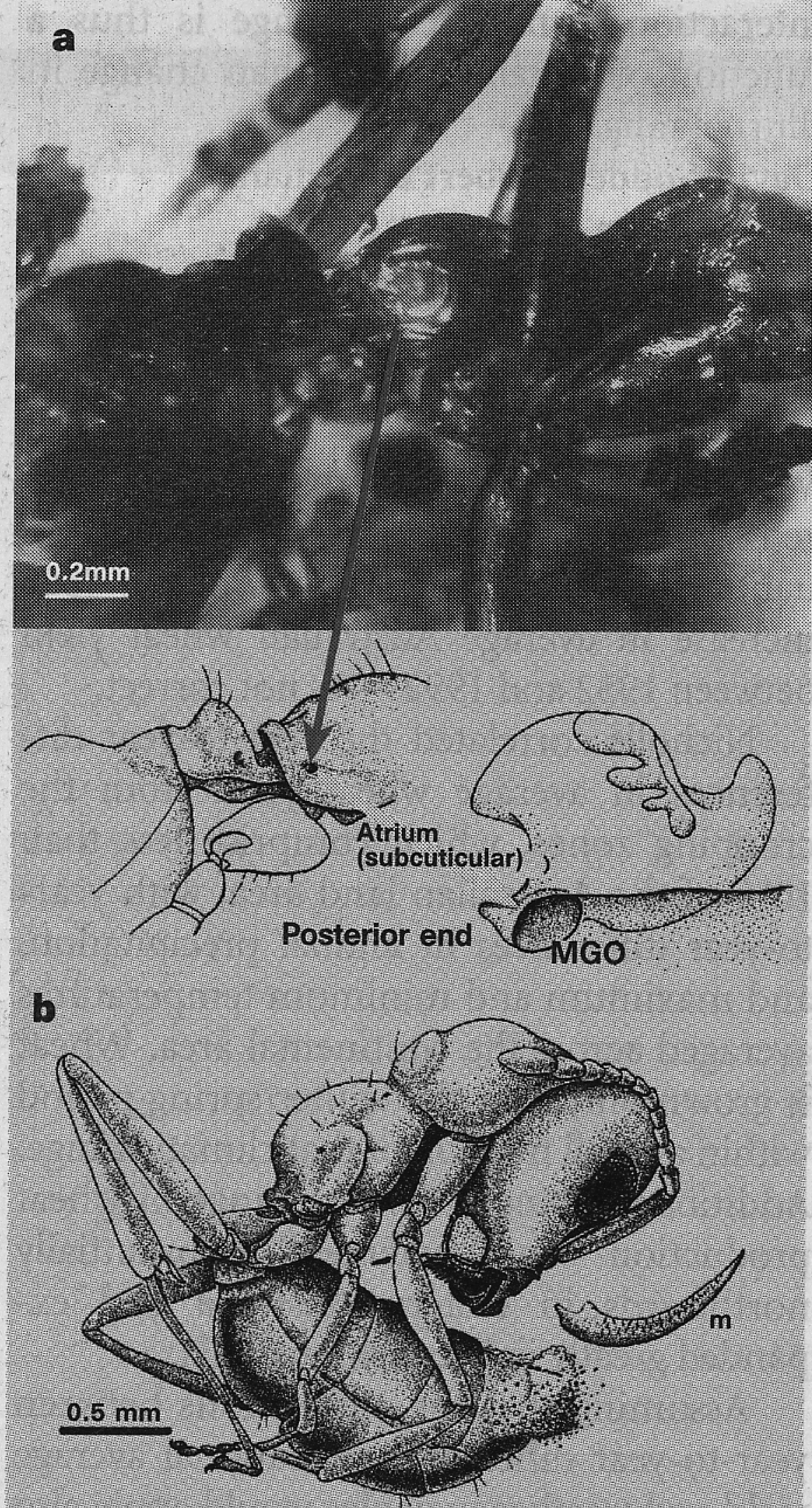

Figure 1 Photomicrographs of New Jersey ant fossils. **a**, Alitrunk and portion of the gaster of the new *S. freyi* worker with a drawing showing the position and structure of its metapleural gland (MGO). **b**, Lateral view of the new Cretaceous ponerine genus (m, mandible in frontal view). A detailed description will be provided elsewhere[6] (http://research.amnh.org/entomology/social_insects).

Another worker represents a new genus, distinguished by its clubbed antennae, proportions of the antennal articles, thin mandibles that lack teeth and cross extensively when closed, and a girdling constriction of the gaster typical of the large modern subfamily, the Ponerinae (Fig. 1b). Furthermore, the broad attachment of the third and fourth abdominal segments, and the apical denticles on the genae, indicate a relationship with ants of the ponerine tribe Amblyoponini.

Addition of these two new taxa confirms the basal position of *Sphecomyrma*[6], but as part of a quadritomy. The position of the new ponerine within one clade of the Ponerinae demonstrates that one major lineage of extant ants was established well before the formation of amber from Sakhalin Island (probably Palaeocene)[7] and of Eocene Baltic amber[8], which are about 50 Myr younger than the New Jersey amber.

A reasonable estimate would thus place the origin of the ants into the lowermost Cretaceous (about 130 Myr ago), but probably no older. This conclusion is consistent with the relationship of the Formicidae to the wasp families Vespidae and Scoliidae[9] and the phylogenetic position of the Cretaceous Vespidae[10]. On this basis, a hypothesis of a Lower Jurassic origin of ants[11], based on estimated divergence time of mitochondrial cytochrome *b* sequences, is unlikely.

Although ants originated in the Cretaceous, it was not until the Tertiary[7] period that they became so dominant and diverse in terrestrial ecosystems, as documented in Baltic[8] and Dominican amber[12]. We are still examining why the radiations were delayed until the Tertiary.

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Climate change and Australian wheat yield

Nicholls[1] reported that 30–50% of the increase in Australian wheat yields in the period 1952–92 resulted from climate change. He estimated a simple linear relationship where a 1 °C fall in diurnal temperature range increased Australian wheat yield by 0.52 t ha^{-1}. This effect, taken with the trend in diurnal range, accounted for 45% of the yield increase between 1952 and 1992. In an extended model with three climate variables, Nicholls found that changes in minimum temperature had had most impact on wheat yield and that rainfall change had contributed little. In our view, Nicholls's results need qualification and should be interpreted with caution. They are only estimates, and do not include standard errors to indicate their precision.

The analytical challenge is to separate the effects of climate change from other factors affecting Australian wheat yields. Non-climate factors include total wheat area, the