

Termites (Isoptera) from the Jurassic/Cretaceous boundary: Evidence for the longevity of their earliest genera

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Abstract. The earliest termite of the extant genus *Mastotermes*, is herein recorded in the Jurassic/Cretaceous (J/K) transitional beds of Chernovskie Kopi in Transbaikalian Russia along with *Santonitermes* of an uncertain family. These records represent the earliest eusocial organisms. No termites have ever been recorded among the hundreds of thousands of fossil insects in the Jurassic/Cretaceous boundary Beds of China and Mongolia or in prior time periods. Both genera indicate that the early termites survived for an extremely long period of time. The present find both provides evidence of the greatest ghost range (60 Mya) of any winged stem cockroach family and indicates that the origin of termites and evolution of eusociality occurred later than the Middle Jurassic.

INTRODUCTION

Superorganismal (Queller & Strassmann, 2002) structure in animals was first achieved by cockroaches during the Late Jurassic/Early Cretaceous transition, when their stem family the *Liberiblattinidae* radiated (Vršanský, 2002, 2010). In the late Early Cretaceous, the major lineages of exclusively eusocial termites had already evolved (Engel et al., 2007, 2009, 2011). Thus, it is important that the general consensus (references above) about the family *Mastotermitidae* (resp. *Cratomastotermitidae*) being the most primitive termite family has now the paleontological support presented in this paper. Both in terms of biomass (20%) (Fittkau & Klinge, 1973) and their ecological importance as principal pollinators, decomposers and predators of herbivores (Zherikhin, 1993) eusocial organisms are very successful animals. Of them, termites comprise 2,958 living and 282 fossil species (Grimaldi et al., 2008; EDNA fossil insect database: active 12 May 2012). Forty four fossil species are known from Mesozoic sediments (Engel et al., 2007; Ren, 1995; EDNA fossil insect database: active 12 May 2012) and 17 from Mesozoic ambers (Engel et al., 2011; Grimaldi et al., 2008; EDNA fossil insect database: active 12 May 2012). Up to now, the earliest record of termites (Engel et al., 2007) is as late as the Valanginian Cretaceous from Baissa in Transbaikalian Russia (Zherikhin et al., 1999), dated in the interval 125–135 Mya. The present two records are at least 15 million years earlier and represent the earliest fossil termites and the first possible Jurassic specimens. No termites are present in coeval fossil records from China and Mongolia (Vršanský, 2008; Ren et al., 2012; Wei & Ren, 2013) and/or earlier.

MATERIAL AND METHODS

Two specimens were preserved in the ?Tithonian Upper Jurassic or Jurassic/Cretaceous transitional locality of Cher-

novskie Kopi (Doronino Formation, Chernovskaya transitional sequence). The assemblage of fossil insects at the Chernovskie Kopi locality is mixed and cannot be assigned to any of the stratigraphic levels recognized in eastern Transbaikalia (Sinitza, 1995; Sinitshenkova, 2000; Vassilenko, 2005). Deposits at this locality are considered to be transitional between the Unda-Daya Group (J3) and the Turga Formation (J3-K1) (Sinitza, 1995). Over 500 specimens, representing 16 insect orders were collected at this locality. Orthoptera, Trichoptera and Ephemeroptera dominate numerically. Coleoptera, Plecoptera, Blattaria, Homoptera and Odonata are comparatively abundant and Diptera, Megaloptera, Heteroptera, Mecoptera, Hymenoptera, Neuroptera and Grylloblattida are rare. Determined caddis-flies (Sukatsheva & Vassilenko, 2011), undescribed ice crawlers of the Permian-Jurassic family Geinitzidae and 17 (of 40) exclusively Jurassic (Toarcian-Tithonian) cockroaches support the Jurassic age of this locality (although the improbable last occurrences across orders can not be definitely excluded; Cretaceous odonates (Vassilenko, 2005) are not contradictory as Tithonian entomofauna already belongs to the Cretaceous type). Eight of the cockroach specimens even belong to a genus absent in the rich J/K boundary beds of the Yixian Formation in China and Shar-Teg in Mongolia, but present at several earlier sites (Barna, in press). The present locality is similar to the former two in the presence of 20 deformities (expressed mutations Vršanský, 2004, 2005, unpubl.) that affect the geometry of 40 fragmented forewings and in the fragmentary character of the preservation. There is a single cockroach hind wings at the present locality ($n = 1/40$). Termites make up less than one per cent of the insect remains and are entirely absent at similarly aged Yixian (Early Cretaceous Ar-Ar- based dating of Yixian was based on the dating of much younger volcanic rocks) and Shar-Teg in spite of the fine preservation at these sites of hundreds of thousands insect fossils. Material is deposited at the Paleontological Institute RAS, Moscow (PIN).

Abbreviations used: CV – cross-veins; Sc – Subcosta; R – radius; M – media; CuA – cubitus anterior; CuP – cubitus posterior; A – anal. The ghost range is any interval from the supposed origin of the taxon uncovered by the fossil record.

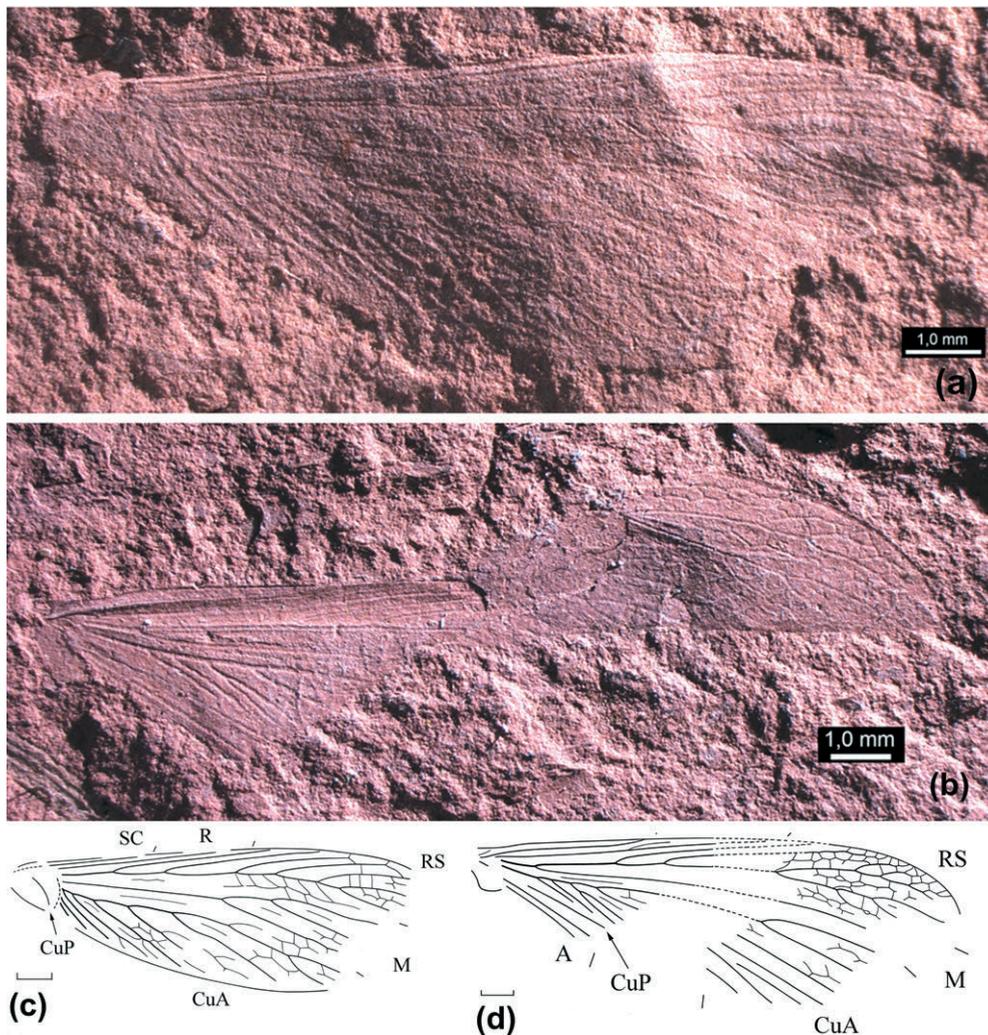


Fig. 1. Two Jurassic termites at the locality Chernovskie Kopi in Transbaikalian Siberia. a, c – *Santonitermes transbaikalicus* sp. n. (?Hodotermitidae), holotype PIN, No 4626/157, forewing: a – photograph, c – drawing. b, d – *Mastotermes nepropadyom* sp. n. (Mastotermitidae), holotype PIN, No 4626/156, hind wing: b – photograph, d – reconstruction. Scale bars: 1 mm.

RESULTS

Order Termitida Latreille, 1802 (= Isoptera Brullé, 1832)

Family Mastotermitidae Silvestri, 1909

Genus *Mastotermes* Froggat, 1897

Species composition: *M. darwiniensis* Froggat, 1897 (living, Australia); *M. bournmouthensis* Rosen, 1913 (Eocene, UK); *M. anglicus* Rosen, 1913 (Eocene or Oligocene, UK); *M. croaticus* Rosen, 1913 (Miocene, Croatia); *M. electrodominicus* Krishna et Grimaldi, 1991 (Miocene, Dominican Republic); *M. electromexicus* Krishna et Emerson, 1983 (Miocene, Mexico); *M. gallicus* Nel, 1986 (Oligocene, France); *M. krishnorum* Wappler et Engel, 2006 (Eocene, Germany); *M. minor* Pongracz, 1928 (Miocene, Croatia); *M. minutus* Nel et Borguet, 2006 (Eocene, France); *M. picardi* Nel et Paicheler, 1993 (Oligocene, France); *M. sarthensis* Schlotter, 1989 (Cenomanian or Albian, France).

Stratigraphic range. Tithonian or Berriasian to present.

Diagnosis of this genus does not have to be expanded (no separate plesiomorphies and/or apomorphies are present).

Mastotermes nepropadyom sp. n.

(Figs 1b, d)

Holotype. Paleontological Institute, Moscow (PIN) 4626/156, counterpart of nearly complete, warped hind wing.

Type locality. Chita Region, Chita District, left bank (stream side) of the Ingoda River; Chernovskie Kopi locality.

Type horizon. Upper Jurassic–Lower Cretaceous, Doronino Formation, Chernovskaya transitional sequence.

Differential diagnosis. The most closely related species within *Mastotermes*, *M. minutus* (Early Eocene) and *M. anglicus*, are symplesiomorphic in their small size and reduced venation, which is not reduced in other small mastotermites [*M. heeri* was not studied as it was transferred from *Mastotermes* to termites incertae sedis by Nel & Paicheler (1993)], but differs in its generally simpler venation (possible symplesiomorphy with Liberiblattiniidae) and comparatively simple (or even a simple) M (autapomorphy or a stochastic variability).

Description. Hind wing length ca. 10 mm, humeral suture present. Sc simple, very short. R branches ascending at a sharp, ca. 20° angle. First branch of R (R1) terminally branched. RS secondarily branched and with a blind posterior branch (a deformity). M descending from RS near base, preserved as simple. CuA with secondary branches, with ca. 7 veins reaching margin. Posterior blind rami also branched. CuP long and straight. A long and simple. Intercalaries apparent among CuA, otherwise reduced. The whole of the remigium is reticulated, especially so at the anterior distal end.

Remarks. The specimen apparently represents a hind wing of a single individual as it was preserved in a single surface and all veins can be easily traced (see reconstruction at Fig. 1d). There are no possible synonymisations of this taxon as its closest relatives occur in strata separated in time by nearly 100-million-years and because of clearly visible (although based on fragmentary material) diagnostic features.

Name derivation. Named after “непропадым” (непропады́м), which is Russian for do not get lost. Indeclinable.

Family ?Hodotermitidae Desneux, 1904

Genus *Santonitermes* Engel, Nel & Perrichot, 2011

Type species. *Santonitermes chloae* Engel, Nel & Perrichot, 2011.

Stratigraphic range. Tithonian or Berriasian to Albian or Cenomanian.

Diagnosis of this genus does not have to be expanded (no separate plesiomorphies and/or apomorphies are present).

Santonitermes transbaikalicus sp. n.

(Figs 1a, c)

Holotype. Paleontological Institute, Moscow (PIN) 4626/157, part of a nearly complete forewing.

Type locality. Chita Region, Chita District, left bank (stream side) of the Ingoda River; Chernovskie Kopi locality.

Type horizon. Upper Jurassic–Lower Cretaceous, Doronino Formation, Chernovskaya transitional sequence.

Differential diagnosis. The present taxon can be categorized as *Santonitermes* based on the regular distance between veins; common reticulations without cross-veins; simple M separated from R and rich CuA; humeral suture nearly completely missing; no clear R2+3; CuA well-developed, with about 10 posterior branches. This species can be differentiated from its only congener by its size (forewing length ca. 10 mm in contrast to 8 mm in *S. chloae*) (Engel et al., 2011). Another difference is the 3-branched M, which is, however, not diagnostic. All the other characters of *S. transbaikalicus* sp. n., such as the structure of the reticulations or blind branch of CuA, are insignificant.

Description. Forewing is wide (over 3.5 mm) and ca. 11 mm long, basal suture present. Sc short, simple and straight. R ascending at a sharp angle and slightly curved towards apical end. M with at least three branches (first dichotomy is in the distal half of the wing). CuA with at least 10 veins that reach the edge of the wing and an ante-

rior blind branch (a deformity). Intercalaries greatly reduced and reticulations present over the whole surface.

Remarks. Size is an important diagnostic character because there is very little variation in the size of Mesozoic species of termite. In addition the size is very different. In combination with non-diagnostic characters absent in *S. chloae* and a time gap of about 20-million-years, the erection of a new species is safe.

Name derivation. Named after Transbaikalian Russia.

DISCUSSION

The forewing of *S. transbaikalicus* sp. n. provides very little phylogenetical information and does not allow definite systematic assignment to a family, although the placement within the Hodotermitidae does not seem contradictory [except for the presence of both occipital carina and completely pentamerous tarsi in *S. chloae* (Engel et al., 2011)]. Numerous Cretaceous taxa (*Jitermes tsaii*, *Yanjingtermes giganteus*, *Yondingia opipara*, *Huaxiatermes huangi*, *Asiatermes reticulatus*, *Mesotermopsis incompleta* and *M. lata*) reported by Ren (1995) differ from *Santonitermes* in that M has strongly developed branches (Engel & Delclos, 2010), with the anterior most vein dominant. *Valditermes brenanae* (Jarzembowski, 1981), which is placed in the same family (Cretatermitinae) and is very similar, except for an expanded M, definitely does not belong to the Mastotermitidae (lacks all plesiomorphies including dense venation).

On the other hand, the hind wing of *Mastotermes nepropadyom* sp. n. (Figs 1b, d) in which the vannus is preserved (apparent in the basal part of Fig. 1b) is apparently different in structure from the forewing and belongs to the Mastotermitidae (both the Socialidae and Cratomastotermitidae can be excluded based on their reduced venation). Mastotermitidae have heterogeneous wings, with the forewing lacking a large anal area. Nevertheless, the attribution of the forewing and the hind wing to the same taxon can be excluded based on size (forewing is significantly larger than the hind wing) and the typical mastotermid structure of the forewing, which is different in having a more dense venation and a distinct anal area. This hind wing is phylogenetically extremely important, because it is of moderate size (similar to that of *M. anglicus* and *M. minutus*) and is most closely related to cockroach hind wings of the termite precursors of the family Liberiblattinidae. Traits found only in cockroaches of the family Liberiblattinidae are: Sc branched, R1 reduced and CuA secondarily branched (and with posterior most branches also branched). On the other hand, the typical traits such as: basal suture, which enables them to shed their wings after the nuptial flight, veins ascending at a sharp, ca. 20° angle, lack of cross-veins (CV) (which is evidence that they do not fly for a prolonged period because CV reduce the incidence of fractures), which result from frequent flights (Dirks & Taylor, 2012) and lack of intercalaries are all characteristics of eusocial Dictyopterans (termites and *Sociala* cockroaches). Presence of apical reticulations is apparently a termite autapomorphy.

M. anglicus provides a particularly nice illustration of the long duration of this taxon, as it survived nearly unchanged from the original *Liberiblattinidae* Baubplan until the Middle Oligocene (in England). *M. darwiniensis* still lives in Australia today (Froggat, 1897). The size, roughly 10 mm, is common for species of *Liberiblattinidae*.

The ghost range in time of the *Mastotermitidae* lasted from the occurrence of *Cratomastotermes* (the Valanginian *Valditermes* is not considered to be a mastotermitid in this manuscript because it lacks the characteristic dense venation). *Cratomastotermes* is sometimes considered to be a representative of a separate family (in which case the ghost range would extend from the occurrence of *M. sarthensis*) closely related to *Mastotermitidae*.

The fact that *Mastotermes*, a genus that was common in the Cenozoic (EDNA fossil insect database: active 12 May 2012) and occurred in the Mesozoic (*M. sarthensis*, and still living today) (Schloter, 1989) was conserved is puzzling. For comparison, Cenozoic and living cockroaches and mantodean genera do not occur in the Mesozoic fossil record. The rest of the termites also evolved rapidly. This may be because of the primitive, opportunistic (and pest) life cycle strategy of *Mastotermes*, which contrasts with the balanced ecology and stable generalist strategy of advanced termites.

The present observation provides significant support for a continuous transition from decomposition-specialist *Liberiblattinidae* cockroaches into the eusocial cockroaches, the *Socialidae* and *Mastotermitidae* termites, during the Late (hypothetically Middle) Jurassic or more precisely during the transition to the Cretaceous. The presence of endosymbionts does not provide evidence of a direct relation between termites and *Cryptocercidae*, as endosymbionts were present in ancestral *Liberiblattinidae* and *Blattulidae* (unpubl. observ.).

Thus the imposing nests of Triassic and Early Jurassic insects (Hasiotis & Dubiel, 1994; Bordy et al., 2009) must have belonged to some other organisms (see also Grimaldi & Engel, 2005), either some unknown eusocial or semisocial cockroaches (candidates are *Blattulidae* and “*Voltziablatta*” group) or to entirely different organisms.

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