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A new primitive termite from the Lower Cretaceous (Albian) Jinju Formation of Korea

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Abstract

A new genus and species of termite is described and figured from the Jinju Formation as *Sclerotermes samsiki* gen. et sp. nov. This new genus and species is left without family attribution because of the lack of information for body characters (*e.g.*, tarsus configuration, pronotum shape). This new taxon differs from all other termites, *inter alia*, owing to its forewing with RA with four main branches and its forewing scale heavily sclerotized. This new species is the first termite described from the Jinju Formation.

Keywords. Isoptera; taxonomy; new genus; Asia; plesiomorphy

Introduction

Termites form a monophyletic lineage within the order Blattodea (Inward et al. 2007; Lo et al. 2007; Engel et al. 2009; Krishna et al. 2013). All extant termite species are highly eusocial (Krishna et al. 2013) and the fossil record seems to convey the same information for early diverged or fossil families (*e.g.*, Zhao et al. 2020; Jouault et al. 2022a,b). As early as the Early Cretaceous, a tripartite caste system was established in termite colonies with reproductives/alates, soldiers, and workers/pseudergates (*e.g.*, Engel et al. 2016; Zhao et al. 2020; Jouault et al. 2021; Jiang et al. 2021).

The phylogeny of termites has been greatly clarified during the past decade with early input from morphological data, later complement with broad molecular-based phylogenetic analyses (*e.g.*, Engel et al. 2009; Krishna et al. 2013; Bourguignon et al. 2015; Legendre et al. 2015; Bucek et al. 2019; Jouault et al. 2021; Wang et al. 2022). Combined with the increase of fossil representatives of modern families, allowing a better delineation of each family, these analyses have greatly contributed to clarify the limits of fossil families. Despite these advances, informal clade such as the '*Meiatermes*-grade' continues to serve as a taxonomic wastebasket, and numerous taxa described a long time ago are poorly placed in the 'termite tree of life'. This issue stems from the reduced number of people working on fossil termites, comparatively poorly studied compared to the other two speciose eusocial lineages: ants and bees (Barden and Engel 2020). As a result, there is an urgent need to document the past diversity of the termite clade to clarify the placements of certain fossil genera.

Embracing this vision, we describe a new genus and species of termite from the Jinju Formation of Korea and provide a detailed comparison with most other Cretaceous termite genera.

Material and Methods

The specimen was collected from the lower part of the Jinju Formation at the Jeongchon section (35°07′45″N, 128°06′02″E), 5.6 km south of the city of Jinju, Republic of Korea (see Park et al. 2019). The most recent detrital zircon analysis shows that the age of the lower boundary of the Jinju

Formation is 112.4 ± 1.3 Ma, while the upper boundary is 108.7 ± 0.5 Ma; hence the age of the formation can be considered early Albian (Lee et al. 2018). The fossil is preserved as a reflective carbonaceous film on different slabs of dark grey shale. The specimen is housed in the Gongju National University of Education, with registration number GNUE218001. The fossil was photographed with a Canon Eos 6D camera with an attached Canon EF 100 mm lens. All images were digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019.

We follow the morphological terminology and the classification of termites as presented in Krishna et al. (2013), with recent additions of Jiang et al. (2021) and Wang et al. (2022), except for modifications to wing venation terms concerning the PCu vein, adapted from Schubnel et al. (2019), and we retain the name Isoptera (Lo et al. 2007), although as subordinate to Blattodea (as advocated by Lo et al. 2007; and Krishna et al. 2013).

Systematic palaeontology

Order: Blattodea Brunner von Wattenwyl 1882

Infraorder: Isoptera Brullé 1832

Family: *Incertae sedis*

Genus: *Sclerotermes* gen. nov.

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Type species. Sclerotermes samsiki sp. nov.

Etymology

The generic name is a combination of the ancient Greek σκληρός (sklērós, ‘hard’, and *Termes* commonly used to designate Isoptera. Gender masculine.

Diagnosis

Imago: wing membranous, long and broad, without ‘crossveins’ present (or archedictyon); all veins similarly sclerotized (radial veins maybe slightly more); forewing with heavily reticulate and sclerotized scale, humeral margin slightly arched, basal suture broadly arched; PCu broadly arched; Sc with two main branches; R with two branches; width of radial field moderate terminating at or slightly before wing apex, RA with four main branches, RP with five main branches, all with additional forks; medial field narrow, not encompassing wing apex, M stem long, M main vein closely parallel to RP and CuA main veins (equidistant from both), with three main branches, first branch of M arising near apical third of wing; CuA emerging from scale in three main branches, apical-most branch of CuA terminating into posterior margin in apical third of forewing length.

Sclerotermes samsiki sp. nov.

Fig. 1

urn:lsid:zoobank.org:act:D328B90B-C933-45DC-BF35-66DDE1E0A2C4

Material

Holotype, GNUE218001, housed in the collection of the Gongju National University of Education, Gongju, South-Korea.

Locality and horizon

Jinju Formation, Jeongchon section, near the city of Jinju, Republic of Korea; early Albian, Early Cretaceous.

Etymology

The specific epithet honors Mr. Lee Samsik who collected and donated the fossil for study, and is to be treated as a noun in a genitive case.

Diagnosis As for the genus (*vide supra*).

Description

Imago: wing membranous; forewing scale ca. 4.05 mm long and ca. 2.77 mm wide, humeral margin slightly damaged; forewing length from apex to basal suture ca. 15.1 mm long and width 6.7 mm, apex rounded, costal margin slightly convex basally then convex, posterior margin evenly convex; forewing Sc short, bifurcate at suture, posterior branch with a faint sub-branch at margin; RA with first branch with a faint sub-branch at margin, terminating anteriad wing mid-length; radial field width moderate, occupying about a quarter of wing area on average; first fork of RP close to basal suture, apical fork close to wing apex; medial field extremely narrow; M fork located near mid-length between third and fourth fork of RP; cubital field occupying about half of wing surface on average; CuA not heavily forked, more proximal branches (three basal ones) loosely sclerotized fading in the membrane, apical-most of these branches virtually terminating on margin near wing mid-length.

Color

No coloration pattern preserved.

Remarks

The forewing venation of the specimen clearly indicates affinities with early diverged termites (see discussion), but the non-preservation of body character precludes safe placement in any of the termite families already described.

Discussion

This specimen is assigned to the Isoptera based on the extremely reduced anal field, the presence of a wing scale with a suture, and is unique among Cretaceous termites because of the strongly sclerotized wing scale (Fig. 1A). In fact, it shares with the early diverged termite families (= non Icoisoptera) a complex wing venation without costalization of veins, and the veins distinct in the scale (Fig. 1B; Krishna et al. 2013). It further differs from the Kalotermitidae because its wing is clearly widened medially, its costal margin faintly arched but also owing to its veins all strongly sclerotized (CuA is not weak as in the Kalotermitidae), and RA and RP with numerous anterior branches (Krishna et al. 2013).

Among the Teletisoptera, the large wing scale, with the basal suture broadly arched and the PCu strongly arched precludes affinities with the Stolotermitidae (in which wing scale is comparatively smaller and the basal suture straight and diagonal; Jiang et al. 2021). Additionally, the vein M and CuA are as sclerotized as RP (*vs*. weak in the Stolotermitidae) and M is not costalized (not closer to CuA than to RP as in the Stolotermitidae) (Fig. 1; Krishna et al. 2013). The new specimen also differs from the Hodotermitidae because of its large scale (*vs.* small in the Hodotermitidae), all veins sclerotized (*vs*. M and CuA weak) (Krishna et al. 2013), and the wing relatively broad (*vs.* elongate). The Hodotermitidae are also characterized by a pectinate series of RP (Figs. 2A, B), but this pattern is not found in the new fossil (Fig. 1).

The internal composition of Archotermopsidae has been modified to resolve paraphyly with Hodotermitidae (Wang et al. 2022), by elevating the Hodotermopsinae and the Archotermopsinae (subfamilies of Archotermopsidae in Jiang et al. 2021) to familial rank: Hodotermopsidae (*Hodotermopsis*) and Archotermopsidae (*Archotermopsis*, and *Zootermopsis*) (Wang et al. 2022). The family Archotermopsidae (*sensu* Wang et al. 2022) is assumed to have its crown group diversifying after the early Eocene, and its ghost lineage (including its stem groups) diverges during the Early Cretaceous (*e.g.*, Bucek et al. 2019; Jouault et al. 2021; Wang et al. 2022).

The new specimen cannot be attributed to the family Archotermopsidae (*Archotermopsis*, and *Zootermopsis*) because the basal suture is broadly arched (*vs.* straight or slightly arched), the complete sclerotization of wing veins (M is not weaker than other veins), M not closer to CuA than to RP, PCu broadly arched (note that it can be straight or slightly arched in Archotermopsidae), RP not distally bend to encompass wing apex (Krishna et al. 2013; Jouault et al. 2022). Jiang et al. (2021) further indicate that the Archotermopsidae tend to have one poorly distinguished inferior branch of RP apically that parallels the main RP branch to or just posteriad the wing apex while the Hodotermopsidae sometimes possess two inferior branches of RP (Engel et al. 2009; Krishna et al. 2013), but this configuration is not found in the new specimen (Fig. 1).

Recently several fossil families have been described to accommodate the particular morphology of fossil taxa from the Cretaceous period (Jiang et al. 2021): Arceotermitidae, Krishnatermitidae, Melqartitermitidae, and Mylacrotermitidae. The family Arceotermitidae has been erected based on soldier characters challenging an in-deep comparison with the new specimen. But, it appears that the latter family is closely related to the Stolotermitidae according to its tarsomere configuration, pronotum shape, and most importantly the configuration of the mandibles of soldiers (Jiang et al. 2021). However, no clear distinction is proposed to separate the alates of Arceotermitidae from those of Stolotermitidae. The sole information regarding the difference between Arceotermitidae and Stolotermitidae concerns the subfamily Cosmotermitinae: the basal suture in alates of *Cosmotermes* is convex rather than straight and diagonal as in Stolotermitidae. The state of this character is not clear in *Cosmotermes* because in Zhang et al. (2020: figs. 3E, J) the basal suture is illustrated as straight and convex. Nevertheless, the overall affinities with Arceotermitidae are precluded because of the similarity between Stolotermitidae and Arceotermitidae. The Krishnatermitidae wing venation is characterized by the vein M as sclerotized as CuA rather than RP (Jiang et al. 2021). In the new specimen, the sclerotization appears to be relatively homogeneous (Fig. 1). The new specimen further differs from Krishnatermitidae because its RP is less parallel to the wing margin and slightly expanded distally (resembling that of

Mastotermes), and M is less developed (Engel et al. 2016). The Melqartitermitidae possess a narrow radial field while it is clearly broad in the new specimen (Engel et al. 2007; Jiang et al. 2021). The new specimen differs from the Mylacrotermitidae owing to its forewing with a clearly defined wing scale i.e., basal suture present (Engel et al. 2007; Jiang et al. 2021). The new fossil clearly differs from the family Termopsidae because of its forewing scale with anterior margin strongly arched (*vs.* only slightly arched, nearly straight), all veins sclerotized (*vs*. M and CuA weak), M not closer to CuA than to RP (*vs*. running closer to CuA than to RP) (Engel et al. 2007a; Krishna et al. 2013). The absence of a developed anal region and the reduced cross-venation (or archedictyon) exclude affinity with Mastotermitidae and Cratomastotermitidae (Fig. 1). Additionally, the anterior branche of the CuA has more posterior branches in the Mastotermitidae. In summary, the new fossil does not fit in any described isopteran family but its complex wing venation and the scale configuration suggest affinities with early diverged termite families (Mastotermitidae, Hodotermitidae, Hodotermitidae, etc.)

We provide hereafter, additional comparison with most of the Cretaceous genera of termites, but the new specimen clearly differs from all of them according to the combination of characters proposed in the diagnosis. The wing venation of the new specimen resembles that of *Baissatermes lapideus* Engel et al., 2007 because of its large scale with a broadly arched basal suture, complex wing venation with RP possessing numerous branches, M field narrow, M with a long stem, CuA well-developed with numerous branches (Engel et al. 2007b). However, the new specimen differs from *Baissatermes lapideus* at least because of its RA with four main branches. Comparison with *Mariconitermes talicei* Fontes and Vulcano, 1998 is difficult because of the poor preservation of the known wings of this species (Fontes and Vulcano 1998; Grimaldi et al. 2008). Nevertheless, the new specimen differs from *M. talicei* because of its wing length ca. 15.1 mm (*vs.* at most 13.8 mm long; Grimaldi et al. 2008: table1). The wing venation of *Meiatermes* species appears to be extremely plastic with variable size of the radial field, and variations in the number of branches of each vein (Grimaldi et al. 2008). However, *Meiatermes* are sp. are comparatively smaller (forewing

length *ca.* 10 mm *vs. ca*. 15 mm in our specimen) and RP nearly always encompasses the wing apex (*vs.* not encompassing wing apex) (Grimaldi et al. 2008: table 1; Bezerra et al. 2021). The new specimen greatly differs from *Carinatermes nascimbeni* Krishna and Grimaldi, 2000 at least because its medial field is narrow (*vs.* broad in *C. nascimbeni*), and the cubital field wide (*vs.* narrow) (Krishna and Grimaldi 2000: fig. 2A). The new specimen strongly differs from *Valditermes brenanae* Jarzembowski, 1981 because of its medial field narrow (*vs.* broad in *V. brenanae*), and M with a reduced number of branches (*vs.* five) (Jarzembowski 1981: figs. 1-6). It also differs from *Khanitermes acutipennis* Ponomarenko, 1988 at least because of its forewing with RA forked (*vs.* simple in *K. acutipennis*), M with first dichotomy far distal wing mid-length (*vs*. near basal suture) (Ponomarenko 1988; Engel et al. 2007: fig. 2A). *Dharmatermes avernalis* Engel et al., 2007 strongly differs from the new specimen, at least because of its basal suture and PCu straight (*vs.* arched), PCu, and the RP parallel to wing margin (Engel et al. 2007: fig. 8). The minute size of *Syagriotermes salomeae* Engel et al., 2011 (forewing ca. 5.8 mm long) and the combination of a feebly arched basal suture, RP close to wing margin preclude affinities with the new specimen (Engel et al. 2011). Our specimen differs from *Santonitermes chloeae* Engel et al., 2011 at least because its forewing scale is heavily sclerotized, and the fork of M is located far distad wing mid-length (*vs.* close to wing mid-length) (Engel et al. 2011; Vršanský and Aristov 2014). The new specimen differs from *Jitermes* Ren, 1995 at least because of its thin medial field (*vs.* occupying an important part of the wing surface in *Jitermes*), the first fork of M located conspicuously distad wing mid-length (*vs.* before wing mid-length), and CuA terminating distad wing mid-length (*vs.* near wing mid-length) (Ren 1995). The wing venation of *Yanjingtermes* Ren, 1995 is poorly preserved but the preserved part strongly differs from that of the new specimen because of the medial field occupying an important surface of the wing (*vs.* reduced in the new specimen), and the first fork of M located conspicuously before wing mid-length (*vs.* distad wing mid-length) (Ren 1995). The wing venation of the new specimen precludes affinities with the genus *Yongdingia* Ren, 1995 because the vein RA is well-developed (*vs*. reduced in *Yongdingia*), the RP without numerous

posterior branches (*vs.* with numerous posterior branches), but also because the basal suture of the wing is broadly arched (*vs.* straight in *Yongdingia*) (Ren 1995). The genus *Huaxiatermes* Ren, 1995 has a quite unique wing venation with the vein M separating from the radius outside wing scale (*vs.* separating in wing scale in the new specimen), medial field occupying an important surface of the wing (*vs.* reduced in the new specimen), and the first fork of M located conspicuously before wing mid-length (*vs.* distad wing mid-length) (Ren 1995). The type specimen of the genus *Asiatermes* Ren, 1995 is poorly preserved and the wing venation is hard to confidently interpret (Ren 1995: fig. 3-15). Nevertheless, the CuA? of *Asiatermes* appears to be heavily pectinate, a configuration absent from our new specimen. A similar configuration of the CuA is found in *Mesotermopsis incompleta* Ren, 1995, which further differs from our new specimen because of its vein medial field occupying an important surface of the wing (*vs.* thin) (Ren 1995).

Sclerotermes gen. nov. is of particular importance because most of the descriptions of Cretaceous termites derive from amber deposits (*e.g.*, Burmese, Lebanon, Charentese, and Spanish). The discovery of additional material from rock deposits enlightens the past diversity of this group during the Cretaceous, providing a glimpse into the diversity of large species. In fact, small species are easily trapped in amber and compose the majority of termite inclusions. Oppositely, rock deposits tend to preserve large specimens. A combination of the data from amber and rock deposit is, therefore, crucial to document the paleoentomofauna as completely as possible. In Asia, the different Burmese ambers (e.g., Tanai, Hkamti) have fossilized a complete isopteran fauna (Jouault et al. 2022b) and are complemented by the deposit of Baissa (Engel et al. 2007b) or Chernovskie Kopi (Vršanský and Aristov 2014) resulting in the best-documented diversity of Isoptera during the Early Cretaceous. Additional descriptions from other deposits such as the Jinju Formation will greatly help in circumscribing the diversity of Isoptera in Asia during the Cretaceous. Surprisingly, only a few termites have been described from the numerous Cretaceous Chinese deposits (Ren, 1995). They all derive from the Lushangfen Formation and to date, no species were described from the fossiliferous Yixian Formation. This lack of specimens of termites from the Yixian Formation,

while many other groups of insects are documented, may result from the absence of publication on specimens already unearthed. We assume that a complete fauna of termites is present in China but not yet described.

Conclusion

The description of *Sclerotermes* gen. nov. serves to increase the diversity of Isoptera documented from Laurasia during the Cretaceous and adds to the morphological diversity of termites of this period. The particular forewing venation of *Sclerotermes* gen. nov. may represent a new family of early diverged termites, but the absence of information for other body parts leads us instead to leave this new genus without attribution to a family. The current increase of known specimens of fossil termites indicates that it is crucial to study the fossil of this group.

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Figure captions:

Figure 1. *Sclerotermes samsiki* gen. et sp. nov., holotype GNUE218001. (A) Photograph of forewing; (B) Interpretative line drawing of wing venation, names of veins labeled; scale bars = 1 mm.

Figure 2. Line drawing reconstructions of wings. (A) *Hodotermes marocanus*; (B) *Anacanthotermes macrocephalus*; scale bars = 4 mm (A); 5 mm (B).