

## OPINION

## Revisiting *Coptotermes* (Isoptera: Rhinotermitidae): a global taxonomic road map for species validity and distribution of an economically important subterranean termite genus

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*Coptotermes* Wasmann (Isoptera: Rhinotermitidae) is one of the most economically important subterranean termite genera and some species are successful invaders. However, despite its important pest status, the taxonomic validity of many named *Coptotermes* species remains unclear. In this study, we reviewed

all named species within the genus and investigated evidence supporting the validity of each named species. Species were systematically scrutinized according to the region of their original description: Southeast Asia, India, China, Africa, the Neotropics, and Australia. We estimate that of the currently 69

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named species described by accepted nomenclatural rules, only 21 taxa have solid evidence for validity, 44 names have uncertain status, and the remaining species names should be synonymized or were made unavailable. Species with high degrees of invasiveness may be known under additional junior synonyms due to independent parochial descriptions. Molecular data for a vast majority of species are scarce and significant effort is needed to complete the taxonomic and phylogenetic revision of the genus. Because of the wide distribution of *Coptotermes*, we advocate for an integrative taxonomic effort to establish the distribution of each putative species, provide specimens and corresponding molecular data, check original descriptions and type specimens (if available), and provide evidence for a more robust phylogenetic position of each species. This study embodies both consensus and contention of those studying *Coptotermes* and thus pinpoints the current uncertainty of many species. This project is intended to be a roadmap for identifying those *Coptotermes* species names that need to be more thoroughly investigated, as an incentive to complete a necessary revision process.

## Introduction

Termites (Isoptera) are a group of eusocial insects traditionally ranked as an insect order, but representing a subgroup within Blattodea, with *Cryptocercus* being their sister taxon (Lo *et al.*, 2000; Inward *et al.*, 2007; Cameron *et al.*, 2012; Djernaes *et al.*, 2015). A recent taxonomic review of termites established that there are currently 2937 described species in the world, with 104 of them considered serious pests (Krishna *et al.*, 2013a). Twenty-three species in the genus *Coptotermes* (Rhinotermitidae) are among the most significant termite pests worldwide for man-made structures. *Coptotermes formosanus* Shiraki and *Coptotermes gestroi* (Wasmann) are of particular economic importance (Rust & Su, 2012) due to their ecological success and invasive ability (Evans *et al.*, 2013). Despite the wide distribution of *Coptotermes* in the world, and the large body of associated scientific literature for population management, the taxonomy of *Coptotermes* remains unsettled and many species names may be synonyms of other species.

In termites, species descriptions have historically relied upon morphological characters of the soldiers and/or alates (Fig. 1), but the seasonal occurrence of alates often prevents simultaneous collection, and therefore the simultaneous description, of both castes (Jones *et al.*, 2005; Yang & Li, 2012). As a result, many original species descriptions are based on the soldier caste alone (Li, 2000) from geographically limited material. For *Coptotermes*, soldier morphology is relatively conserved across the genus, presenting a major challenge to species identification. The overdependence on soldier head shape and the number of setae around the fontanelle has resulted in taxonomic confusion – as, for example, the controversy regarding distinguishing *C. formosanus* and *C. gestroi* in Taiwan based solely on soldier morphology, which was ultimately solved by the alate morphology and additional molecular data (Li *et al.*, 2010). Intraspecific variation in morphological characters

in soldiers also complicates species identification (Emerson, 1971; Husseneder & Grace, 2001). Soldiers in *Coptotermes* are produced from different developmental pathways which are colony-age dependent, contributing to intracolony variability (Ferraz & Cancellato, 2004; Chouvenc & Su, 2014). Furthermore, exacerbating the confusion is the unavailability of voucher specimens with all castes in sufficient number for comparison and description of the given variability. In addition, transport by ships has led to the spread of several invasive species throughout the world (Scheffrahn, 2013). This complicates termite species identification further, as many identification guides only cover regional faunas (Kirton & Brown, 2003; Scheffrahn *et al.*, 2004; Austin *et al.*, 2005; Jenkins *et al.*, 2007; Yeap *et al.*, 2007; Husseneder *et al.*, 2012). As a result, there are many synonyms in *Coptotermes* (more than 40 junior synonyms), and thus resolving *Coptotermes* nomenclature is a work in progress (Krishna *et al.*, 2013b).

Krishna *et al.* (2013b) listed 110 species names within *Coptotermes* that conformed to the rules of the International Code of Zoological Nomenclature (ICZN) and, among them, 69 were regarded as valid in the taxonomic literature, and 42 were listed as subjective synonyms. The list also included four objective synonyms and ten *nomina nuda* (not treated herein). Out of the 69 species listed as valid by Krishna *et al.* (2013b), about half of the species are known only from limited material (e.g., one caste described, single colony of origin, or a single alate, no comparison with previously described specimen, etc.). Some descriptions are over a century old and may not meet modern rigour. Although molecular taxonomy offers tools to validate species or synonymization, such data have yet to be collected for most species. As a result, the validity of many species names as real biological taxa is uncertain. For example, the unusually high species diversity of described *Coptotermes* in China (22 species) represents an anomaly that requires close scrutiny (Eggleton, 1999; Wang & Grace, 1999; Li, 2000; Yeap *et al.*, 2009; Li *et al.*, 2011). Krishna *et al.* (2013a) provided an invaluable



Fig. 1. *Coptotermes gestroi*, alates (winged), soldiers (orange head capsule) and workers (white head capsule). Picture: R. Scheffrahn.

contemporary catalogue of the Isoptera worldwide, and building on that, we focus here on the *Coptotermes* species names for which there is little evidence to support their validity as a biological species in light of current knowledge of inter- and intraspecific variability and worldwide geographical distribution.

The phylogenetic relationships within *Coptotermes* are currently fragmentary and focused on a limited number of species and just a few DNA sequences per species (Lo *et al.*, 2006; Yeap *et al.*, 2009; Scheffrahn *et al.*, 2015). A recent analysis using the available molecular data (Lee *et al.*, 2015) has provided some insight into *Coptotermes* phylogenetics and its radiation, especially in Australian species. In light of the work by Krishna *et al.* (2013b), and Lee *et al.* (2015), it is clear that a taxonomic revision of *Coptotermes* is urgently needed, especially as accurate species identification can have important implications for control practices, as highlighted by Kirton (2005). However, the task will require morphological and genetic analyses from a large geographical survey that are beyond the capability of a single, localized research group. In addition, the recent phylogeny proposed by Lee *et al.* (2015) revealed discrepancies depending on the genetic marker used, and the limited number of DNA sequences available for most species currently prevents a robust and definitive analysis. The goal of this study is to investigate the current status of all described *Coptotermes* species names as a step toward a comprehensive taxonomy of the genus. Although the investigation of species names is only the first part of this conundrum, it provides a framework that focuses the attention on uncertain species names. Ultimately, we propose a road map for the taxonomic revision of the genus based on modern phylogenetic methods.

### Determining if a species name is valid

We gathered the information available on all named species, using Krishna *et al.* (2013b) as a starting resource for *Coptotermes* nomenclature, and consulted original descriptions of species when available. The 69 species names given by Krishna *et al.* (2013b) are assumed to be valid based on their original author's scholarship. Likewise, some names listed as subjective synonyms by Krishna *et al.* (2013b) might actually be valid, and, conversely, some currently valid species names may actually be junior synonyms. The list includes all available names currently recognized as valid and all subjective, potentially valid, junior synonyms. There are currently many grey areas in the *Coptotermes* taxonomy (and more broadly in overall termite taxonomy), and we express caution from making definite statements about the validity of any given species names, as in many cases it is still a work in progress.

We have compiled a list of species names that were considered to have questionable or uncertain status, based on a review of the literature about *Coptotermes* and the distribution of the genus. Considerations were based on the comparison of original and later descriptions, along with recent genetic data, and personal

observations from various authors of this study. All 69 species names were investigated and categorized as 'valid,' 'uncertain' or 'other' according to the following guidelines, and the category attribution was the result of a consensus among all authors using these guidelines (a full description of the analysis is available in Appendix S1). Ultimately, the decision to place a species in a given category was the result of a discussion among all authors in this study and represents a compromise on the overall agreement about the uncertain status of some species.

### Valid species names

While validity of a species and quality of its description may be unrelated, the species names placed in the 'valid' category all include description of the soldier caste and/or imago, and comparisons with sympatric or widespread species. Many of these names are also well established in the *Coptotermes* literature and most have a well-known distribution. The intraspecific morphological variability was expanded over time due to author interpretation and known range expansion. Most species in this category were also confirmed using molecular tools. Historically, there is a long list of names that were synonymized owing to the precedence of older names. Therefore, currently valid species names may be junior synonyms of less well known older names, but availability, quality and erosion of samples may preclude such synonymization. To our current knowledge, there is sufficient evidence to confirm their validity, although we do not exclude potential synonymization in light of future morphological and/or molecular studies. The status of subspecies was also discussed when necessary.

### Uncertain species names

For the majority of uncertain species, type specimens were not compared with any other material at the time of their description or subsequently. Some species in this category were only mentioned in various catalogues and no specimens were independently collected to confirm their validity. Moreover, there are currently no available molecular data to support their validity. Species in this category will require further study to confirm their validity, or to relegate them to junior synonym status. Alternatively, such poorly defined species may be senior synonyms of currently 'valid' species, but the current absence of data forced us to place these species names in the 'uncertain' list by default, at least until further investigation is performed. In this respect, while we may suspect a case of senior synonymy for a name that was not used for several decades, we presently consider them as 'uncertain' in the hope that future work will resolve their nomenclatural position. When a synonymy is suspected for a questionable name, we indicate if junior or senior synonymy would apply. Although there is currently little evidence to support the validity of some taxa, we express caution about interpreting our opinion as a 'nonvalid' statement, because there are simply not enough data to resolve the ambiguity.

**Table 1.** List of *Coptotermes* species names (updated from Krishna et al., 2013b).

Species name <sup>a</sup>	Putative native area
<i>Coptotermes acinaciformis acinaciformis</i> (Froggatt) 1898	Australia
<i>Coptotermes acinaciformis raffrayi</i> <sup>b</sup> Wasmann 1900	Western Australia
<i>Coptotermes amanii</i> (Sjöstedt) 1911	Ethiopian region
<i>Coptotermes amboinensis</i> <sup>b</sup> Kemner 1931	Indonesia: Maluku
<i>Coptotermes bannaensis</i> <sup>b</sup> Xia and He 1986	China: Yunnan
<i>Coptotermes beckeri</i> <sup>b</sup> Mathur and Chhotani 1969	South India
<i>Coptotermes bentongensis</i> <sup>b</sup> Krishna 1956	Malaysia
<i>Coptotermes boetonensis</i> <sup>b</sup> Kemner 1934	Indonesia: Java
<i>Coptotermes brunneus</i> Gay 1955	Western Australia
<i>Coptotermes ceylonicus</i> <sup>b</sup> Holmgren 1911	South India, Sri Lanka
<i>Coptotermes changtaiensis</i> <sup>b</sup> Xia and He 1986	China: Anhui
<i>Coptotermes chaoxianensis</i> <sup>b</sup> Huang and Li 1985	China: Anhui
<i>Coptotermes cochlearius</i> <sup>b</sup> Xia and He 1986	China: Anhui
<i>Coptotermes crassus</i> <sup>b</sup> Snyder 1922	Neotropics
<i>Coptotermes curvignathus</i> <sup>b</sup> Holmgren 1913	Indonesia, Vietnam,
<i>Coptotermes cyclocoryphus</i> <sup>b</sup> Zhu et al 1984	China: Guangdong
<i>Coptotermes dimorphus</i> <sup>b</sup> Xia and He 1986	China: Yunnan
<i>Coptotermes dobonicus</i> <sup>b</sup> Oshima 1914	Papua New Guinea
<i>Coptotermes dregghorni</i> Hill 1942	Queensland
<i>Coptotermes elisae</i> (Desneux) 1905	Indonesia, Malaysia
<i>Coptotermes emersoni</i> <sup>b</sup> Ahmad 1953	Sri Lanka
<i>Coptotermes formosanus</i> Shiraki 1909	Mainland China and Taiwan
<i>Coptotermes frenchi</i> Hill 1932	Australia
<i>Coptotermes fumipennis</i> <sup>b</sup> (Walker) 1853	Unknown (Australia?)
<i>Coptotermes gambrinus</i> Bourguignon and Roisin 2011	Papua New Guinea
<i>Coptotermes gaurii</i> <sup>b</sup> Roonwal and Krishna 1955	Sri Lanka, Nicobar
<i>Coptotermes gestroi</i> (Wasmann) 1896	Indonesia, Malaysia, Philippines
<i>Coptotermes grandiceps</i> Snyder 1925	Papua New Guinea
<i>Coptotermes grandis</i> <sup>b</sup> Li and Huang 1985	China: Fujian
<i>Coptotermes guangdongensis</i> <sup>b</sup> Ping 1985	China: Guangdong
<i>Coptotermes guizhouensis</i> <sup>b</sup> He and Qui 1982	China: Guizhou
<i>Coptotermes gulangyuensis</i> <sup>b</sup> Li and Huang 1986	China: Fujian
<i>Coptotermes hainanensis</i> <sup>b</sup> Li and Tsai 1985	China: Hainan
<i>Coptotermes heimi</i> (Wasmann) 1902	India, Pakistan, Nepal
<i>Coptotermes hekouensis</i> <sup>b</sup> Xia and He 1986	China: Yunnan
<i>Coptotermes intermedius</i> Silvestri 1912	West Africa
<i>Coptotermes kalshoveni</i> Kemner 1934	Indonesia, Malaysia
<i>Coptotermes kishori</i> <sup>b</sup> Roonwal and Chhotani 1962	India
<i>Coptotermes lacteus</i> (Froggatt) 1898	Eastern Australia
<i>Coptotermes longignathus</i> <sup>b</sup> Xia and He 1986	China: Yunnan
<i>Coptotermes longistriatus</i> <sup>b</sup> Li and Huang 1985	China: Guangdong
<i>Coptotermes mauricianus</i> <sup>b</sup> (Rambur) 1842	Mauritius
<i>Coptotermes melanoistriatus</i> <sup>b</sup> Gao et al 1995	China: Hong Kong
<i>Coptotermes menadoae</i> <sup>b</sup> Oshima 1914	Indonesia: Sulawesi
<i>Coptotermes michaelsoni</i> Silvestri 1909	Western Australia
<i>Coptotermes minutissimus</i> <sup>b</sup> Kemner 1934	Indonesia: Sulawesi
<i>Coptotermes monosetosus</i> <sup>b</sup> Tsai and Li 1985	China: Yunnan
<i>Coptotermes niger</i> <sup>b</sup> Snyder 1922	Neotropics
<i>Coptotermes ochraceus</i> <sup>b</sup> Ping and Xu 1986	China: Guizhou
<i>Coptotermes oshimai</i> <sup>b</sup> Light and Davis 1929	Indonesia: Sulawesi
<i>Coptotermes pamuae</i> Snyder 1925	Papua New Guinea
<i>Coptotermes paradoxus</i> <sup>b</sup> (Sjöstedt) 1911	Ethiopian region
<i>Coptotermes peregrinator</i> <sup>b</sup> Kemner 1934	Indonesia: Sulawesi
<i>Coptotermes premrasmi</i> <sup>b</sup> Ahmad 1965	Thailand
<i>Coptotermes remotus</i> <sup>b</sup> Hill 1927	Papua New Guinea
<i>Coptotermes sepagensis</i> Krishna 1956	Indonesia, Malaysia
<i>Coptotermes shanghaiensis</i> <sup>b</sup> Xia and He 1986	China: Shanghai
<i>Coptotermes silvaticus</i> <sup>b</sup> Harris 1968	Ethiopian region
<i>Coptotermes sinabangensis</i> <sup>b</sup> Oshima 1923	Sumatra, Malaysia

Table 1. Continued

Species name <sup>a</sup>	Putative native area
<i>Coptotermes sjostedti</i> Holmgren 1911	Ethiopian region to Senegal
<i>Coptotermes suzhouensis</i> <sup>b</sup> Xia and He 1986	China: Jiangsu
<i>Coptotermes testaceus</i> (Linnaeus) 1758	Neotropics
<i>Coptotermes travians</i> (Haviland 1898)	Sumatra, Malaysia
<i>Coptotermes truncatus</i> (Wasmann) 1897	Madagascar
<i>Coptotermes varicapitatus</i> <sup>b</sup> Tsai and Li 1985	China: Guangdong

<sup>a</sup>Bold species indicates that there is strong evidence for species validity.

<sup>b</sup>Uncertain status concerning validity as a species, with potential for synonymy.

#### Other species: nonvalid and fossil species names

Species listed as *nomina nuda* by Krishna *et al.* (2013b) and species names due to misspellings (*lapsus calami*) are unavailable and therefore ten names were not included in the current study. Fossil species are included in this study.

#### Evidence for species validity

A consensus regarding the evidence for the validity of all potential *Coptotermes* species was formulated in Appendix S1. The analysis was structured by grouping species by their putative geographical origin. To summarize, out of 69 *Coptotermes* species, only 21 species currently have some evidence to support their validity (Table 1), 44 names need additional work to confirm their validity or their potential junior/senior synonymy (24 outside China, 20 from China), and all remaining species names were confirmed as junior synonyms or were unavailable. Type localities and putative distributions of all 69 potential species are shown in Fig. 2, with an emphasis on their validity status. Among the 21 species with a valid status, eight are native to Southeast Asia, one is from China, one from India, four from Africa, one from the Neotropics, and six are from Australia. All 44 species with uncertain status, fossils and all junior synonyms are discussed in Appendix S1.

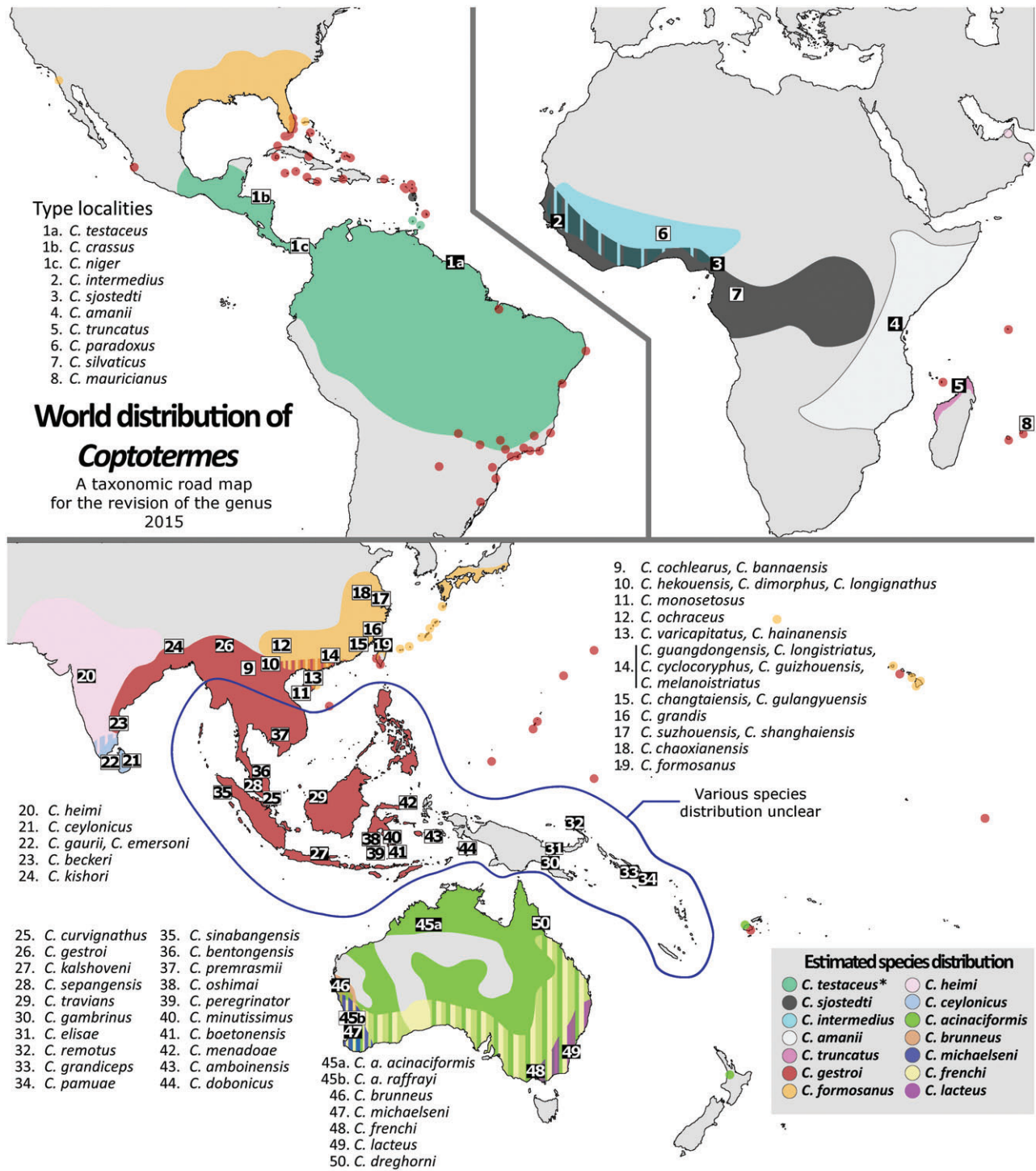
#### Is *Coptotermes* invasive as a genus?

Of the 21 *Coptotermes* species we considered valid, 16 species currently have major pest status according to Krishna *et al.* (2013a). This observation supports the ecological success of the genus and its ability to establish in disturbed environments. It also confirms the economic impact the genus has around the world (Rust & Su, 2012). However, the general perception that the genus is a major invader may have been distorted due to the extensive research of some of these species in non-native areas. While it is widely accepted that *Coptotermes* is a 'great invader' when associated with human activity (Evans, 2011; Evans *et al.*, 2013), our review actually points toward only two species that have this ability: *C. formosanus* and *C. gestroi*. The invasive status of *C. formosanus* and *C. gestroi* has long been a source of taxonomic confusion in many parts of the world, and, to some extent, still is. Historically, both species have at least eight junior

synonyms. Both species were themselves confused as a single species in Taiwan for a long time (Li *et al.*, 2010). As discussed in this study, there is a strong suspicion that several species described from India, from the islands around Madagascar and some islands from Southeast Asia could be synonyms of *C. gestroi*.

*Coptotermes heimi* is invasive to the Arabian subcontinent to a small extent, whereas *C. acinaciformis* in New Zealand and the Pacific Islands, and *C. sjostedti* in Guadeloupe could be considered as 'chance invasions' with little to no local expansion. Therefore, besides *C. formosanus* and *C. gestroi*, *Coptotermes* as a genus has very few species with a history of successful introduction and establishment. It may be that the number of introductions by *Coptotermes* is correlated with the amount of historical sea travel between areas, where the propagule pressure is different (Lockwood *et al.*, 2005; Su, 2013). Alternatively, the dispersal flight behaviour (diurnal vs nocturnal) of some species may influence the chance for alates to fly towards artificial lights. For example, *C. testaceus* is a diurnal flier and may not have had many opportunities to infest boats (Scheffrahn *et al.*, 2015). In addition to its underground foraging ability, *Coptotermes* is also a genus where most species have evolved to eat heartwood in living trees, with extreme examples in some Australian 'tree-piping' termites. Such a trait could have allowed for the transport of infested logs and good survival of colonies for the establishment in non-native areas. Future studies should focus on the differences in biology of all described species to explain why these two species are exceptions and why they thrive so well when associated with human activity.

Movement of species around the world and novel interactions among allopatric species may also have unexpected consequences. Chouvenc *et al.* (2015) recently observed in south Florida (where both species are invasive) that *C. formosanus* and *C. gestroi* have a long overlapping swarming season in south Florida with field observation of interspecies mating behaviour. Colonies with high hybrid vigour were obtained under laboratory conditions, which raises questions about the barriers between species in endemic areas that are potentially absent in their invasive range. It also implies that gene flow among various populations might have occurred in the past among other *Coptotermes* species. However, genetic determination of taxa has historically used mitochondrial markers, comparing maternal lineage, which cannot be used for the investigation of potential gene flow among different populations of



**Fig. 2.** Putative distributions of species within the genus *Coptotermes*. Numbers refer to type localities of each described species. Black backgrounds indicate species with valid status, and white backgrounds indicate species whose validity is uncertain. Distribution of species within the Southeast Asian archipelago was not presented due to the complexity of the visual representation and the uncertainty of the distribution of local species. \*Includes the *C. testaceus*–*C. crassus*–*C. niger* complex.

*Coptotermes*. The future clarification of the species complex within *Coptotermes* will provide valuable insight into the definition of species in *Coptotermes*, as seen in *C. acinaciformis* (Lee *et al.*, 2015), and could solve the question of how *Coptotermes* evolved and radiated in the past, and predict how it will spread in the future.

### **Coptotermes, a global taxonomic challenge**

Our study reveals major problems in *Coptotermes* taxonomy. The validity of each described species name as a biological taxon varies tremendously in level of support, from full evidence to no data. Krishna *et al.* (2013b) listed 69 *Coptotermes* names that were regarded as valid in the taxonomic literature and took into account various subjective synonymies over the past century. While the nomenclatural work of Krishna *et al.* (2013b) provides the biogeographical details concerning all known *Coptotermes* species names, there is still research needed to clarify the biological reality of each *Coptotermes* species name. The current effort to clarify the taxonomy of the *Coptotermes* genus needs to be intensified, as the use of molecular tools now enables us to distinguish taxa with much greater certainty (Bourguignon *et al.*, 2015). Such tools should also allow for the discovery of potentially new cryptic species (Lee *et al.*, 2015). In addition, recent surveys revealed that some species have yet to be discovered (Bourguignon & Roisin, 2011), while more synonymy is expected to be found (Scheffrahn *et al.*, 2015). We assume that a clarification of the taxonomic status of species within the *Coptotermes* genus will take place in the near future. Clearly, soldier morphology alone is insufficient to establish a species, as the wide intraspecific soldier morphological variability has long been the source of inaccurate species descriptions. Alate descriptions should be encouraged in the description process along with soldiers, and molecular data using a range of genetic markers. Any novel description, synonymizations or re-descriptions may also use quantitative morphometrics in the case of large samplings. As the number of diagnostic sequences available to termite researchers will inevitably increase in the foreseeable future, this is a good time to clarify the taxonomy of this important pest genus and to complete the story of the evolutionary radiation of the genus throughout the world.

Owing to the high number of available species names from Southeast Asia, Emerson (1971) suggested that *Coptotermes* may have originated from this area and then radiated to the rest of the world. However, we argue in this review that the diversity in Southeast Asia may be lower than previously accepted. Genetic data from African termites (*C. sjostedti*, *C. amanii*, *C. intermedius*) suggest that they are basal within the *Coptotermes* phylogeny, followed by the Neotropical *Coptotermes*, and then went through rapid radiation throughout Asia and Australia (Lee *et al.*, 2015). The phylogeography of *Coptotermes* is still in its infancy, as the taxonomic complexity of geographic populations within a species has only been partially described in Australian termites (Brown *et al.*, 2004; Lee *et al.*, 2015). However, such studies offer unique perspectives on other *Coptotermes* species (Vargo & Husseneder, 2009). We therefore expect

extensive taxonomic and phylogeographic studies of *Coptotermes* on a global scale in the near future and we hope that the consensus reached in this article concerning the uncertain status of some species will provide an incentive to achieve this goal.

### **Supporting Information**

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12157

**Appendix S1.** Revisiting *Coptotermes* (Isoptera: Rhinotermitidae): a global taxonomic road map for species validity and distribution of an economically important subterranean termite genus.

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## Chouvenc et al. Supplementary material S1

### Systematic Entomology

#### Revisiting *Coptotermes* (Isoptera: Rhinotermitidae): a global taxonomic roadmap for species validity and distribution of an economically important subterranean termite genus

##### Additional resources

We investigated all available sequences to date (July 2015) from GenBank for mitochondrial DNA 12S, 16S, and COII sequences. All sequences were compared to determine the number of unique haplotypes published for each species (summarized in Tables S1, S2, S5-8). While 154 (12S), 333 (16S) and 414 (COII) verified sequences were deposited in GenBank, about 74% of all sequences are identical to one or more other sequences, reflecting a relatively low genetic diversity in sequenced *Coptotermes*. We used the topology proposed by Lee et al. (2015) as the most current *Coptotermes* phylogeny (Figure S1).

Measurements of soldiers and alates from all species described from China were gathered from the original literature (in Chinese) and were summarized in Table S3 and Table S4. Soldiers and alates of *C. formosanus* and *C. gestroi* were also collected in Taiwan (H-F Li) and measurements of all characters were added to the tables for comparison with all Chinese species. For *C. formosanus*, we obtained measurements from 30 soldiers from 10 different locations and 30 alates from 11 different locations. For *C. gestroi*, we obtained measurements from 30 soldiers from 10 different locations and 17 alates from 5 different locations. In addition, Xia and He (1986) proposed the number of setae around the fontanelle of *Coptotermes* soldiers can separate two subgenera (unavailable nomenclature), *Oligocrinitermes* (one pair of setae) and *Polycrinitermes* (two pair of setae). We therefore counted the number of setae around the fontanelle of *Coptotermes* soldiers from the termite collection located at the University of Florida Ft. Lauderdale Research and Education Center (R. Scheffrahn, curator) and from the resources summarized by Krishna et al. (2013b) to investigate the status of the two subgenera.

##### Geographical overview of *Coptotermes* taxonomy, evidence for validity or lack thereof.

###### *Coptotermes* from Southeast Asia

The Southeast Asian region has been described as one of the world's major biodiversity hot spots (Mittermeier et al. 1999) because the insular rain forest has served as a source of refugia during prehistoric environmental disturbances for many animal species, including termites (Gathorne-Hardy et al. 2002). The *Coptotermes* diversity reported in this region follows this general trend of speciation and radiation typical for the area with more than 20 described species (Table S1). However, the high diversity and large distribution area of some species has come with many synonymies and we here argue that, while nine species may well be valid, another eleven species names have uncertain status.

*Coptotermes gestroi* is the most important subterranean termite as a structural and forestry pest throughout Southeast Asia (Rust and Su 2012, Evans et al. 2013). Its wide distribution, including Burma (Wasmann 1896), Thailand, Vietnam, Malaysia, the Philippines and Indonesia, has probably led many overlapping descriptions, with at least eight recognized junior synonyms (*C. havilandi* Holmgren (Kirton and Brown 2003) and *C. vastator* Light (Yeap et al. 2007) being the most common junior synonyms cited in the literature from non-native areas, as both names were still considered valid by Krishna et al. 2013b). It has been introduced to many parts of the world, including Eastern India, South China, Taiwan, French Polynesia, Fiji, Réunion Island, Brazil, Hawaii, the Caribbean, and South Florida. The wide distribution of *C. gestroi* and its pest status has motivated active research on the genetic variation of this species, and *C. gestroi* is currently the *Coptotermes* species with the highest level of

intraspecific mitochondrial DNA sequence variation reported in GenBank.

Along with *C. gestroi*, *C. curvignathus* (Holmgren) is a major tree pest in Southeast Asia and both species apparently have a wide distribution overlap in their native range. In Malaysia, *C. curvignathus* is an important pest of rubber and oil palm plantation (Lee et al. 2007). A preliminary morphological and genetic investigation study of *C. elisae* (Desneux) from New Guinea matched the morphology and the sequences deposited for *C. curvignathus* (T. Bourguignon, *pers. obs.*). If confirmed, the seniority of *C. elisae* means that *C. curvignathus* is a junior synonym, and we therefore gave *C. curvignathus* an uncertain status.

*Coptotermes kalshoveni* Kemner, *C. sepangensis* Krishna, and *C. travians* (Haviland), are three other taxa in the region commonly found in the literature; their validity has been supported by molecular data (Lee et al. 2015), although additional genetic and morphologic survey are needed, as the number of available samples is low in comparison to *C. gestroi* and *C. curvignathus*.

Species previously described from Papua New Guinea have received little attention since the 1930s, but *C. elisae*, *C. grandiceps* Snyder, *C. pamuae* Snyder and *C. remotus* Hill were collected and re-described by Bourguignon and Roisin (2011), confirming their validity on morphological ground, although Hill (1942) suggested that *C. pamuae* and *C. remotus* could be the same species. In addition, a new species, *C. gambrinus* Bourguignon and Roisin was described during the same survey. However, no genetic sequences are yet available from these species. *Coptotermes* soldiers collected in New Caledonia are similar to *C. grandiceps* (morphologically, A. Robert, C. Bordereau, *Pers. Obs.*) but the identification and the presence of the species on that island remains to be confirmed.

There are also a dozen species names for which the validity is uncertain because so little data are available. Specimens of *C. amboinensis* Kemner were collected in Maluku and described once in 1931, but have never been reported again. A number of species suffer from the same problem: *Coptotermes bentongensis* Krishna from Malaysia, *C. boetonensis* Kemner from Sulawesi, *C. dobonicus* Oshima from Papua New Guinea, *C. menadoae* Oshima from Sulawesi, *C. minutissimus*

Kemner from Sulawesi, *C. oshimai* Light and Davis from Sulawesi, *C. peregrinator* Kemner from Sulawesi, *C. premrasmii* Ahmad from Thailand, and *C. sinabangensis* Oshima from Sumatra. There is a need to investigate this group of species as a whole.

### ***Coptotermes* from China**

*Coptotermes formosanus* is endemic to mainland China and Taiwan and is now a major invasive pest in Japan, Hawaii, Southeast US and most recently Grand Bahama Island (Scheffrahn et al. 2015). Its status as an invasive pest in urban areas is comparable to that of *C. gestroi* (Rust and Su 2012). However, both species have distinct ecological requirements and have different distributions, with *C. gestroi* a tropical species while *C. formosanus* is a subtropical and warm temperate species (Li et al. 2009, Grace 2014, Chouvenec et al. 2015). With *C. formosanus* widely distributed throughout mainland China, and *C. gestroi* invading from the southern regions, these are the only two species in mainland China whose presence and validity is beyond questions (Li 2000).

The taxonomic status of *Coptotermes* in mainland China is unique from a historical perspective (Table S2) (Eggleton 1999). With very few exceptions, all *Coptotermes* species described outside mainland China were named before the 1960's. However, among species reported from mainland China, only *C. formosanus* was described in 1909 (originally reported in Taiwan, formerly known as Formosa, Shiraki 1909), and all other 30+ Chinese species were described after 1982. The sudden surge of species description in China in the 1980's is a clear anomaly and coincides with the surge in interest in this genus during that period, but raises questions concerning the validity of the new taxa, as explained by Eggleton (1999). From 30+ originally described species in China, 22 Chinese *Coptotermes* species names remain listed in the revision by Krishna et al. (2013b). Except for *C. gestroi* and *C. formosanus*, the other 20 species were described in a handful of publications between 1984 and 1995 (Zhu et al. 1984, Ping 1985, Tsai et al. 1985, Li 1986 Li and Huang 1986, Ping et al. 1986, Xia et al. 1986, He and Qiu 1992, Gao et al. 1995), and 18 of the 20 species were described in a three-year period (1984-1986).

All 20 species exclusively reported in China were described with the soldier caste but only nine of them were described with both soldiers and winged imagoes. However, winged imagoes provided more specific diagnostic characters that point toward synonymy with *C. formosanus* or *C. gestroi* (Li et al 2010). Eight of the 20 Chinese species were described with soldier polymorphisms (*i.e.*, different morphological castes), usually based on the shape of soldier head capsule. These shapes included rounded, elongated, elliptic, pear-shaped, egg-shaped etc., but no clear definition or morphometrical analyses was provided to classify each head-shape type. Because the number of observed individuals from each described species was small and specimens were generally collected from a single nest location (Table S3), soldier polymorphism is dubious.

Out of all *Coptotermes* species previously described in the area, *C. formosanus* and *C. gestroi* are the only two *Coptotermes* species not exclusively reported from mainland China (Huang et al. 2000). With the description of so many *Coptotermes* species in just a few years, it is likely that the morphological characteristics of all these species were not carefully examined and compared. For example, *C. formosanus* was the first reported *Coptotermes* species in China, but only six of the newer species have been compared with *C. formosanus* in their original descriptions. Of the 20 *Coptotermes* species exclusively reported in China, seven were never compared with other Chinese species, ten were compared with one Chinese species and three were compared with two other Chinese species in their original descriptions, respectively.

When comparing the morphometric characters among the 20 exclusively Chinese species with the two well-described species *C. gestroi* and *C. formosanus*, the ranges for character measurements among the former of the characteristics of the 20 exclusive Chinese species were much smaller than those of *C. gestroi* and *C. formosanus* in the current study. Such small ranges probably reflect the poor sampling used to describe the Chinese species (Table S3, soldier morphometrics, Table S4, alate morphometrics), resulting in a bias for interpretation of morphometrics data and choosing diagnostic characteristics.

Despite nomenclature inaccuracy, species from mainland China with a single pair of setae were placed in the *Oligocrinitermes* subgenus (unavailable), while species with two pairs were placed in the *Polycrinitermes* subgenus (unavailable) (Xia and He 1986). Soldiers from *C. formosanus* have two pairs of setae present around the fontanelle, while soldiers from *C. gestroi* have a single pair of setae. This trait has been proven useful because of the invasive status of *C. formosanus* and *C. gestroi*: in areas of the world where both species are established, the number of setae around the soldier fontanelle remains the best method to quickly differentiate the two species (Scheffrahn and Su 2005). Based on the available Chinese *Coptotermes* soldier morphomatrix data, we found many of the exclusive Chinese species are likely junior synonyms of *C. formosanus* or *C. gestroi*. For morphological comparison, we divided the Chinese species into two groups, the soldier with one pair and two pairs of setae around the fontanelle. The morphomatrix data of the five species with one pair of setae was compared with that of *C. gestroi* (Table S3, soldier morphomatrix). The three species, *C. bannaensis*, *C. cochlearus*, and *C. dimorphus*, are larger than *C. gestroi*. The range of pronotum width and head width of the two species, *C. longignathus*, and *C. monosetosus*, are similar to that of *C. gestroi*, with over 64% and 100% overlap, respectively. The morphomatrix data of the fifteen species with two pairs of setae was compared with that of *C. formosanus*. Five species, *C. changtaiensis*, *C. grandis*, *C. hainanensis*, *C. longistriatus*, and *C. ochraceus*, are larger than *C. formosanus*. *C. shanghaiensis*, is much smaller than *C. formosanus*. The head width and pronotum width of other nine species, including *C. chaoxianensis*, *C. cyclocoryphus*, *C. guangdongensis*, *C. guizhouensis*, *C. gulangyuensis*, *C. hekouensis*, *C. melanoistriatus*, *C. suzhouensis*, and *C. varicapitatus*, overlapped with that of *C. formosanus* by over 76%. Because there were no distinct characteristic to differentiate these nine species from *C. formosanus*, they are likely junior synonyms of *C. formosanus*. The limited alate morphometric data (Table S4, alate morphometrics) conforms with our junior synonym prediction.

In addition, there are hundreds of DNA sequences of Chinese *Coptotermes* samples available on GenBank, but none showed much variability (<1%) from either *C. formosanus* or *C. gestroi*. The high ratio of species exclusive to China and the absence of genetic variability from hundreds of samples make the validity of these Chinese species even more suspect. However, there are a couple of exceptions that present some problem with our general approach. Both *C. cochlearus* and *C. dimorphus* were originally described with a single pair of setae around the fontanelle, which suggests that they could be junior synonyms of *C. gestroi*. However, 16S and 12S sequences obtained by Yeap et al. (2009) suggest they are junior synonyms of *C. formosanus*. This contradiction could be due to the misidentification of the old specimen and the limited number of sample ( $n = 1$ , C.Y. Lee, *Pers. Obs.*) that was procured for the work reported in Yeap et al. (2009).

On a side note, as we investigated the number of setae around the fontanelle of soldiers from various species, we noticed that there was no clear conservation of the trait within the *Coptotermes* phylogeny (Figure S1). The presence of three pairs of setae in mature soldiers of the Neotropical *C. testaceus* (L.), two pairs of setae in *C. formosanus* and *C. curvignathus*, and one pair of setae for all other observed species in the phylogeny suggests that the change in number of setae around the fontanelle may have evolved multiple times in *Coptotermes* (Chouvenc et al. 2014). As discussed above, Xia and He (1986) proposed two subgenera within *Coptotermes* based on the number of setae around the fontanelle of soldiers. Our observation therefore implies that, beside the fact that *Oligocrinitermes* and *Polycrinitermes* are unavailable (on type designation) (Krishna et al. 2013b), they do not represent two independent clades.

A comprehensive revision of the genus with molecular and caste morphological data is required in China. Herein, we suggest a possible pathway to clarify the taxonomic status of Chinese *Coptotermes*. First, based on the two well-described species present in China, *C. formosanus* and *C. gestroi*, there is a need to measure major characteristics of soldier and alate castes of multiple colonies collected from multiple locations in order to obtain the morphological range of the

major diagnostic characters for both species. Second, the commonly used genes (12S, 16S, COI, COII, or full mitochondrial genome, as used in Bourguignon et al. 2015) could be analyzed to confirm that these referenced specimens are *C. formosanus* or *C. gestroi*. Third, we could compare the referenced specimens and type specimens of the 20 Chinese endemic species, side by side; however, accessing holotypes and/or paratypes of all 20 species may be challenging. If any distinctly different characteristics between referenced specimens and type specimens are found, further re-collection, gene sequencing, and morphological re-description should be undertaken. Most, if not all of the Chinese species names may ultimately be considered as junior synonyms of *C. formosanus* or *C. gestroi*.

### ***Coptotermes* from the Indian region**

There are currently five *Coptotermes* species described from India. However, the available evidence suggests that *C. heimi* (Wasmann) is a valid native species (Table S5), with *C. gestroi* also present at its westernmost distribution in Asia. *Coptotermes heimi* appears to be the dominant species, with a wide distribution from Pakistan Indus River valley to Nepal and most of India. This is also the only species, owing to its pest status, that has received extensive investigation, including molecular genetic analysis. Because of its close genetic resemblance to *C. gestroi* ( $\approx 3\%$  difference), both taxa have been confused as a single species (Yeap et al. 2010, Li et al. 2013, Harit et al. 2014); however, they are genetically different and have distinct ecological requirements. *Coptotermes heimi* is the only *Coptotermes* species to thrive in desert conditions, apart from some Australian species. In comparison, *C. gestroi* is distributed in more humid areas. *Coptotermes heimi* has also been found in the United Arab Emirates (R. Scheffrhan, *Pers. Obs.*) and in Oman (Chhotani 1988), in both cases it appears to have been introduced in recent times.

*Coptotermes ceylonicus* Holmgren is recorded from southern India and Sri Lanka, but there are no recent descriptions or molecular data for this species. *Coptotermes ceylonicus* might be a synonym of *C. gestroi*, because both species show little morphological divergence and live in similar habitats. *Coptotermes gaurii* Roonwal and

Krishna was described as being distinct from *C. ceylonicus* in Sri Lanka but only on the basis of soldier morphology from a single locality (Roonwal and Krishna 1955); however, samples subsequently collected from the Nicobar Island (where *C. gestroi* is established), were identified as *C. gaurii* (Maiti 1979). The observation by Maiti (1979) suggests that *C. gaurii* may actually be a synonym of *C. gestroi*.

*Coptotermes kishori* Roonwal and Chhotani has been reported throughout northeastern India (Sen-Sarma et al. 1975); however, the description of this species was based exclusively on soldiers showing little morphological difference from *C. gestroi*. It is currently difficult to confirm that *C. kishori* is a good species or if this species has been confused with *C. heimi* or *C. gestroi*. *Coptotermes beckeri* Mathur and Chhotani was described based on soldiers collected in southern India, but has not been reported for almost 60 years. Similarly, *C. emersoni* Ahmad, originally collected in Sri Lanka, like *C. beckeri*, has never been re-collected. We therefore question the validity of both *C. emersoni* and *C. beckeri*. Finally, *C. travians* was long thought to be established throughout eastern India and Burma (Roonwal and Chhotani 1962, 1989, Tho 1992) but Kirton and Brown (2003) determined that samples were misidentified and were in fact *C. gestroi*. If confirmed that *C. emersoni*, *C. beckeri*, *C. gaurii* and *C. ceylonicus* are junior synonyms to *C. gestroi*, the distribution of *C. gestroi* in Asia would be expanded further eastward than previously thought. It is unknown if this is part of its invasive range due to human activity, or its natural range.

#### ***Coptotermes* from the African region**

Few species have received extensive documentation in the African region (Table S6). Three species, *C. sjostedti* Holmgren, *C. amanii* (Sjöstedt) and *C. intermedius* Silvestri, have wide distributions with some level of range overlap (Harris 1966), from Senegal to Tanzania, Ethiopia and south to Namibia and Zimbabwe (Uys 2002). The few mtDNA COII or 16S sequences available from these three species suggest that they are in a monophyletic clade within *Coptotermes* (T. Chouvenc, *Pers Obs*) although there are currently too few sequences to confirm. We cannot exclude

the existence of undescribed species because of the wide distribution of the three species and the relative paucity of molecular data from African *Coptotermes*. There has also been some confusion about the taxonomic status of *C. intermedius* var. *subintacta*. Originally described as variety of *C. intermedius* (Silvestri 1914), Sjöstedt (1926), referred to it as a variety of *C. sjostedti*, then it was synonymized with *C. intermedius* by Roy-Noël (1966), and finally cited as a synonym of *C. sjostedti* by Bouillon and Mathot (1971), with no further reference mentioned concerning this variety. There is therefore a need to address the status of “*subintacta*” as a potential species, a synonym of one named species, a subspecies of *C. intermedius*, or a subspecies of another African *Coptotermes*. A population survey on the genetic basis of the *C. intermedius* – *C. sjostedti* – *C. amanii* complex is warranted in Africa to clarify this confusion. In addition, it was suggested that this tri-species African group is the most basal *Coptotermes* clade (Lee et al. 2015), which implies that contrary to Emerson’s (1971) hypothesis, the initial radiation of *Coptotermes* may not have originated from Asia (Figure S1). Due to the current absence of *Coptotermes* molecular data from the African region, we can only speculate on the origin of *Coptotermes*.

A fourth species, *C. truncatus* (Wasmann) was found in Madagascar and in some associated coastal islands in 1897. The only available COII sequence suggests that *C. truncatus* is related to the Asian *Coptotermes* clade, not to the African clade (Lee et al. 2015), therefore its establishment in Madagascar appears to be a more recent event in comparison to the original African *Coptotermes* radiation (Paulian 1970). Little research has been conducted on *C. truncatus* since the 1970’s (Eggleton and Davies 2003), but the validity of its taxonomic status was supported by Holmgren (1909) and Cachan (1949), and confirmed by COII sequence divergence (Lee et al. 2015). However, because of the genetic similarity of *C. truncatus* to the Asian clade, it is also possible that it is a synonym to one of the Southeast Asian species for which we have little molecular data. Despite the apparent validity of *C. truncatus*, the recent nomenclatural revival by Krishna et al. (2013b) of *C. mauricianus* (Rambur) from Mauritius Island (described from imagos in 1842 as *Termes mauricianus* by Rambur), raises questions and it

was suggested to be a potential synonym of *C. truncatus* (Emerson, cited in Krishna et al. 2013b). The proximity to Madagascar and the complete absence of any description since Sjöstedt (1900) suggests that *C. mauricianus* may be a senior synonym of *C. truncatus*. However, we failed to find any records of *C. truncatus* on Mauritius, while *C. gestroi* (introduced from Southeast Asia) is currently fully established on this island. If *C. truncatus* is not found on Mauritius and no other *Coptotermes* other than *C. gestroi* are found, *C. mauricianus* may in fact be an unexpected senior synonym of *C. gestroi*. We here argue in case of such synonymy that, because of the worldwide pest status of *C. gestroi*, now established and recognized for more than a century, and the fact that *C. mauricianus* was never used, *C. gestroi* name's should be retained as a valid name (*nomen protectum*), and *C. mauricianus* would therefore be a *nomen oblitum* according to ICZN art. 23.9.

In a similar problem of priority, a single specimen described as *C. paradoxus* (Sjöstedt) from Togo was suggested to be a synonym of *C. intermedius* (Emerson, cited in Krishna et al. 2013b), but the synonymy remains unclear and no specimens have been identified since 1926. It is therefore possible that *C. paradoxus* would take precedence over its potential junior synonym *C. intermedius* if further examined. From a description of soldiers from Gabon, Harris (1968) described *C. silvaticus*; however, this species has never subsequently been found. The collection locality of the holotype was within the southern distribution of *C. sjostedti*, and the lack of any evidence about its existence since 1968 raises concerns. Investigating the collection specimens of *C. silvaticus* would prove useful to determine if it is a valid taxon or a junior synonym of *C. sjostedti*.

Of the named *Coptotermes* species in Africa and Madagascar, we suggest that only four species currently have a solid taxonomic basis (*C. amanii*, *C. intermedius*, *C. sjostedti* and *C. truncatus*); however, three species from collection specimens need further investigation (*C. mauricianus*, *C. paradoxus*, and *C. silvaticus*) to investigate potential senior or junior synonymy. In addition to the native *Coptotermes* species, there are occurrences of human-aided introduction of *Coptotermes* species in the African region. *Coptotermes formosanus* was detected in South

Africa, but the early detection resulted in action being taken and its probable eradication (Uys 2002). However, *C. gestroi* was introduced and established on Réunion Island (Bordereau et al. 1999), Mayotte, and Mauritius. Samples from the Seychelles, originally thought to be *C. truncatus* may possibly be *C. gestroi* because of the frequent occurrence of *C. gestroi* on moist tropical islands around the world, including the surrounding islands of Madagascar.

#### ***Coptotermes* from the Neotropical region**

Three native *Coptotermes* species were described from the New World. However, Scheffrahn et al. (2015) suggested that, *C. niger* Snyder and *C. crassus* Snyder are both be junior synonyms of *C. testaceus* (Table S7). The distribution of the *C. testaceus* – *C. niger* – *C. crassus* complex extends from the southern part of lowland Mexico to Brazil and is the only known *Coptotermes* taxa to display three pairs of setae around the fontanelle. *Coptotermes marabitanas* (Hagen) is a junior synonym of *C. testaceus* following Adamson (1937) but has continued to be listed in regional checklists, as the synonymy was questioned by Mathews (1977). *Coptotermes sucineus* Emerson, one of the four known *Coptotermes* fossils (Emerson 1971, Krishna and Grimaldi 2009), was found within the current distribution of *C. testaceus* in Mexico from Miocene amber. Scheffrahn et al. (2015) suggested that this fossil specimen compares morphologically favorably with modern day *C. testaceus*. Three additional fossil species, *C. priscus* Emerson, *C. hirsutus* Krishna and Grimaldi, and *C. paleodominicanus* Krishna and Grimaldi have been found in Dominican amber, which implies the presence of *Coptotermes* in the Caribbean region during the Miocene. Further studies should investigate the population structure of *C. testaceus* in the Neotropics to confirm if it represents a single taxon or determine if some populations are reproductively isolated and represent separate species. Despite its extensive range in the Neotropics, the *C. testaceus* complex has not been documented as an invasive species in other parts of the world.

Beginning in the 1930's with Barbados, humans may have introduced the Asian *C. gestroi* throughout the West Indies, some areas of Brazil and Paraguay, and south Florida (Constantino

2002, Scheffrahn and Su 2005). In the U.S.A., *C. formosanus* is one of the most economically important invasive species throughout southeastern states (Rust and Su 2012, Corn and Johnson 2013). A local infestation of *C. formosanus* were detected in San Diego (California), but it is unclear if the species is still established in the area (Haagsma et al. 1995) and like South Africa, the population appears to have been extirpated (Scheffrahn et al. 2015). Finally, *C. sjostedti*, an African species, has been recorded on Guadeloupe (Scheffrahn et al. 2004).

### ***Coptotermes* from the Australian region**

The active termite research in Australia offers insights on the genetics of *Coptotermes* at a much finer resolution than for *Coptotermes* from most other areas (Table S8). There are currently six described *Coptotermes* species in Australia, with *C. acinaciformis* (Froggatt) receiving the most attention. At present two subspecies within *C. acinaciformis* are recognized: *C. a. acinaciformis* and *C. a. raffrayi*, however, the status of *C. a. raffrayi* as either a full- or subspecies has varied between authors since Calaby and Gay (1956) first designated it as a subspecies. There is, however, a strong geographic pattern to genetic variation within *C. acinaciformis sensu lato* with pronounced western (*C. a. raffrayi*), southeastern and northern (both currently classified as *C. a. acinaciformis*), that correspond to differences in epigeal mound structures, (only Australian *Coptotermes* species build mounds). Lee et al. (2015) suggest that *C. acinaciformis sensu lato* consists of at least three species and further genetic and environmental niche analyses involving sampling across the entire range of these taxa, in particular in Central Australia, are underway to investigate this further.

The five remaining species are well established in the literature (Watson and Abbey 1993), and their taxonomic status has also been examined by genetic data (Lee et al. 2015). *Coptotermes dreghorni* Hill, which has a limited distribution in wet-tropical, northeastern Australia (Watson and Abbey 1993) and unique biological traits, is the sister-group of *C. acinaciformis sensu lato* (Lee et al. 2015). *Coptotermes brunneus* Gay, also has a narrow, possibly relictual, distribution in coastal western Australia. *Coptotermes michaelsoni* Silvestri, has at times been considered

a synonym or western subspecies of *C. lacteus* (Froggatt), however genetic data firmly establishes that the two are not closely related; *C. michaelsoni* groups with the clade that includes *C. acinaciformis* and relatives whereas *C. lacteus* groups with *C. frenchi*. The status of the remaining two described species, *C. lacteus* and *C. frenchi* requires additional investigation. Lee et al. (2015) found that *C. lacteus* rendered *C. frenchi* paraphyletic and that there is considerable variation within each species, mirroring earlier analyses of cuticular hydrocarbon diversity in these species (Brown et al. 1990). Lee et al. (2015) included insufficient sampling to fully resolve species-limits in *C. lacteus/C. frenchi* and additional dense geographic sampling in southeastern Australia is needed. Finally, the survey by Lee et al. (2015) revealed the presence of two potential new *Coptotermes* species in Australia, closely related to *C. frenchi* / *C. lacteus*. These species have much smaller soldiers than the other Australian *Coptotermes*, and are genetically distinct, but have yet to be formally described (Lee et al., *in prep.*). There is currently no known invasive *Coptotermes* species established in Australia; however, *C. acinaciformis* was found in a limited area in New Zealand (Ross 2005) and other Pacific islands (Evans 2010). Finally, specimens named *C. fumipennis* (Walker) originally thought to be described from Australia were suggested to be from another location, which remains unknown (Watson and Gay 1980).

### **Additional References**

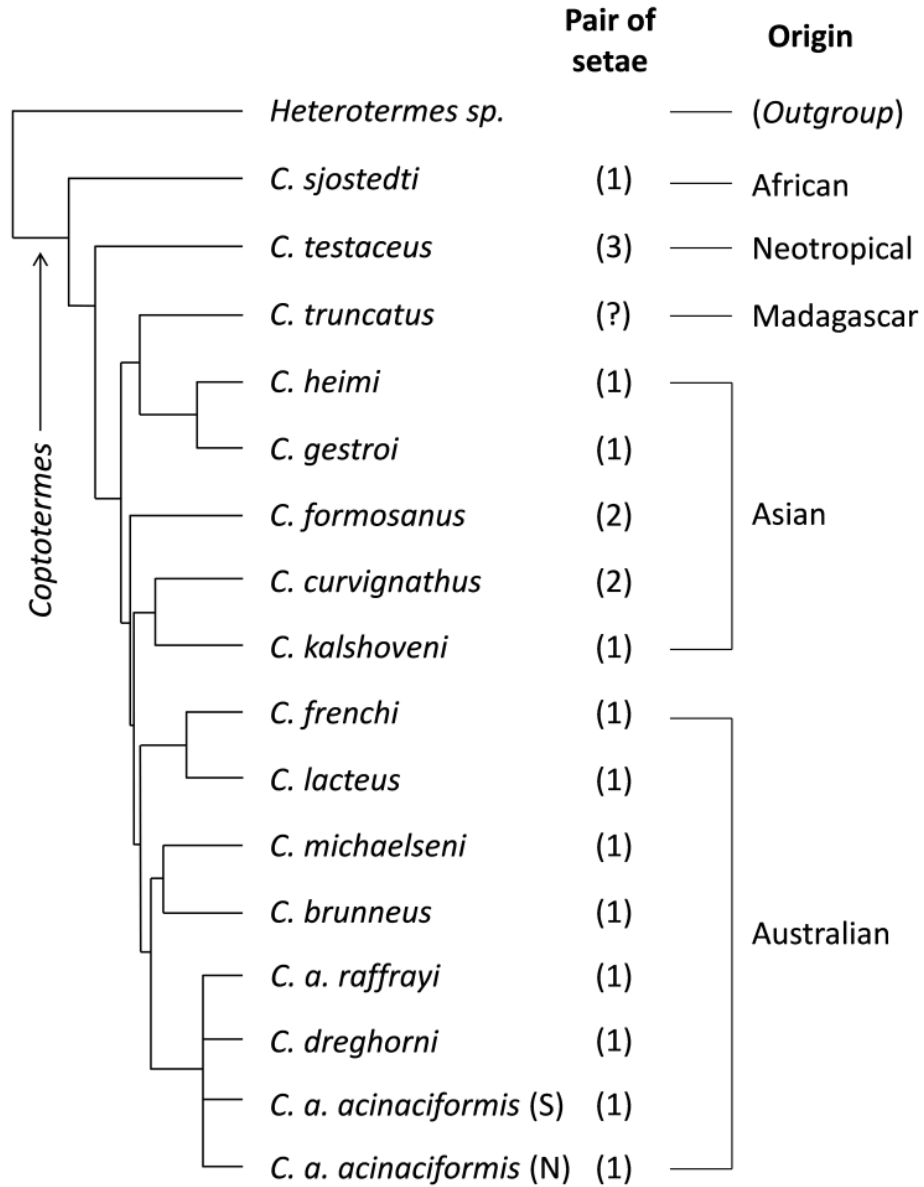
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**Figure S1:** Partial phylogeny of *Coptotermes* using 12S,16S and COII sequences, topology modified from Lee et al. (2015). Numbers indicate the characteristic pair of setae around the fontanelle of soldiers from a given species.

**Table S1. List of *Coptotermes* species names from Southeast Asia**

Species	Authority	Species status	Junior synonyms	Putative native area	Notes	Sequences available*		
						12S	16S	COII
<i>Coptotermes elisae</i>	(Desneux) 1905	Valid ✓	<i>C. hyaloapex</i>	Indonesia, Malaysia	Senior synonym of <i>C. curvignathus</i> ?	4(6)	0	0
<i>Coptotermes gambrinus</i>	Bourguignon and Roisin 2011	Valid ✓		Papua New Guinea		0	0	0
<i>Coptotermes gestroi</i>	(Wasmann) 1896	Valid ✓	<i>C. havilandi</i> , <i>C. javanicus</i> , <i>C. monosetosus</i> , <i>C. meglunensis</i> , <i>C. obliquus</i> , <i>C. pacificus</i> , <i>C. vastator</i> , <i>C. yaxianensis</i>	Indonesia, Malaysia, Philippines, Indochina peninsula	Presumably the most invasive subterranean termite species in the tropics	5(35)	12(134)	8(67)
<i>Coptotermes grandiceps</i>	Snyder 1925	Valid ✓	<i>C. froggatti</i> , <i>C. hilli</i> , <i>C. solomonensis</i> , <i>C. obiratus</i>	Papua New Guinea		0	0	0
<i>Coptotermes kalshoveni</i>	Kemner 1934	Valid ✓		Indonesia, Malaysia		1(2)	4(4)	4(4)
<i>Coptotermes pamuae</i>	Snyder 1925	Valid ✓		Papua New Guinea		1(1)	0	0
<i>Coptotermes sepangensis</i>	Krishna 1956	Valid ✓	<i>C. alfredi</i>	Indonesia, Malaysia		0	1(2)	8(8)
<i>Coptotermes travians</i>	(Haviland 1898)	Valid ✓	<i>C. bornensis</i>	Sumatra, Malaysia		1(1)	2(2)	1(2)
<i>Coptotermes amboinensis</i>	Kemner 1931	Uncertain ?		Indonesia: Maluku		0	0	0
<i>Coptotermes bentongensis</i>	Krishna 1956	Uncertain ?		Malaysia	Junior synonym of <i>C. sepangensis</i> ?	0	0	0
<i>Coptotermes boetonensis</i>	Kemner 1934	Uncertain ?		Indonesia: Java		0	0	0
<i>Coptotermes curvignathus</i>	Holmgren 1913	Uncertain ?	<i>C. robustus</i> , <i>C. flavicephalus</i>	Indonesia, Vietnam, Philippines	Junior synonym of <i>C. elisae</i> ?	3(3)	5(10)	4(8)
<i>Coptotermes dobonicus</i>	Oshima 1914	Uncertain ?		Papua New Guinea		0	0	0
<i>Coptotermes menadoae</i>	Oshima 1914	Uncertain ?		Indonesia: Sulawesi		0	0	0
<i>Coptotermes minutissimus</i>	Kemner 1934	Uncertain ?		Indonesia: Sulawesi		0	0	0
<i>Coptotermes oshimai</i>	Light and Davis 1929	Uncertain ?		Indonesia: Sulawesi		0	0	0
<i>Coptotermes peregrinator</i>	Kemner 1934	Uncertain ?		Indonesia: Sulawesi		0	0	0
<i>Coptotermes premasmii</i>	Ahmad 1965	Uncertain ?		Thailand		0	0	0
<i>Coptotermes remotus</i>	Hill 1927	Uncertain ?		Papua New Guinea	Junior synonym of <i>C. pamuae</i> ?	0	0	0
<i>Coptotermes sinabangensis</i>	Oshima 1923	Uncertain ?		Sumatra, Malaysia		0	0	0

\*number of unique genotypes (total number of sequences for the species) deposited in Genbank as of July 2015 for three common mitochondrial markers (12S, 16S, COII).

**Table S2. List of *Coptotermes* species names from China**

Species	Authority	Species status	Junior synonyms	Putative native area	Notes	Sequences available*		
						12S	16S	COII
<i>Coptotermes formosanus</i>	Shiraki 1909	Valid ✓	<i>C. formosae</i> , <i>C. hongkonensis</i> , <i>C. intrudens</i> , <i>C. eucalyptus</i> , <i>C. xiaoliangensis</i> , <i>C. guangzhouensis</i> , <i>C. heteromorphus</i> , <i>C. communis</i> , <i>C. rectangularis</i>	Mainland China and Taiwan	Presumably the only valid native <i>Coptotermes</i> in mainland China	3(40)	6(87)	14(170)
<i>Coptotermes bannaensis</i>	Xia and He 1986	Uncertain ?		Yunnan	Jr. synonym of <i>C. gestroi</i> ?	0	0	0
<i>Coptotermes changtaiensis</i>	Xia and He 1986	Uncertain ?	<i>C. setosus</i>	Anhui	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes chaoxianensis</i>	Huang and Li 1985	Uncertain ?	<i>C. varicapitatus minutus</i>	Anhui	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes cochlearus</i>	Xia and He 1986	Uncertain ?		Anhui	Contradicting data	1(1)	1(1)	0
<i>Coptotermes cyclocoryphus</i>	Zhu et al 1984	Uncertain ?		Guangdong	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes dimorphus</i>	Xia and He 1986	Uncertain ?		Yunnan	Contradicting data	1(1)	1(1)	0
<i>Coptotermes grandis</i>	Li and Huang 1985	Uncertain ?		Fujian	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes guangdongensis</i>	Ping 1985	Uncertain ?	<i>C. pingi</i>	Guangdong	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes guizhouensis</i>	He and Qui 1982	Uncertain ?		Guizhou	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes gulangyuensis</i>	Li and Huang 1986	Uncertain ?		Fujian	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes hainanensis</i>	Li and Tsai 1985	Uncertain ?	<i>C. jiaxingensis</i>	Hainan	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes hekouensis</i>	Xia and He 1986	Uncertain ?		Yunnan	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes longignathus</i>	Xia and He 1986	Uncertain ?		Yunnan	Jr. synonym of <i>C. gestroi</i> ?	0	0	0
<i>Coptotermes longistriatus</i>	Li and Huang 1985	Uncertain ?		Guangdong	Jr. synonym of <i>C. formosanus</i> ?	1(1)	0	0
<i>Coptotermes melanoistriatus</i>	Gao et al 1995	Uncertain ?		Hong kong	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes monosetosus</i>	Tsai and Li 1985	Uncertain ?		Yunnan	Jr. synonym of <i>C. gestroi</i> ?	0	0	0
<i>Coptotermes ochraceus</i>	Ping and Xu 1986	Uncertain ?	<i>C. zhenyuanensis</i>	Guizhou	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes shanghaiensis</i>	Xia and He 1986	Uncertain ?		Shanghai	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes suzhouensis</i>	Xia and He 1986	Uncertain ?	<i>C. xianrendongensis</i> , <i>C. anglefontanalis</i>	Jiangsu	Jr. synonym of <i>C. formosanus</i> ?	0	0	0
<i>Coptotermes varicapitatus</i>	Tsai and Li 1985	Uncertain ?		Guangdong	Jr. synonym of <i>C. formosanus</i> ?	0	0	0

\*number of unique genotypes (total number of sequences for the species) deposited in Genbank as of July 2015 for three common mitochondrial markers (12S, 16S, COII).

**Table S3.** Measurements of 20 Chinese-exclusive *Coptotermes* based on original description and two widely distributed species, *C. formosanus* and *C. gestroi* based on 30 individuals from 10 colonies collected in Taiwan. The six characters shown were commonly used in the 8 original descriptions. Range (mm) and average in parentheses are listed.

	No. of measured individual	No. of collecting location	Length of head to lateral base of mandible	Maximum width of head	Length of left mandible	Maximum width of postmentum	Minimum width of postmentum	Width of pronotum
<i>C. bannaensis</i>	?	1	1.55 - 1.625	1.25 - 1.425	0.813 - 0.938	0.45 - 0.475	0.288 - 0.338	0.938 - 1.063
<i>C. changtaiensis</i> *	?	1	1.575 - 1.70	1.30 - 1.50	1.00 - 1.025	0.438 - 0.463	0.275 - 0.282	0.938 - 0.963
<i>C. chaoxianensis</i> *	10	1	1.29 - 1.43 (1.39)	1.14 - 1.27 (1.20)	0.82 - 0.93 (0.88)	0.36 - 0.40 (0.38)	0.20 - 0.22 (0.21)	0.82 - 0.83 (0.82)
<i>C. cochlearus</i>	?	1	1.50 - 1.575	1.20 - 1.30	0.90 - 0.963	0.425 - 0.438	0.25 - 0.275	0.875 - 0.938
<i>C. cyclocoryphus</i> *	?	1	1.39 - 1.528 (1.476)	1.22 - 1.38 (1.28)	0.930 - 0.991 (0.9705)	0.342 - 0.416 (0.3875)	0.217 - 0.239 (0.226)	0.797 - 0.878 (0.851)
<i>C. dimorphus</i> *	?	1	1.25 - 1.575	1.175 - 1.40	0.938 - 1.00	0.438 - 0.45	0.238 - 0.313	0.938 - 1.063
<i>C. grandis</i>	10	1	1.68 - 1.87 (1.77)	1.33 - 1.54 (1.44)	1.04 - 1.14 (1.08)	0.46 - 0.54 (0.50)	0.26 - 0.32 (0.30)	0.96 - 1.14 (1.06)
<i>C. guangdongensis</i>	?	1	1.53 - 1.55	1.33 - 1.35	1.07 - 1.07	0.43 - 0.45	0.25 - 0.25	0.94 - 0.99
<i>C. guizhouensis</i> *	?	1	1.416 - 1.512	1.20 - 1.272	0.912 - 0.912	0.408 - 0.432	0.24 - 0.264	0.774 - 0.792
<i>C. gulangyuensis</i>	13	1	1.25 - 1.50 (1.375)	1.15 - 1.33 (1.25)	0.88 - 0.96 (0.91)	0.33 - 0.42 (0.37)	0.20 - 0.25 (0.22)	0.75 - 0.88 (0.80)
<i>C. hainanensis</i>	10	1	1.57 - 1.68 (1.63)	1.33 - 1.47 (1.39)	1.04 - 1.07 (1.05)	0.43 - 0.47 (0.45)	0.25 - 0.29 (0.27)	0.93 - 1.18 (1.02)
<i>C. hekouensis</i> *	?	1	1.55 - 1.675	1.275 - 1.375	0.963 - 1.00	0.413 - 0.475	0.213 - 0.25	0.875 - 0.938
<i>C. longignathus</i>	?	1	1.35 - 1.475	1.075 - 1.20	1.00 - 1.025	0.40 - 0.45	0.25 - 0.25	0.838 - 0.863
<i>C. longistriatus</i>	4	1	1.60 - 1.61 (1.61)	1.36 - 1.39 (1.375)	1.00 - 1.04 (1.03)	0.46 - 0.51 (0.48)	0.25 - 0.26 (0.255)	0.96 - 1.02 (1.00)
<i>C. melanoistriatus</i>	?	1	1.56 - 1.584	1.284 - 1.296	0.984 - 1.008	0.408 - 0.432	0.24 - 0.264	0.864 - 0.888
<i>C. monosetosus</i> *	10	1	1.25 - 1.28 (1.26)	1.14 - 1.28 (1.20)	0.83 - 0.89 (0.86)	0.36 - 0.39 (0.37)	0.22 - 0.25 (0.24)	0.79 - 0.86 (0.83)
<i>C. ochraceus</i>	10	1	1.66 - 1.80 (1.74)	1.28 - 1.43 (1.35)	0.99 - 1.04 (1.02)	0.43 - 0.47 (0.44)	0.25 - 0.29 (0.27)	0.9 - 1.02 (0.95)
<i>C. shanghaiensis</i>	?	1	1.25 - 1.375	1.025 - 1.05	0.875 - 0.925	0.40 - 0.40	0.225 - 0.225	0.70 - 0.725
<i>C. suzhouensis</i>	?	1	1.60 - 1.675	1.25 - 1.35	0.963 - 1.025	0.438 - 0.50	0.275 - 0.288	0.875 - 0.975
<i>C. varicapitatus</i> *	10	1	1.36 - 1.43 (1.40)	1.18 - 1.43 (1.32)	0.89 - 0.96 (0.92)	0.39 - 0.43 (0.40)	0.21 - 0.23 (0.22)	0.87 - 0.89 (0.88)
<i>C. formosanus</i>	30	10	1.048 - 1.694 (1.402)	1.058 - 1.372 (1.169)	0.766 - 1.022 (0.877)	0.362 - 0.461 (0.400)	0.207 - 0.284 (0.239)	0.678 - 0.978 (0.812)
<i>C. gestroi</i>	30	10	1.267 - 1.472 (1.374)	1.081 - 1.23 (1.164)	0.753 - 0.904 (0.849)	0.37 - 0.447 (0.410)	0.224 - 0.302 (0.265)	0.755 - 0.921 (0.851)

\* Species described with polymorphic soldier castes. For each character measured, the range covered all types of soldiers.

**Table S4.** Measurements of 9 Chinese-exclusive *Coptotermes* winged imago based on original description and two widely distributed species, *C. formosanus* and *C. gestroi* based on 30 and 17 individuals collected in Taiwan, respectively. The five characters shown were commonly used in the original descriptions. Range (mm) are listed.

	No. of measured individual	No. of collecting location	Length of head to tip of labrum	Maximum width of head with eyes	Distance between compound eye to head capsule margin	Maximum length of pronotum	Maximum width of pronotum
<i>C. changtaiensis</i>	?	?	1.70-1.89	1.58-1.68	0.18-0.21	0.8-0.82	1.4-1.5
<i>C. chaoxianensis</i>	3	1	1.40-1.43	1.39-1.43	0.14-0.17	N/A	1.25-1.32
<i>C. cyclocoryphus</i>	?	1	1.56-1.66	1.537-1.586	N/A	0.88-0.9	1.342-1.42
<i>C. dimorphus</i>	?	1	1.50-1.55	1.375-1.45	0.156-0.18	0.75-0.8	1.35-1.4
<i>C. guizhouensis</i>	?	1	1.512	1.368-1.392	0.144	0.768	1.272
<i>C. hekouensis</i>	?	1	1.625-1.75	1.5-1.625	0.144	0.8	1.3-1.4
<i>C. monosetosus</i>	10	1	1.4-1.46	1.33-1.43	0.14-0.18	N/A	1.32-1.36
<i>C. shanghaiensis</i>	?	1	1.5-1.575	1.35-1.4	0.12	0.65-0.7	1.125-1.2
<i>C. suzhouensis</i>	?	1	1.65-1.75	1.575-1.625	0.12-0.156	0.85-0.9	1.45-1.5
<i>C. formosanus</i>	30	11	1.260-1.698	1.398-1.626	0.093-0.184	0.789-0.953	1.217-1.44
<i>C. gestroi</i>	17	5	1.298-1.527	1.311-1.442	0.087-0.147	0.789-0.87	1.207-1.384

**Table S5. List of *Coptotermes* species names from the Indian region**

Species	Authority	Species status	Junior synonyms	Putative native area	Notes	Sequences available*		
						12S	16S	COII
<i>Coptotermes heimi</i>	(Wasmann) 1902	Valid ✓	<i>C. parvulus</i>	India, Pakistan, Nepal	Sometimes confused with <i>C. gestroi</i>	6(15)	3(17)	2(13)
<i>Coptotermes ceylonicus</i>	Holmgren 1911	Uncertain ?		South India, Sri Lanka	Need to check relation with <i>C. gestroi</i>	0	0	0
<i>Coptotermes beckeri</i>	Mathur and Chhotani 1969	Uncertain ?		South India		0	0	0
<i>Coptotermes emersoni</i>	Ahmad 1953	Uncertain ?		Sri Lanka		0	0	0
<i>Coptotermes gaurii</i>	Roonwal and Krishna 1955	Uncertain ?		Sri Lanka, Nicobar	Junior synonym of <i>C. ceylonicus</i> ?	0	0	0
<i>Coptotermes kishori</i>	Roonwal and Chhotani 1962	Uncertain ?		India		0	0	0

\*number of unique genotypes (total number of sequences for the species) deposited in Genbank as of July 2015 for three common mitochondrial markers (12S, 16S, COII).

**Table S6. List of *Coptotermes* species names from the African region**

Species	Authority	Species status	Junior synonyms	Putative native area	Notes	Sequences available*		
						12S	16S	COII
<i>Coptotermes amanii</i>	(Sjöstedt) 1911	Valid ✓		Ethiopian region		0	0	2(4)
<i>Coptotermes intermedius</i>	Silvestri 1912	Valid ✓	<i>C. intermedius subintacta</i> , <i>C. reductus</i>	West Africa		0	1(1)	0
<i>Coptotermes sjostedti</i>	Holmgren 1911	Valid ✓	<i>C. sjostedti modica</i>	Ethiopian region to Senegal		1(1)	2(2)	1(1)
<i>Coptotermes truncatus</i>	(Wasmann) 1897	Valid ✓		Madagascar	Closely related to Asian species	1(2)	1(2)	1(6)
<i>Coptotermes mauricianus</i>	(Rambur) 1842	Uncertain ?		Mauritius	Senior synonym of <i>C. truncatus</i> or <i>C. gestroi</i> ?	0	0	0
<i>Coptotermes paradoxus</i>	(Sjöstedt) 1911	Uncertain ?		Ethiopian region	Senior synonym of <i>C. intermedius</i> ?	0	0	0
<i>Coptotermes silvaticus</i>	Harris 1968	Uncertain ?		Ethiopian region	Junior synonym of <i>C. sjostedti</i> ?	1(1)	0	0

\*number of unique genotypes (total number of sequences for the species) deposited in Genbank as of July 2015 for three common mitochondrial markers (12S, 16S, COII).



**Table S7. List of *Coptotermes* species names from the Neotropical region**

Species	Authority	Species status	Junior synonyms	Putative native area	Notes	Sequences available*		
						12S	16S	COII
<i>Coptotermes testaceus</i>	(Linnaeus) 1758	Valid ✓	<i>C. marabitanas</i> <i>Perla fusca</i> <i>Termes morio</i>	Central and South America		1(1)	17(33)	4(4)
<i>Coptotermes crassus</i>	Snyder 1922	Uncertain ?			Junior synonym of <i>C. testaceus</i> ?	0	1(1)	0
<i>Coptotermes niger</i>	Snyder 1922	Uncertain ?			Junior synonym of <i>C. testaceus</i> ?	1(1)	0	1(1)
<i>Coptotermes hirsutus</i>	Krishna and Grimaldi 2009	Fossil †		Dominican Republic	Miocene	0	0	0
<i>Coptotermes paleodominicanus</i>	Krishna and Grimaldi 2009	Fossil †		Dominican Republic	Miocene	0	0	0
<i>Coptotermes priscus</i>	Emerson 1971	Fossil †		Dominican Republic	Miocene	0	0	0
<i>Coptotermes sucineus</i>	Emerson 1971	Fossil †		Mexico	Miocene	0	0	0

\*number of unique genotypes (total number of sequences for the species) deposited in Genbank as of July 2015 for three common mitochondrial markers (12S, 16S, COII).

**Table S8. List of *Coptotermes* species names from the Australian region**

Species	Authority	Species status	Junior synonyms	Putative native area	Notes	Sequences available*		
						12S	16S	COII
<i>Coptotermes a. acinaciformis</i>	(Froggatt) 1898	Valid ✓		Australia	Potential complex of species or subspecies	6(17)	13(13)	28(71)
<i>Coptotermes brunneus</i>	Gay 1955	Valid ✓		Western Australia		1(1)	1(1)	1(1)
<i>Coptotermes dreghorni</i>	Hill 1942	Valid ✓		Queensland	Closely allied with <i>C. acinaciformis</i> ; Additional work needed to establish the <i>C. acinaciformis</i> species complex	1(1)	1(1)	1(1)
<i>Coptotermes frenchi</i>	Hill 1932	Valid ✓	<i>C. flavus</i> , <i>C. labiosus</i>	Australia	Paraphyletic with respect to <i>C. lacteus</i> ; may represent a species complex	8(8)	3(5)	4(10)
<i>Coptotermes lacteus</i>	(Froggatt) 1898	Valid ✓	<i>C. sedulus</i>	Eastern Australia		3(7)	3(10)	6(16)
<i>Coptotermes michaelsoni</i>	Silvestri 1909	Valid ✓		Western Australia		3(4)	2(3)	2(7)
<i>Coptotermes a. raffrayi</i>	Wasmann 1900	Uncertain ?		Western Australia	Potential junior synonym or subspecies of <i>C. acinaciformis</i>	3(4)	3(3)	7(20)
<i>Coptotermes fumipennis</i>	(Walker) 1853	Uncertain ?		Unknown	Incorrect location for type material	0	0	0

\*number of unique genotypes (total number of sequences for the species) deposited in Genbank as of July 2015 for three common mitochondrial markers (12S, 16S, COII).