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

Table 1. Continued

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

[a]Bold species indicates that there is strong evidence for species validity.
[b]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 specie 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

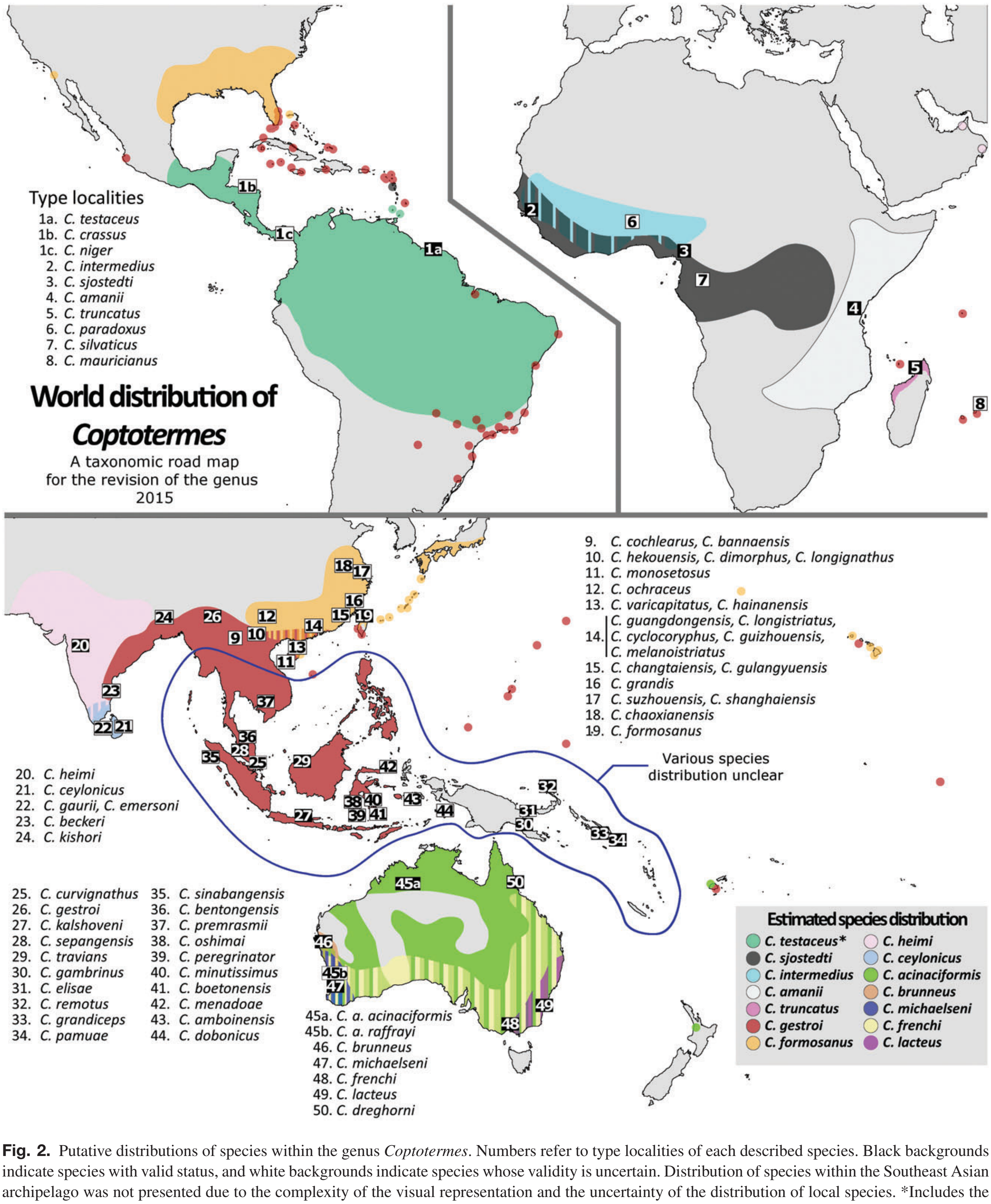

Fig. 2. Putative distributions of species within the genus *Coptotermes*. Numbers refer to type localities of each described species. Black backgrounds indicate species with valid status, and white backgrounds indicate species whose validity is uncertain. Distribution of species within the Southeast 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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References

Austin, J.W., Szalanski, A.L., Scheffrahn, R.H., Messenger, M.T., Dronnet, S. & Bagnères, A.G. (2005) Genetic evidence for the synonymy of two *Reticulitermes* species: *Reticulitermes flavipes* and *Reticulitermes santonensis*. *Annals of the Entomological Society of America*, **98**, 395–401.

Bourguignon, T. & Roisin, Y. (2011) Revision of the termite family Rhinotermitidae (Isoptera) in New Guinea. *ZooKeys*, **148**, 55–103.

Bourguignon, T., Lo, N., Cameron, S.L. *et al.* (2015) The evolutionary history of termites as inferred from 66 mitochondrial genomes. *Molecular Biology and Evolution*, **32**, 406–421.

Brown, W.V., Lacey, M.J. & Lenz, M. (2004) Further examination of cuticular hydrocarbons of worker termites of Australian *Coptotermes* (Isoptera: Rhinotermitidae) reveals greater taxonomic complexity within species. *Sociobiology*, **44**, 623–658.

Cameron, S.L., Lo, N., Bourguignon, T., Svenson, G.J. & Evans, T.A. (2012) A mitochondrial genome phylogeny of termites (Blattodea: Termitoidae): robust support for interfamilial relationships and molecular synapomorphies define major clades. *Molecular Phylogenetics and Evolution*, **65**, 163–173.

Chouvenc, T. & Su, N.Y. (2014) Colony age-dependent pathway in caste development of *Coptotermes formosanus* Shiraki. *Insectes Sociaux*, **61**, 171–182.

Chouvenc, T., Helmick, E.E. & Su, N.Y. (2015) Hybridization of two major termite invaders as a consequence of human activity. *PLoS ONE*, **10**, e0120745.

Djernaes, M., Klass, K.-D. & Eggleton, P. (2015) Identifying possible sister groups of Cryptocercidae + Isoptera: a combined molecular and morphological phylogeny of Dictyoptera. *Molecular Phylogenetics and Evolution*, **84**, 284–303.

Eggleton, P. (1999) Termite species description rates and the state of termite taxonomy. *Insectes Sociaux*, **46**, 1–5.

Emerson, A.E. (1971) Tertiary fossil species of the Rhinotermitidae (Isoptera), phylogeny of genera, and reciprocal phylogeny of associated Flagellata (Protozoa) and the Staphylinidae (Coleoptera). *Bulletin of the American Museum of Natural History*, **146**, 243–304.

Evans, T.A. (2011) Invasive termites. *Biology of Termites: A Modern Synthesis* (ed. by D.E. Bignell, Y. Roisin and N. Lo), pp. 519–562. Springer, the Netherlands.

Evans, T.A., Forschler, B.T. & Grace, J.K. (2013) Biology of invasive termites: a worldwide review. *Annual Review of Entomology*, **58**, 455–474.

Ferraz, M.F. & Cancello, E.M. (2004) Strategies on the developmental biology of incipient colonies of *Coptotermes gestroi* (Isoptera: Rhinotermitidae), in different substrates. *Sociobiology*, **44**, 109–122.

Husseneder, C. & Grace, J.K. (2001) Evaluation of DNA fingerprinting, aggression tests, and morphometry as tools for colony delineation of the Formosan subterranean termite. *Journal of Insect Behavior*, **14**, 173–186.

Husseneder, C., Simms, D.M., Delatte, J.R., Wang, C., Grace, J.K. & Vargo, E.L. (2012) Genetic diversity and colony breeding structure in native and introduced ranges of the Formosan subterranean termite, *Coptotermes formosanus*. *Biological Invasions*, **14**, 419–437.

Inward, D., Beccaloni, G. & Eggleton, P. (2007) Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biology Letters*, **3**, 331–335.

Jenkins, T.M., Jones, S.C., Lee, C.Y. *et al.* (2007) Phylogeography illuminates maternal origins of exotic *Coptotermes gestroi* (Isoptera: Rhinotermitidae). *Molecular Phylogenetics and Evolution*, **42**, 612–621.

Jones, D.T., Verkerk, R.H.J. & Eggleton, P. (2005) Methods for sampling termites. *Insect Sampling in Forest Ecosystems* (ed. by S. Leather), pp. 221–253. Blackwell Science Ltd, Oxford.

Kirton, L.G. (2005) The importance of accurate termite taxonomy in the broader perspective of termite management. *Proceedings of the Fifth International Conference on Urban Pests*, pp. 1–7. P&Y Design Network, Penang.

Kirton, L.G. & Brown, V.K. (2003) The taxonomic status of pest species of *Coptotermes* in Southeast Asia: Resolving the paradox in the pest status of the termites, *Coptotermes gestroi, C. havilandi and C. travians* (Isoptera: Rhinotermitidae). *Sociobiology*, **42**, 43–63.

Krishna, K., Grimaldi, D.A., Krishna, V. & Engel, M.S. (2013a) Treatise on the Isoptera of the World: Vol. 1. *Bulletin of the American Museum of Natural History*, **377**, 1–200.

Krishna, K., Grimaldi, D.A., Krishna, V. & Engel, M.S. (2013b) Treatise on the Isoptera of the World: Vol. 3. *Bulletin of the American Museum of Natural History*, **377**, 623–973.

Lee, T.R., Cameron, S.L., Evans, T.A., Ho, S.Y. & Lo, N. (2015) The origins and radiation of Australian *Coptotermes* termites: from rainforest to desert dwellers. *Molecular Phylogenetics and Evolution*, **82**, 234–244.

Li, G. (2000) Coptotermes. *Fauna Sinica, Isoptera*, Vol. **17** (ed. by F. Huang, S. Zhu, Z. Ping, X. He, G. Li and F. Gao), pp. 299–341. Science Press, Beijing.

Li, H.F., Su, N.Y. & Wu, W.J. (2010) Solving the hundred-year controversy of *Coptotermes* taxonomy in Taiwan. *American Entomologist*, **56**, 222–227.

Li, H.F., Su, N.Y., Wu, W.J. & Hsu, E.L. (2011) Termite pests and their control in Taiwan. *Sociobiology*, **57**, 575–586.

Lo, N., Tokuda, G., Watanabe, H. *et al.* (2000) Evidence from multiple gene sequences indicates that termites evolved from wood-feeding cockroaches. *Current Biology*, **10**, 801–804.

Lo, N., Eldridge, R.H. & Lenz, M. (2006) Phylogeny of Australian *Coptotermes* (Isoptera: Rhinotermitidae) species inferred from mitochondrial COII sequences. *Bulletin of Entomological Research*, **96**, 433–437.

Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223–228.

Rust, M.K. & Su, N.Y. (2012) Managing social insects of urban importance. *Annual Review of Entomology*, **57**, 355–375.

Scheffrahn, R.H. (2013) Overview and current status of non-native termites (Isoptera) in Florida. *Florida Entomologist*, **96**, 781–788.

Scheffrahn, R.H., Krecek, J., Maharajh, B. *et al.* (2004) Establishment of the African termite, *Coptotermes sjostedti* (Isoptera: Rhinotermitidae), on the Island of Guadeloupe, French West Indies. *Annals of the Entomological Society of America*, **97**, 872–876.

Scheffrahn, R.H., Carrijo, T.F., Křeček, J. *et al.* (2015) A single endemic and three exotic species of the termite genus *Coptotermes* (Isoptera, Rhinotermitidae) in the New World. *Arthropod Systematics & Phylogeny*, **73**, 333–348.

Su, N.Y. (2013) How to become a successful invader. *Florida Entomologist*, **96**, 765–769.

Vargo, E.L. & Husseneder, C. (2009) Biology of subterranean termites: insights from molecular studies of *Reticulitermes* and *Coptotermes*. *Annual Review of Entomology*, **54**, 379–403.

Wang, J. & Grace, J.K. (1999) Current status of *Coptotermes* wasmann (lsoptera: Rhinotermitidae) in China, Japan, Australia and the American Pacific. *Sociobiology*, **33**, 295–305.

Yang, R.L. & Li, H.F. (2012) Taxonomy and identification of the five common termite species in Taiwan. *Formosan Entomolology*, **32**, 169–198.

Yeap, B.K., Othman, A.S., Lee, V.S. & Lee, C.Y. (2007) Genetic relationship between *Coptotermes gestroi* and *Coptotermes vastator* (Isoptera: Rhinotermitidae). *Journal of Economic Entomology*, **100**, 467–474.

Yeap, B.K., Othman, A.S. & Lee, C.Y. (2009) Molecular systematics of *Coptotermes* (Isoptera: Rhinotermitidae) from East Asia and Australia. *Annals of the Entomological Society of America*, **102**, 1077–1090.

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