Genomic data provide insights into the classification of extant termites

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The higher classification of termites requires substantial revision as the Neoisoptera, the most diverse termite lineage, comprise many paraphyletic and polyphyletic higher taxa. Here, we produce an updated termite classification using genomic-scale analyses. We reconstruct phylogenies under diverse substitution models with ultraconserved elements analyzed as concatenated matrices or within the multi-species coalescence framework. Our classification is further supported by analyses controlling for rogue loci and taxa, and topological tests. We show that the Neoisoptera are composed of seven family-level monophyletic lineages, including the Heterotermitidae Froggatt, Psammotermitidae Holmgren, and Termitogetonidae Holmgren, raised from subfamilial rank. The species-rich Termitidae are composed of 18 subfamily-level monophyletic lineages, including the new subfamilies Crepititermitinae, Cylindrotermitinae, Forficulitermitinae, Neocapritermitinae, Protohamitermitinae, and Promirotermitinae; and the revived Amitermitinae Kemner, Microcerotermitinae Holmgren, and Mirocapritermitinae Kemner. Building an updated taxonomic classification on the foundation of unambiguously supported monophyletic lineages makes it highly resilient to potential destabilization caused by the future availability of novel phylogenetic markers and methods. The taxonomic stability is further guaranteed by the modularity of the new termite classification, designed to accommodate as-yet undescribed species with uncertain affinities to the herein delimited monophyletic lineages in the form of new families or subfamilies.

Termites, or Isoptera, are a clade of eusocial cockroaches in a sister-group relationship with the subsocial *Cryptocercus* wood roaches[1–6]. With over 3000 described species[7], the diversity of termites is relatively low compared to hyper-diverse insect clades (*e.g.*, Coleoptera or Lepidoptera). Termites achieve critical ecosystem functions, such as decomposing plant material, providing bioturbation of soils, and influencing water infiltration in soils of tropical and subtropical terrestrial ecosystems, where they are amongst the most abundant animals[8–15]. Termites are also well-known as major pests of wood in service, such as in buildings and constructions, utility poles, fencing, etc.[7,16]. In regions where they are found, they account for over half of total urban pest control costs[17–19], excluding costs from insect-

vectored diseases. Consequently, public opinion on termites has been shaped by, and the bulk of termite biology research has focused on, a handful of pestiferous termite genera. The combination of moderate species diversity and high abundance, leading to economic and ecological importance, has made termites of considerable interest to insect taxonomists. The discovery of new extant taxa is rare at the supra-generic level (but see Romero Arias et al.[20]), although it is relatively common at genus and species levels.

The higher classification of termites has undergone substantial changes since its inception more than a century ago[21–31]. In the *Treatise on the Isoptera of the World*, the last comprehensive catalogue published on the global termite fauna, extant termites were divided into

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nine families: Archotermopsidae, Hodotermitidae, Kalotermitidae, Mastotermitidae, Rhinotermitidae, Serritermitidae, Stolotermitidae, Stylotermitidae, and Termitidae[7]. An additional family was subsequently erected for *Hodotermopsis*, the Hodotermopsidae[32,33], resolving the paraphyly of Archotermopsidae with respect to Hodotermitidae identified by preceding molecular phylogenies[3,34–37]. Molecular phylogenetic analyses have identified additional non-monophyletic termite families and subfamilies, indicating that additional augmentations of termite classification are required.

All ten currently recognised extant termite families (*sensu* Krishna et al.[7], modified by Wang et al.[33]) are monophyletic, except for the Rhinotermitidae, which is paraphyletic with respect to Serritermitidae and Termitidae. The non-monophyletic status of Rhinotermitidae has been evidenced in numerous phylogenetic studies based on morphological characters[38,39], a few molecular markers[34,40,41], or a combination of both[3,35,42]. Phylogenetic reconstructions performed with complete mitogenomes[36,37] and, more recently, with thousands of nuclear markers obtained from transcriptomes[43] or Ultraconserved Elements (UCEs)[44], confirmed the paraphyly of Rhinotermitidae. In addition, molecular phylogenies indicate that the rhinotermitid subfamily Heterotermitinae is paraphyletic with respect to Coptotermitinae[43,44]. A taxonomic revision of these family and subfamily names is required, and phylogenies inferred from many independent nuclear markers, which yield robust reconstructions, provide an ideal framework.

One additional polyphyletic subfamily requires attention within the Termitidae. Nine subfamilies of Termitidae are currently recognised: Apicotermitinae, Cubitermitinae, Engelitermitinae, Foraminitermitinae, Macrotermitinae, Nasutitermitinae, Sphaerotermitinae, Syntermitinae, and Termitinae[7,20]. All subfamilies were consistently retrieved as monophyletic, with the notable exception of Termitinae, which has consistently been found to be polyphyletic[34,37,41,43–45]. Indeed, the Cubitermitinae, Engelitermitinae, Nasutitermitinae, and Syntermitinae are all nested within the traditional concept of Termitinae. The early diversification of crown Termitidae presumably occurred at a fast pace, leaving termitid lineages separated by short, unresolved internodes, along with significant discordance among individual gene trees[43,44], suggestive of incomplete lineage sorting and hybridisation. While the relationships among the main termitid lineages are unclear in many cases, UCE phylogenies may allow for the identification of monophyletic lineages and their elevation to a subfamilial rank.

The purpose of this study is to revise termites at the family and subfamily levels and to produce a robust classification only composed of monophyletic groups. To achieve this, we thoroughly inspect the termite tree of life through the computation of 30 phylogenetic trees reconstructed from concatenated sequence supermatrices and 21 trees reconstructed within the multi-species coalescence framework. Our maximum-likelihood reconstructions use UCEs and diverse nucleotide, codon, and amino acid substitution models. UCEs are ideal markers to build robust phylogenetic trees, as they are highly conserved nuclear markers spread across all chromosomes. In arthropods, most UCEs are found in exons[44,46–49]. Our sampling includes 135 termite species, covering the breadth of the termite tree of life, and is especially exhaustive for the Rhinotermitidae and Termitinae. We delineate new circumscriptions for all families and subfamilies to abide by the monophyly criterion and corroborate our taxonomic amendments with analyses of rogue loci and taxa and topological tests. These comprehensive phylogenetic analyses provide a robust framework to create a lasting global taxonomic classification of termites.

Results
Phylogenetic analyses and their implication on the higher classification of termites
Our phylogenetic reconstructions support the monophyly of all currently recognised termite families (*sensu* Krishna et al.[7], modified by Wang et al.[33]), except Rhinotermitidae, which is paraphyletic with respect to Serritermitidae and Termitidae, as previously acknowledged[3,34–44].

The Rhinotermitidae (*sensu* Krishna et al.[7]) can be divided into four monophyletic lineages diverging early alongside Serritermitidae and Termitidae (Figs. 1, 2): Heterotermitinae Froggatt + Coptotermitinae Holmgren, Psammotermitinae Holmgren + Prorhinotermitinae Quennedey & Deligne, Rhinotermitinae Froggatt, and Termitogetoninae Holmgren. All our analyses supported the monophyly of these four clades, and our analyses with RogueNaRok found no evidence of rogue taxa within these clades. Assigning each of these four clades a familial rank resolves the challenges embodied in Rhinotermitidae as traditionally conceived. Accordingly, we raise these four lineages to familial rank. We restrict Rhinotermitidae to *Acorhinotermes*, *Dolichorhinotermes*, *Parrhinotermes*, *Rhinotermes*, and *Schedorhinotermes*, the five genera composing the Rhinotermitinae (*i.e.*, Rhinotermitidae Froggatt, **sensu novo**). We synonymise the two largely unused names Arrhinotermitinae and Leucotermitinae with Coptotermitinae and Heterotermitinae, respectively. We further synonymise Coptotermitinae with Heterotermitinae. The synonymy of the monogeneric Coptotermitinae (*Coptotermes*) with Heterotermitinae is justified by the paraphyly of Heterotermitinae, within which Coptotermitinae are nested. Heterotermitinae, having precedence over the other names, is here elevated to familial rank (*i.e.*, elevated as Heterotermitidae Froggatt, **stat. nov.**). The monogeneric subfamilies Prorhinotermitinae and Psammotermitinae are together raised to familial rank, the latter having precedence (*i.e.*, Psammotermitidae Holmgren, **stat. nov.**). Lastly, we elevate Termitogetoninae to Termitogetonidae Holmgren, **stat. nov.** (see Systematics, *infra*).

The phylogenetic relationships of Psammotermitidae and Termitogetonidae, which diverged shortly after the origin of the clade Serritermitidae + Rhinotermitidae + Termitogetonidae + Psammotermitidae + Heterotermitidae + Termitidae, are unresolved and variable among analyses (Fig. 1). Our phylogenetic analyses placed Termitogetonidae in four potential topological conformations, being sister to: Psammotermitidae (analyses on concatenated data: UFBs = 49–93, $n = 7/30$ analyses; coalescence analyses: LPP = 0.49, $n = 1/21$); Serritermitidae + Rhinotermitidae (UFBs = 60–99, $n = 13/30$; LPPs = 0.35–0.54, 6/21); Heterotermitidae + Termitidae (LPPs = 0.49–0.90, $n = 6/21$); and Psammotermitidae + Heterotermitidae + Termitidae (UFBs = 52–99, $n = 10/30$; LPPs = 0.38–0.88, $n = 8/21$). The latter branching was recovered in both majority rule consensus trees, but with sCFs close to 33.3% (32.1–32.5%; Figs. 1, 2), the values obtained for alignments generated at random, indicating the absence of signal for this node in the alignments[50]. To assess the anomaly zone surrounding the origin of Termitogetonidae and Psammotermitidae, we performed a series of topology tests displacing Termitogetonidae. Topology tests indicated that Termitogetonidae could be sister to non-Stylotermitidae Neoisoptera and Psammotermitidae + Heterotermitidae + Termitidae, as reported in some mitogenome-based Bayesian phylogenies[51], but it was never in a direct sister relationship with any of these families (AU tests; Supplementary Data 6).

Our sampling of Termitidae included a total of 77 representative genera. Notably, the Syntermitinae were found to be paraphyletic and include the enigmatic monotypic genus *Genuotermes* Emerson (see Fig. 1). Although sharing key features with the Syntermitinae, *Genuotermes* was first tentatively assigned to the Termitinae[52], based on similar soldier morphologies (Fig. 3 and Supplementary Figs. 17, 18). *Genuotermes* was identified as a rogue taxon by RogueNaRok in one analysis performed on concatenated sequence data (Fig. 1 and Supplementary Data 5). *Genuotermes* was also retrieved sister to *Onkotermes* in one coalescence analysis (Fig. 2; tree 36 in "File 4: trees.tar", available on Dryad at https://doi.org/10.5061/dryad.02v6wwqbm; LPP = 0.66), both genera forming a clade outside the Syntermitinae and the *Microcerotermes* clade. The phylogenetic position of
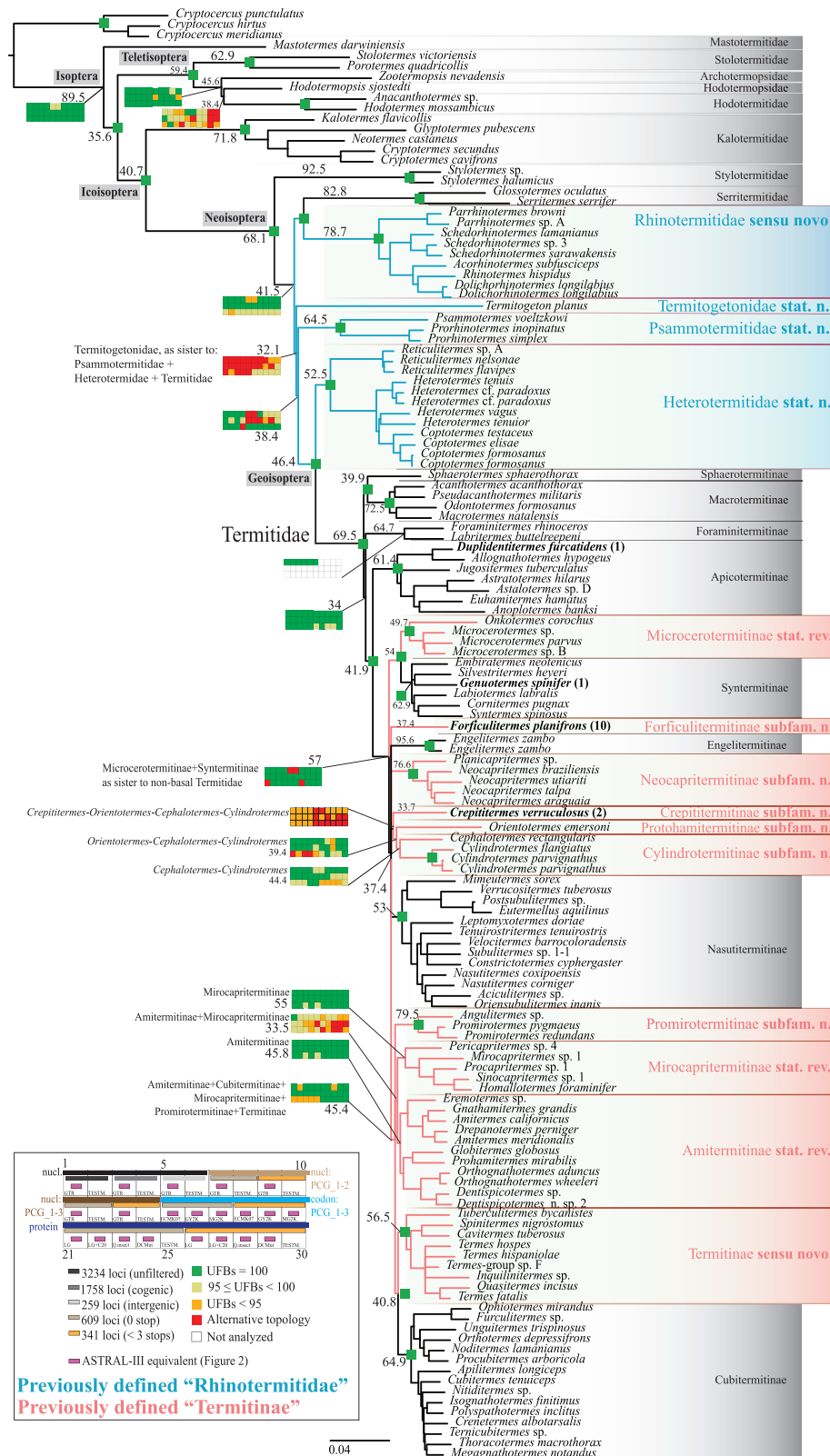
Fig. 1 | Majority rule consensus summary tree produced from 30 maximum-likelihood phylogenetic reconstructions performed with IQ-TREE on concatenated sequence matrices using various nucleotide, codon, and protein models (for details, see Supplementary Data 5). For readability, we only provided support values (UFBs, ultrafast bootstraps) for nodes representing families and subfamilies. Node labels are site concordance factors (sCFs) calculated on the majority rule consensus tree and the unfiltered UCE supermatrix. Species whose names are in bold were identified as rogue taxa by RogueNaRok (number of times under parentheses; for details, see Supplementary Data 5). The source data used for this figure can be found in the Dryad repository at https://doi.org/10.5061/dryad.02v6wwqbm (trees 1-30 in "File 4: trees.tar").
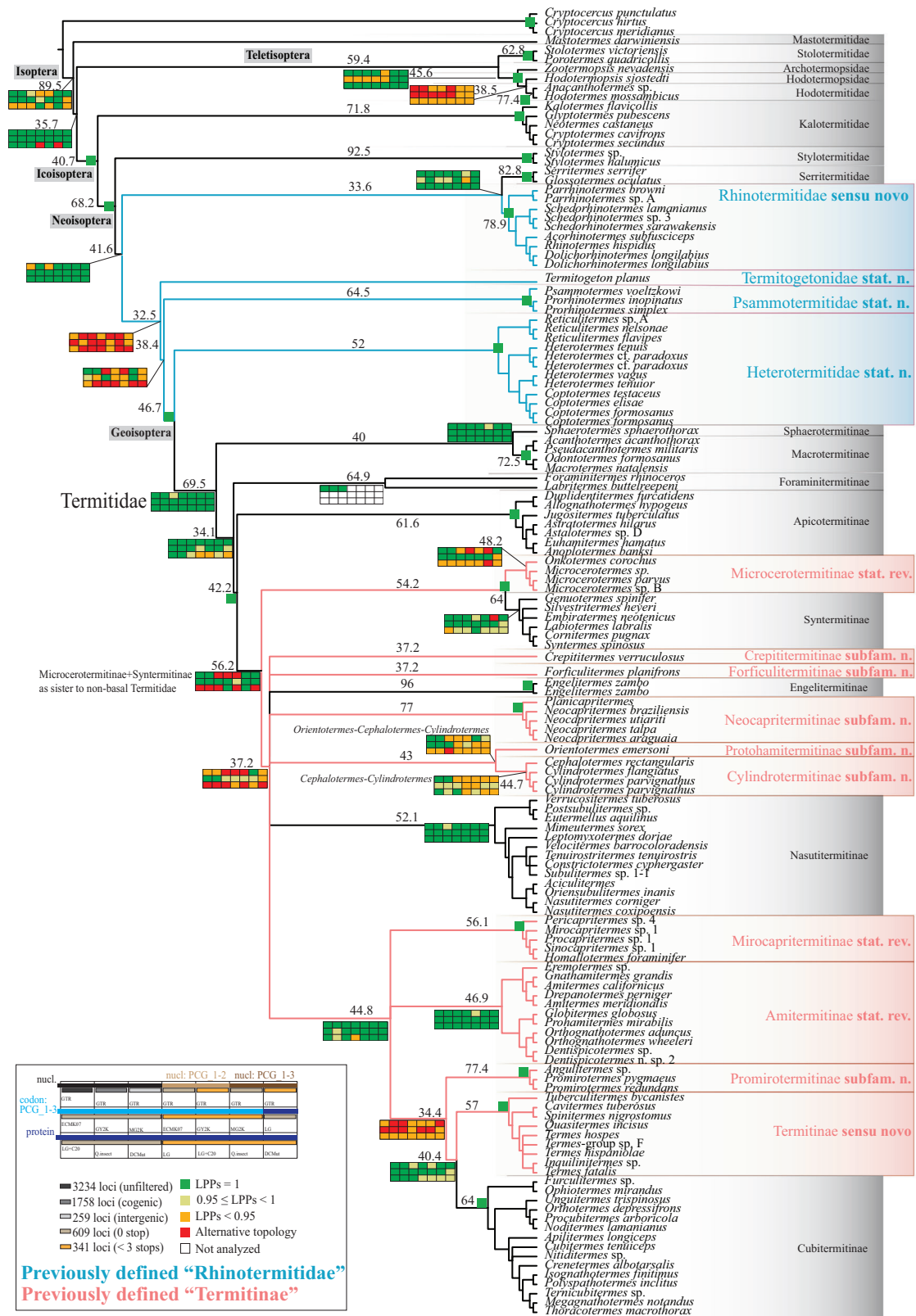
Fig. 2 | Majority rule consensus summary cladogram produced from 21 multi-species coalescence phylogenetic reconstructions with ASTRAL-III using various nucleotide, codon, and protein models (for details, see Supplementary Data 5). The tree presented herein (tree 75 in File 4 on Dryad) was constructed from gene trees for which outliers were pruned with TreeShrink (trees 52–72). The summary topology without pruning outliers is identical for all but one intrasubfamilial node (see tree 74 built from trees 31–51 on Dryad: File 4). For readability, we only provided support values (LPPs, local posterior probabilities) for nodes representing families and subfamilies. Node labels are site concordance factors (sCFs) calculated on the majority rule consensus tree and the unfiltered UCE supermatrix. The source data used for this figure can be found in the Dryad repository at https://doi.org/10.5061/dryad.02v6wwqbm ("File 4: trees.tar").
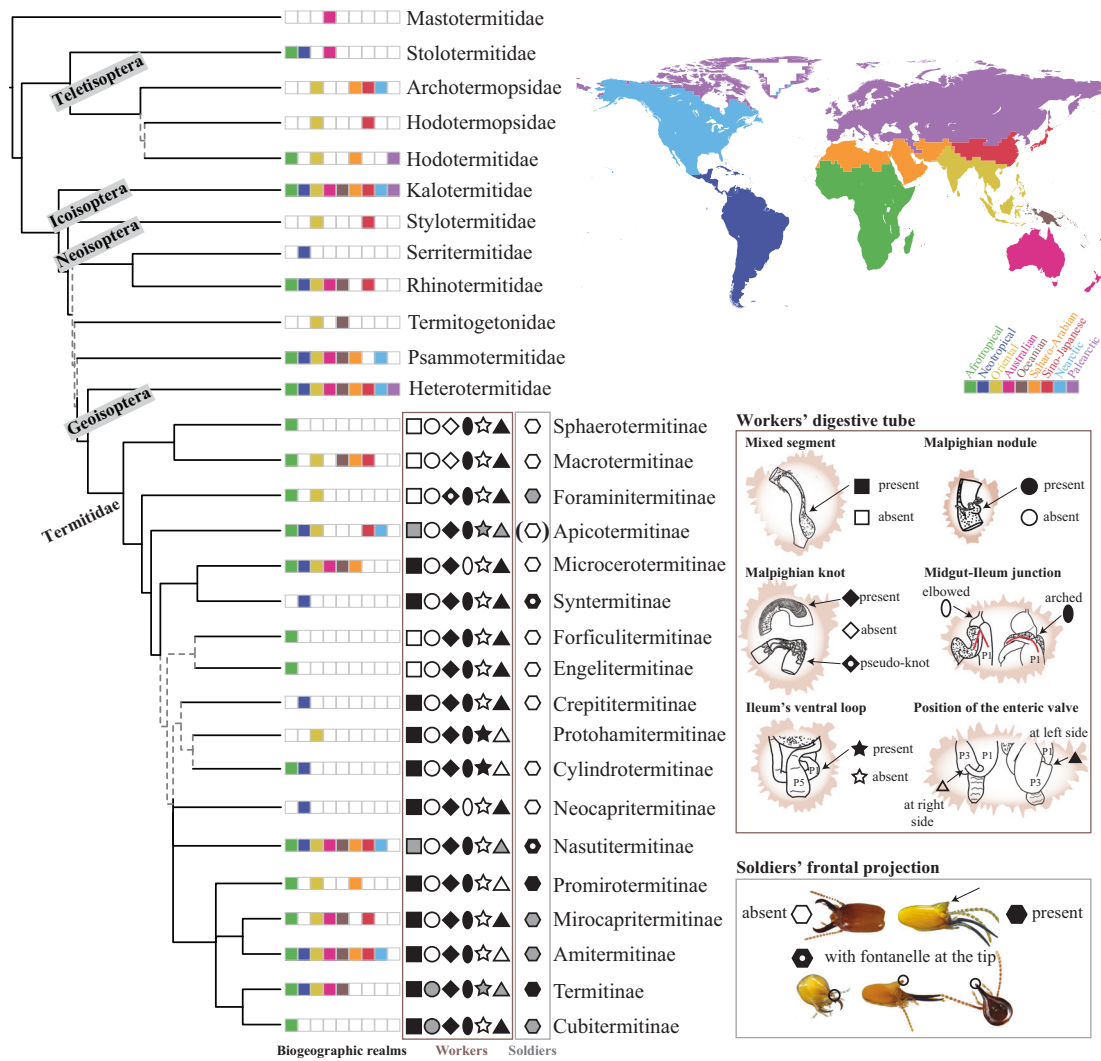
Fig. 3 | Summary cladogram of Isoptera. This cladogram integrates topologies summarised from analyses performed on concatenated data and coalescence analyses. The preferred topology within anomaly zones estimated from approximately unbiased topological tests is indicated in dashed grey. The biogeographic matrix indicates the realms occupied by extant members of all isopteran families and termitid subfamilies (adapted from Krishna et al. [7]). Here, we recognise nine realms (*sensu* Holt et al.[54]): Afrotropical (including Madagascan), Neotropical (incl. Panamanian), Oriental, Australian, Oceanian, Saharo-Arabian, Sino-Japanese, Nearctic, and Palaearctic. For termitid subfamilies, we report the main diagnostic features based on workers' digestive tubes and soldiers' heads. These features are summarised from Supplementary Notes 1 and 3, and Supplementary Figs. 1–18. (i) For workers' midgut-hindgut junction, we indicate: the presence of a mixed segment (square; stippled section), the presence of Malpighian nodules (circle); the presence of a Malpighian knot (full diamond) or pseudo-knot (full diamond with empty circle); the shape of the junction between the mixed segment and the ileum (P1) either elbowed (empty oval) or arched (full oval). For the hindgut, we indicate the presence of a ventral loop (star) formed under the rectum (P5) by P1; and the position (triangle) of the enteric valve (P2, indicated by an arrow) at the insertion of P1 into the paunch (P3). (ii) For termitid soldiers, we indicate the presence of a frontal projection (hexagon) and whether the fontanelle opens at the tip of the projection (full hexagon with empty circle), or at its base (full hexagon). Greyed shapes indicate that both trait states occur within the considered subfamily. Diagnostic features for all subfamilies are extensively presented in Supplementary Figs. 1–18. Soldier pictures, from left to right: (1) *Microcerotermes* sp. (Microcerotermitinae); (2) *Termes fatalis* (Termitinae); (3) *Silvestritermes heyeri* (Syntermitinae), (4) *Genuotermes spinifer* (Syntermitinae); (5) *Nasutitermes* sp. (Nasutitermitinae). Picture credits: M. M. Rocha (4); R. H. Scheffrahn (2,3); J. Šobotník (1,5).

Genuotermes is, therefore, not entirely resolved; however, our analyses generally placed *Genuotermes* within the Syntermitinae[53], and we hereby formally transfer this genus to the subfamily Syntermitinae.

Our phylogenetic analyses indicate that all other subfamilies of Termitidae are monophyletic, with the exception of the polyphyletic Termitinae, within which four other subfamilies are nested: Cubitermitinae, Engelitermitinae, Nasutitermitinae, and Syntermitinae. The relationships within the Termitinae + Cubitermitinae + Engelitermitinae + Nasutitermitinae + Syntermitinae clade are largely unresolved. This clade is composed of a dozen monophyletic lineages with uncertain relationships and separated by exceedingly short internodes (see Figs. 1, 2). Based on our phylogenetic reconstructions, we recognise 18 major monophyletic lineages within

Termitidae, eight of which already have subfamilial status. Giving subfamilial ranks to the other ten lineages resolves the polyphyly of Termitinae while simultaneously retaining the subfamilial status of four subfamilies supported as monophyletic: Cubitermitinae (UFBs = 100; LPPs = 1; sCFs = 64–64.9%), Engelitermitinae, Nasutitermitinae (UFBs = 100; LPPs = 0.99–1; sCFs = 52.1–53%), and Syntermitinae (UFBs = 100; LPPs = 0.92–1; sCFs = 62.9–64%). Accordingly, we redefine Termitinae Latreille **sensu novo** and restrict it to *Termes* and related genera, which unambiguously formed a monophyletic group in all our analyses (UFBs = 100; LPPs = 1; sCFs = 56.5–57%). We advocate the resurrection of three monophyletic subfamilies: Microcerotermitinae Holmgren **stat. rev.** (UFBs = 100; LPPs = 0.74–1; sCFs = 48.2–49.7%), Mirocapritermitinae

Kemner **stat. rev**. (UFBs = 99–100; LPPs = 1; sCFs = 55–56.1%), and Amitermitinae Kemner **stat. rev**. (UFBs = 99–100; LPPs = 0.98–1; sCFs = 45.8–46.9%). The aforementioned subfamilies were found monophyletic across all analyses, with the exception of Microcerotermitinae, as *Onkotermes* was placed sister to *Microcerotermes* + Syntermitinae in two coalescence analyses (LPPs = 1; trees 34, 50 in "File 4: trees.tar", available on Dryad at https://doi.org/10.5061/dryad.02v6wwqbm) and sister to *Genuotermes* in one coalescence analysis (see above). Although not entirely supported by our phylogenetic analyses, the placement of *Onkotermes* within Microcerotermitinae is also justified by their similar gut morphologies, with a characteristic elbowed junction between the mixed segment and the ileum (Fig. 3). Our topology tests did not reject Microcerotermitinae + Syntermitinae as sisters to other non-Sphaerotermitinae, non-Macrotermitinae, non-Foraminitermitinae and non-Apicotermitinae Termitidae (Supplementary Data 6), while coalescence analyses placed the clade on a polytomy in 8 of 21 coalescence analyses run with diverse sequence matrices and substitution models (Fig. 2).

Lastly, we propose to erect six monophyletic lineages to new subfamilies in Termitidae: Crepititermitinae **subfam. nov**., Cylindrotermitinae **subfam. nov**. (UFBs = 78–100; LPPs = 0.70–1; sCFs = 44.4–44.7%), Forficulitermitinae **subfam. nov**., Neocapritermitinae **subfam. nov**. (UFBs = 100; LPPs = 1; sCFs = 76.6–77%), Protohamitermitinae **subfam. nov**., and Promirotermitinae **subfam. nov**. (UFBs = 100; LPPs = 1; sCFs = 77.4–79.5%). These six subfamilies were placed on a polytomy, reflecting their uncertain phylogenetic positions, varying among analyses. The monotypic subfamilies Crepititermitinae and Forficulitermitinae were identified as rogue taxa in, respectively, two and ten analyses performed on concatenated sequence data from edge-trimmed protein-coding loci (Fig. 1 and Supplementary Data 5). Our topology tests did not reject Engelitermitinae and Forficulitermitinae as forming a clade sister to other non-Sphaerotermitinae, non-Macrotermitinae, non-Foraminitermitinae, non-Apicotermitinae, non-Microcerotermitinae and non-Syntermitinae Termitidae (AU tests; Supplementary Data 6). The Crepititermitinae were retrieved as sister to Cylindrotermitinae + Protohamitermitinae in 18 of 30 analyses performed on concatenated sequence data (Fig. 1; UFBs = 51–87), a scenario absent in our coalescence analyses (Fig. 2). The uncertain phylogenetic positions of Crepititermitinae and Forficulitermitinae, together with their unique combinations of morphological and biological characteristics (see the Systematics section below; Fig. 3), justified their placements in two separate subfamilies.

Systematics

We present the revised classification of extant Isoptera in Table 1. The diagnoses and distribution maps of Neoisoptera families and subfamilies presented herein are based on and modified from Krishna et al.[7]. The biogeographic boundaries follow Holt et al.[54]. The descriptions of digestive tubes follow Noirot[55].

Family-level classification changes for Neoisoptera. In the following, we provide abridged diagnoses for families with changes. Please refer to Supplementary Note 1 for extended diagnoses of all neoisopteran families and Supplementary Note 2 for a revised identification key to all families of Isoptera.

Family Rhinotermitidae Froggatt, sensu novo. The subfamily Rhinotermitinae Froggatt[21], 1897: 518, is herein elevated to the familial rank.

> **Type genus:** *Rhinotermes* Hagen[56], 1858.
> **Included genera (5):** *Acorhinotermes* Emerson, *Dolichorhinotermes* Snyder & Emerson, *Parrhinotermes* Holmgren, *Rhinotermes* Hagen, and *Schedorhinotermes* Silvestri (*Macrorhinotermes* Holmgren, **syn. nov**.).

Diagnosis: Imagoes with inflated clypeus, slightly or not at all drawn out over the labrum −reminiscent of a "nose-like" projection; and a narrow groove running from the fontanelle to the clypeus. Imago-worker left mandible with an apical tooth, followed by three distinct (unequal) marginal teeth. Imagoes, workers, and soldiers with anterior margin of postclypeus convex. Soldiers without setae surrounding the fontanelle. Soldier labrum elongated, forming a brush apically and endowed with a groove in the centre along which the chemical secretion of the frontal gland flows from the fontanelle.

Remarks: *Macrorhinotermes* was initially described as a subgenus of *Rhinotermes*[57]. Snyder[26] considered *Macrorhinotermes* as a potential synonym of *Schedorhinotermes* but did not unambiguously synonymize the two names, and *Macrorhinotermes* has remained a valid genus name. Here, we formally synonymize *Macrorhinotermes* and *Schedorhinotermes*, the latter having precedence over the former. There is an interesting diversity of soldier morphologies among Rhinotermitidae. Soldiers can be monomorphic as in *Acorhinotermes* and *Parrhinotermes*; dimorphic as in *Dolichorhinotermes*, *Rhinotermes*, and most *Schedorhinotermes*; or trimorphic as in some *Schedorhinotermes*. Rhinotermitidae occur in the Australian, Afrotropical, Neotropical, Oriental, Palaearctic (Sino-Japanese), and Oceanian realms.

Family Termitogetonidae Holmgren, stat. nov. The subfamily Termitogetoninae Holmgren[23], 1910: 286, is herein elevated to the familial rank.

> **Type genus:** *Termitogeton* Desneux[58], 1904
> **Included genus:** monogeneric.

Diagnosis: Imagoes densely hairy. Head subtriangular with posterior margin sinuate. Pronotum small, with median projections from anterior margins. Soldiers are densely hairy with a heart-shaped head. Soldier mandibles elongated without marginal teeth. Soldier legs with two protibial apical spurs. All castes dorso-ventrally flattened.

Remarks: *Termitogeton* is a wood-feeding termite known from the Oriental and Oceanian realms. It is composed of only two known extant species.

Family Psammotermitidae Holmgren, stat. nov. The family Psammotermitidae regroups the Psammotermitinae and Prorhinotermitinae subfamilies.

> **Subfamily Psammotermitinae Holmgren[24], 1911: 64**.
> **Type genus:** *Psammotermes* Desneux[59], 1902
> **Subfamily Prorhinotermitinae Quennedey & Deligne[60], 1975: 265.**
> **Type genus:** *Prorhinotermes* Silvestri[61], 1909.
> **Included extant genera (2):** *Psammotermes* Desneux and *Prorhinotermes* Silvestri.

Diagnosis: Imagoes with pronotum flat; tarsi tetramerous. Wings with all veins arising independently from inside the wing scales. Nymphs with fused wing buds forming two shield-looking structures on the mesothorax and metathorax. Imago-worker left mandible with an apical tooth followed by three distinct marginal teeth. Soldiers with tibial spurs formula 3:2:2; presenting a more or less marked groove from the fontanelle to clypeus[60].

Remarks: The extinct genus †*Zophotermes* Engel, 2011 is included in the Psammotermitidae. The distribution of *Prorhinotermes* is mostly insular. This distribution has fuelled speculation that colonies can be transported in driftwood by ocean currents, thus accounting for such a wide distribution on islands of the South Pacific. In sharp contrast, *Psammotermes* is a desert dweller occurring in the Afrotropical (incl. Madagascan), Saharo-Arabian and Oriental realms.

Clade Geoisoptera Engel, Hellemans, & Bourguignon, nov. This is an important group of termites as it includes the Termitidae, the most species-rich family of Isoptera, and the Heterotermitidae, which include some of the most widespread and critical pest species. In this clade, the

Table 1 | Revised higher-level classification of the extant Isoptera Brullé, 1832

	Family	Subfamily	Type genus	
	Mastotermitidae Desneux[22]: 282, 284	–	*Mastotermes* Froggatt[21]: 517	
	Hodotermitidae Desneux[22]: 284, 286	–	*Hodotermes* Hagen[123]: 480	
	Hodotermopsidae Engel *in* Jiang et al.[32]: 379, 383	–	*Hodotermopsis* Holmgren[24]: 38	
	Archotermopsidae Engel, Grimaldi & Krishna[31]: 9, 11	–	*Archotermopsis* Desneux[124]: 13	
	Stolotermitidae Holmgren[23]: 285	Porotermitinae Emerson[125]: 10 Stolotermitinae Holmgren[23]: 285	*Porotermes* Hagen[56]: 101 *Stolotermes* Hagen[56]: 105	
	Kalotermitidae Froggatt[21]: 516	–	*Kalotermes* Hagen[123]: 479, 480	
Nanorder Neoisoptera Engel et al.[31]	Stylotermitidae Holmgren & Holmgren[126]: 141	–	*Stylotermes* Holmgren & Holmgren[126]: 141	
	Serritermitidae Holmgren[23]: 285	–	*Serritermes* Wasmann[84]: 150	
	Termitogetonidae Holmgren[23]: 286, **stat. nov**	–	*Termitogeton* Desneux[58]: 373, 374	**Formerly Rhino-termitidae**
	Psammotermitidae Holmgren[24]: 64, **stat. nov**.	Prorhinotermitinae Quennedey & Deligne[60]: 265 Psammotermitinae Holmgren[24]: 64	*Prorhinotermes* Silvestri[61]: 286 *Psammotermes* Desneux[59]: 436	
	Rhinotermitidae Froggatt[21]: 518, **sensu novo**	–	*Rhinotermes* Hagen[56]: 233	
	Heterotermitidae Froggatt[21]: 550, **stat. nov**.	–	*Heterotermes* Froggatt[21]: 518, 550	
	Termitidae Latreille[80]	Sphaerotermitinae Engel & Krishna[127]: 6	*Sphaerotermes* Holmgren[25]: 33	
		Macrotermitinae Kemner[69]: 69	*Macrotermes* Holmgren[128]: 193	
		Foraminitermitinae Holmgren[25]: 125	*Foraminitermes* Holmgren[25]: 125	
		Apicotermitinae Grassé & Noirot[129]: 345, 360	*Apicotermes* Holmgren[25]: 104–105	
		Nasutitermitinae Hare[84]: 462	*Nasutitermes* Dudley[130]: 158	
		Syntermitinae Engel & Krishna[127]: 6	*Syntermes* Holmgren[128]: 193	
		Microcerotermitinae Holmgren[76]: 145, **stat. rev**.	*Microcerotermes* Silvestri[64]: 3	**Formerly Termitinae**
		Amitermitinae Kemner[69]: 110, **stat. rev**.	*Amitermes* Silvestri[64]: 4	
		Crepititermitinae **subfam. nov**.	*Crepititermes* Emerson[72]: 433	
		Cylindrotermitinae **subfam. nov**.	*Cylindrotermes* Holmgren[74]: 542	
		Forficulitermitinae **subfam. nov**.	*Forficulitermes* Emerson[75]: 44–47	
		Mirocapritermitinae Kemner[69]: 166, **stat. rev**.	*Mirocapritermes* Holmgren[77]: 277	
		Neocapritermitinae **subfam. nov**.	*Neocapritermes* Holmgren[25]: 115–116	
		Protohamitermitinae **subfam. nov**.	*Protohamitermes* Holmgren[25]: 76–78	
		Promirotermitinae **subfam. nov**.	*Promirotermes* Silvestri[79]: 131–132	
		Termitinae Latreille[80]: 293, **sensu novo**	*Termes* Linnaeus[81]: 609	
		Cubitermitinae Weidner[82]: 99	*Cubitermes* Wasmann[131]: 573	
		Engelitermitinae Romero Arias, Roisin & Scheffrahn *in* Romero Arias et al.[20]: 74	*Engelitermes* Romero Arias, Roisin & Scheffrahn *in* Romero Arias et al.[20]: 78	

Polyphyletic lineages (*i.e.*, Rhinotermitidae and Termitinae), which remained from the comprehensive revision of Isoptera by Krishna et al.[7], are resolved herein.

number of chromosomes is fixed to $2n = 42$ (reviewed in Jankásek et al.[62]), and their mitogenomes are characterised by a complex repeat structure in their control region[36]. Additionally, all species of this clade have a true worker caste (as in Mastotermitidae, Hodotermitidae, and Rhinotermitidae *sensu novo*) and typically live in large colonies.

Etymology: The clade name is a combination of the Ancient Greek prefix *geo–* (γεω–, from *gê* / γῆ), meaning "soil," "land," or "earth") and Isoptera. The name references the growing reliance on organically rich soil as a source of nitrogen[63].

Family Heterotermitidae Froggatt[21], **stat. nov.** The subfamily Heterotermitinae Froggatt[21],1897: 550, is herein elevated to the familial rank.

Heterotermitinae Froggatt[21], 1897: 550. Type genus: *Heterotermes* Froggatt[21].

Leucotermitinae Holmgren[23], 1910: 285. Type genus: *Leucotermes* Silvestri[64], 1901 [= *Heterotermes* Froggatt[21], 1897].

Coptotermitinae Holmgren[23], 1910: 285. Type genus: *Coptotermes* Wasmann[65], 1896. **Syn. nov.**

Arrhinotermitinae Sjöstedt[66], 1926: 8. Type genus: *Arrhinotermes* Wasmann[67], 1902 [= *Coptotermes* Wasmann]. **Syn. nov**.

Type genus: *Heterotermes* Froggatt[21], 1897

Included genera (3): *Coptotermes* Wasmann, *Heterotermes* Froggatt, and *Reticulitermes* Holmgren. †*Lukotermes* Perkovsky & Nel, **syn. nov.** is an extinct member of Heterotermitidae.

Diagnosis: Imagoes with postclypeus devoid of nose-like projection or groove extending from the fontanelle. Head round in *Coptotermes* and oval with even posterior margin in *Heterotermes* and *Reticulitermes*. Pronotum without median projection on the anterior margin; tarsi tetramerous. Workers and soldiers with anterior margin of postclypeus flat or concave. Soldiers with fontanelle surrounded by setae and katana-shaped mandibles devoid of marginal teeth (though with basal serrations); protibia with more than three protibial apical spurs. Soldiers of *Coptotermes* displaying an egg-shaped head with a large fontanelle directed forward and oozing latex-appearing secretions. Soldiers of *Heterotermes* and *Reticulitermes* exhibit a rectangular head with a small indistinct fontanelle.

Remarks: Some species exhibit slightly dimorphic soldiers[68]. The Heterotermitidae now encompass the three genera often referred to as "subterranean termites", a term historically associated with "Rhinotermitidae" with an extensive pest status in the literature. The Heterotermitidae occur across most temperate and tropical regions.

Subfamily-level classification changes for Termitidae Latreille. The number of subfamilies within the Termitidae is expanded given that the current Termitinae are demonstrably polyphyletic. We describe the new subfamilies of Termitidae erected in this paper and redescribe the Termitinae. We do not address the Syntermitinae, as the inclusion of *Genuotermes* does not alter the diagnosis of the subfamily. We do not address the other seven subfamilies of Termitinae, as they remain unaltered (*i.e.*, Sphaerotermitinae Engel & Krishna; Macrotermitinae Kemner; Foraminitermitinae Holmgren; Apicotermitinae Grassé & Noirot; Engelitermitinae Romero Arias, Roisin, & Scheffrahn; Nasutitermitinae Hare; and Cubitermitinae Weidner). Diagnoses for these subfamilies can be found in Krishna et al.[7] and Romero Arias et al.[20]. An updated key for all subfamilies of Termitidae is given in Supplementary Note 3. An updated list of all genera of extant Isoptera currently recognised is given in Supplementary Note 4. A list of the top 20 UCEs diagnostic for each subfamily of Termitidae (excluding subfamilies represented by only one sample, *i.e.*, Crepititermitinae, Forficulitermitinae, and Protohamitermitinae) is provided in Supplementary Data 7. An accompanying diagnostic tool is available on the Termite UCE Database (in "File 5: termitidae_diagnosing_database_v1.fasta.gz" available on Dryad at https://doi.org/10.5061/dryad.02v6wwqbm; also available at: https://github.com/sihellem/TER-UCE-DB/). Diagnostic features for each of the 18 subfamilies are given in Supplementary Figs. 1–18.

Subfamily Amitermitinae Kemner, stat. nov. Amitermitinae Kemner[69], 1934: 110.

Type genus: *Amitermes* Silvestri[64], 1901.

Included genera (14): *Ahamitermes* Mjöberg, *Amitermes* Silvestri, *Dentispicotermes* Emerson, *Drepanotermes* Silvestri, *Eremotermes* Silvestri, *Globitermes* Holmgren, *Gnathamitermes* Light, *Hoplotermes* Light, *Incolitermes* Gay, *Invasitermes* Miller, *Orthognathotermes* Holmgren, *Prohamitermes* Holmgren, *Pseudhamitermes* Holmgren, and *Synhamitermes* Holmgren.

Diagnosis: Imago-worker left mandible with apical tooth (LAt) shorter than marginal teeth (LMt), except in a few genera such as: *Ahamitermes* and *Invasitermes*[70], or *Orthognathotermes* (see Supplementary Fig. 1i). Worker gut with ileum (P1) tubular, dilated, or globular, without loop ventrally; each pair of Malpighian tubules united in one base (or nodule), except in *Prohamitermes* in which each tubule ends in its own nodule. Soldiers generally have a pear-shaped head and are devoid of frontal projection (except in *Eremotermes* and

Dentispicotermes). Diagnostic UCE loci are listed in Supplementary Data 7. Diagnostic features are given in Supplementary Fig. 1.

The subfamily is most similar to the Promirotermitinae, whose enteric valve (P2) position, *i.e.* the insertion of P1 into the paunch (P3), occurs on the right side of the abdomen (rather than the left side, as in Microcerotermitinae, Mirocapritermitinae, and Neocapritermitinae; Fig. 3). The Amitermitinae can be distinguished from the promirotermitines by: P1 tubular to inflated (always inflated in Promirotermitinae); soldier mandibles of various forms, ranging from crushing, piercing, slashing, or symmetrical snapping (always symmetrical snapping in Promirotermitinae); and soldier head pear-shaped without frontal projection (a notable frontal hump or projection is present in Promirotermitinae).

Remarks: Amitermitinae are widespread across every tropical and subtropical biogeographic realm. Species feed on various substrates, including mounds, soil, wood (incl. dry grasses), and the soil-wood interface. The genus *Invasitermes* is reported as soldierless.

Subfamily Crepititermitinae Hellemans, Engel, & Bourguignon, subfam. nov. Zoobank registration: https://zoobank.org/urn:lsid:zoobank.org:act:5F7D1841-7543-4914-B552-10318E2224C2.

Type genus: *Crepititermes* Emerson[71], 1925.

Included genera: monogeneric.

Diagnosis: Imago-worker left mandible lacks a third marginal tooth (LMt3). Right mandible lacking second marginal tooth (RMt$_2$). Worker gut with a blind diverticulum or caecum on P3; Malpighian tubules forming two pairs attached individually. Soldiers with sub-rectangular heads, labrums with concave apical margins and sharp apicolateral points, flattened frons, and symmetrical snapping mandibles. Diagnostic features are given in Supplementary Fig. 3.

The presence of a blind diverticulum on P3 and the absence of an indentation between LMt$_3$ and LMt$_{1+2}$ in Crepititermitinae are reminiscent of the Cubitermitinae, but the former can be distinguished by: the presence of a columnar belt (of the generalised type) in the gizzard (absent in Cubitermitinae); P1 tubular (P1 inflated in Cubitermitinae); the absence of intermediate cushions on the enteric valve armature (intermediate cushions present in Cubitermitinae; see Supplementary Fig. 4j, k); and the blind diverticulum on P3 occurring dorsally (ventrally in Cubitermitinae).

Remarks: *Crepititermes* was previously assigned to the *Termes*-group. A comprehensive re-description of *Crepititermes* was provided by Rocha & Cuezzo[72]. The genus is exclusively Neotropical, with species that feed on humus. *Crepititermes* workers use an autothysis mechanism that involves the rupture of the upper side of the abdomen, near the junction with the thorax, to expose their sticky gut for colony defence.

Subfamily Cylindrotermitinae Hellemans, Engel, & Bourguignon, subfam. nov. Zoobank registration: https://zoobank.org/urn:lsid:zoobank.org:act:DEEDCE51-6696-4C97-BB2E-654EF86C8F9F.

Type genus: *Cylindrotermes* Holmgren[73], 1906.

Included genera (2): *Cephalotermes* Silvestri and *Cylindrotermes* Holmgren.

Diagnosis: Imago-worker left mandible with apical tooth (LAt) roughly equal or shorter than LMt$_{1+2}$ and LMt$_3$ well-developed. Worker gut with long, P1 tubular, forming a loop ventrally under the rectum (P5). Enteric valve bearing six unequal cushions. Soldier head elongated, subrectangular, devoid of frontal projection, covered by short bristles; mandibles short, robust, of biting/slashing type; weak humps on the frons located immediately between the antennae above the basolateral corners of clypeus. Diagnostic UCE loci are listed in Supplementary Data 7. Diagnostic features are given in Supplementary Fig. 5.

The Cylindrotermitinae can be differentiated from the Amitermitinae as in the latter, P1 forms a loop ventrally under P5 and P2 occurs on the left side of the abdomen (Fig. 3).

Remarks: The two genera of Cylindrotermitinae were previously assigned to the *Amitermes*-group *sensu* Krishna et al.[7]. Cylindrotermitinae are wood-feeding termite genera from separate biogeographic regions: *Cephalotermes* is Afrotropical, while *Cylindrotermes* is Neotropical. *Cephalotermes* builds mounds, and forms populous colonies with few soldiers, headed by one king and one extremely physogastric queen that loses the ability to crawl as the colony matures (J. Šobotník, pers. obs.). *Cylindrotermes* are found in dead wood and form small colonies.

Subfamily Forficulitermitinae Hellemans, Engel, & Bourguignon, subfam. nov. Zoobank registration: https://zoobank.org/urn:lsid:zoobank.org:act:429D8F1D-1D78-44AD-BF91-4AAE9492251F.

Type genus: *Forficulitermes* Emerson[74], 1960.

Included genera: monogeneric.

Diagnosis: Imago-worker right mandible with well-developed second marginal tooth (RMt$_2$). Worker gut with four Malpighian tubules attached in pairs at the junction of the mixed segment. Soldier head subquadrangular with fontanelle located in a small depression, with two flat longitudinal ridges located in front of the opening on each side and forming a faint groove-like structure leading to the base of the clypeus; small, elevated humps on each side between the fontanelle and antennal base; mandibles elongate and slender, without marginal teeth, used to bite and unable to snap; apical margin of the labrum with medioapical convexity and sharply pointed apicolateral angles. Diagnostic features are given in Supplementary Fig. 8.

The Forficulitermitinae can be distinguished from termites in their newly restricted circumscription by the absence of a Malpighian nodule (generally present in Termitinae *sensu novo*). In addition, the soldier mandibles are elongated and not of snapping type, while in Termitinae the mandibles are generally snapping (except in three genera with biting/slashing mandibles: *Divinotermes*, *Spinitermes*, and *Tuberculitermes*). Lastly, the soldier head has a faint groove running from the fontanelle, which sits in a shallow depression, to the clypeal base and with small humps on either side of the channel between the fontanelle and the antennal toruli, while termites lack such a groove, depression, or lateral humps and instead have a medial frontal prominence of varying degrees of development.

Remarks: *Forficulitermes* was previously assigned to the *Termes*-group *sensu* Krishna et al.[7]. It is an exclusively Afrotropical genus, including species that feed on soil. A comprehensive re-description of *Forficulitermes* was provided by Scheffrahn & Křeček[75].

Subfamily Microcerotermitinae Holmgren, stat. nov. Microcerotermitinae Holmgren[76], 1910: 145.

Type genus: *Microcerotermes* Silvestri[64], 1901.

Included genera (2): *Microcerotermes* Silvestri and *Onkotermes* Constantino.

Diagnosis: Imago-worker left mandible with third marginal tooth (LMt$_3$) well developed, right mandible with posterior margin of LMt$_2$ long and straight. Worker gut with a conspicuous Malpighian knot; junction of the mixed segment with P1 constricted and elbowed, not fully visible in ventral view; P1 tubular, dilated anteriorly, constricted posteriorly at the connection with P2 on the left side of the abdomen, without loop ventrally. P2 is constricted and poorly ornamented. Soldier devoid of frontal projection, head generally long and narrow. Imago head subrectangular. Diagnostic UCE loci are listed in Supplementary Data 7. Diagnostic features are given in Supplementary Fig. 10.

Microcerotermitines are similar to Amitermitinae but have P1 inserted on P3 on the left side of the abdomen rather than the right in the latter clade (Fig. 3). In addition, the soldier head of Microcerotermitinae is subrectangular rather than the pear-shaped form of Amitermitinae.

Remarks: Species of this group were previously assigned to the *Amitermes*-group but were found to consistently form a sister relationship with Syntermitinae. The microcerotermitines are pantropical wood feeders (*sensu lato*: wood and grass).

Subfamily Mirocapritermitinae Kemner, stat. nov. Mirocapritermitinae Kemner[69], 1934: 166.

Type genus: *Mirocapritermes* Holmgren[76], 1914.

Included genera (14): *Dicuspiditermes* Krishna, *Homallotermes* John, *Indocapritermes* Chhotani, *Kemneritermes* Ahmad & Akhtar, *Krishnacapritermes* Chhotani, *Labiocapritermes* Krishna, *Mirocapritermes* Holmgren, *Oriencapritermes* Ahmad & Akhtar, *Pericapritermes* Silvestri, *Procapritermes* Holmgren, *Pseudocapritermes* Kemner, *Rinacapritermes* Amina & Rajmohana, *Sinocapritermes* Ping & Xu, and *Syncapritermes* Ahmad & Akhtar.

Diagnosis: Imago-worker right mandible with anterior margin of RMt$_2$ convex or straight, posterior margin concave. Worker gut with Malpighian tubules attached in two separate pairs fused proximally, devoid of Malpighian nodules. Soldiers with rectangular heads and snapping mandibles are generally asymmetrical (symmetrical in some species of *Procapritermes*). Soldier head devoid of frontal projection (except in *Mirocapritermes*). Diagnostic UCE loci are listed in Supplementary Data 7. Diagnostic features are given in Supplementary Fig. 11.

Mirocapritermitinae can be distinguished from the termitines in their restricted sense by the absence of a Malpighian nodule (present in Termitinae *sensu novo*) and the absence of a frontal projection (generally present in Termitinae). In the imago-worker mandible, RMt$_2$ is distinctly present and with a concave posterior margin, while it is absent or vestigial with a straight posterior margin in Termitinae *sensu novo*.

Remarks: Mirocapritermitinae include species previously assigned to the *Pericapritermes*-group. Their distribution is restricted to the Oriental region, with the exception of *Pericapritermes*, which is also found in the Australian, Afrotropical, Palaearctic (Sino-Japanese), and Oceanian regions. Mirocapritermitines feed on soil or at the soil-wood interface.

Subfamily Neocapritermitinae Hellemans, Engel, & Bourguignon, subfam. nov. Zoobank registration: https://zoobank.org/urn:lsid:zoobank.org:act:B9567537-33EF-4B4D-992F-34E0C16B8701.

Type genus: *Neocapritermes* Holmgren[25], 1912.

Included genera (3): *Neocapritermes* Holmgren, *Planicapritermes* Emerson, and *Schievitermes* Roisin.

Diagnosis: Imago-worker left mandible with apical tooth (LAt) shorter than LMt$_{1+2}$; right mandible with RMt$_2$ slightly reduced, posterior margin straight. Worker gut with two pairs of Malpighian tubules fused anteriorly and inserted in a single point at the mixed segment junction, devoid of Malpighian nodule; mixed segment long, distally bilobed into mesenteric sacs in *Neocapritermes* and *Schievitermes* (see Roisin[77]); junction of the mixed segment with P1 constricted and elbowed; P3 inflated, with wall bearing numerous spines. Soldiers with asymmetrical snapping mandibles and subrectangular heads devoid of frontal projection. Diagnostic UCE loci are listed in Supplementary Data 7. Diagnostic features are given in Supplementary Fig. 13.

Like the Termitinae, the imago-worker mandible has RMt$_2$ reduced and with a straight posterior margin but can be distinguished by the absence of a Malpighian nodule (present in Termitinae *sensu novo*) and the absence of a frontal prominence on the soldier head (generally present to varying degrees in Termitinae). The Neocapritermitinae differ from the Old World Mirocapritermitinae in three ways: the posterior margin of RMt$_2$ is straight (rather than concave in mirocapritermitines); the molar area has distinct ridges (molar area smooth to faint and reduced striations in mirocapritermitines); the enteric valve armature is composed of three folds (six in mirocapritermitines). The Neocapritermitinae exhibit an elbowed midgut-P1 junction as the Microcerotermitinae but can be distinguished by their soldiers (snapping in Neocapritermitinae, piercing/slashing in Microcerotermitinae).

Remarks: The species of Neocapritermitinae were previously assigned to the *Termes*-group. The subfamily is exclusively Neotropical, with species that feed on decayed wood or at the wood-soil interface.

Subfamily Promirotermitinae Hellemans, Engel, & Bourguignon, subfam. nov. Zoobank registration: https://zoobank.org/urn:lsid:zoobank.org:act:1F08A9B3-6F94-498C-A8B4-78ABF508FDA6.

Type genus: *Promirotermes* Silvestri[78], 1914.

Included genera (2): *Angulitermes* Sjöstedt and *Promirotermes* Silvestri.

Diagnosis: Imago-worker right mandible with well-developed RMt$_2$. Worker gut with two pairs of Malpighian tubules fused in a common base. Soldier head is subrectangular to egg-shaped (*Promirotermes*), with symmetrical snapping mandibles and either a pointed frontal projection (*Angulitermes*) or a blunt frontal hump (*Promirotermes*). Diagnostic features are given in Supplementary Fig. 14.

The subfamily can be distinguished from Termitinae *sensu novo* by its imago-worker mandible with well-developed RMt$_2$, which is otherwise absent or at least considerably reduced in termitines. The subfamily is most easily distinguished from Amitermitinae by its subrectangular soldier heads with a frontal process (generally absent in Amitermitinae) and bifurcate labrum (rounded, or with slightly pointed tips in Amitermitinae).

Remarks: The species of this group were previously assigned to the *Termes*-group (*sensu* Krishna et al.[7]) and are humus-feeders. *Promirotermes* is exclusively Afrotropical, while *Angulitermes* is also distributed across the Oriental region, the Middle East, and Africa.

Subfamily Protohamitermitinae Hellemans, Engel, & Bourguignon, subfam. nov. Zoobank registration: https://zoobank.org/urn:lsid:zoobank.org:act:2C4DDA82-D86C-40CA-BCB9-F5CD5AA60E7B.

Type genus: *Protohamitermes* Holmgren[25], 1912.

Included genera (2): *Orientotermes* Ahmad and *Protohamitermes* Holmgren.

Diagnosis: Imago-worker right mandible with well-developed subsidiary tooth at the base of the first and second marginal teeth (RMt$_1$ and RMt$_2$), with anterior margin angular and posterior margin curved. Worker gut with two pairs of Malpighian tubules connected to the mixed segment by two nodules, one for each pair; with long, tubular ileum (P1), forming a loop ventrally under the rectum (P5) (as in Cylindrotermitinae and part of the Apicotermitinae). Diagnostic features are given in Supplementary Fig. 15.

The Protohamitermitinae can be distinguished from the Amitermitinae by the presence of a long P1 that loops ventrally under P5 (ventral loop absent in Amitermitinae) and by the presence of a subsidiary tooth on the right imago-worker mandible (absent in Amitermitinae). The subfamily differs from Cylindrotermitinae by the presence of the subsidiary tooth and the absence of soldiers.

Remarks: The Protohamitermitinae include two Oriental soldierless species feeding on wood. They were previously assigned to the *Amitermes*-group *sensu* Krishna et al.[7]. Although the type-genus *Protohamitermes* was not included in our analyses, its relationship with *Orientotermes* is known from previous phylogenetic analyses[3].

Subfamily Termitinae Latreille, sensu novo. Termitina Latreille[80], 1802: 293. Type genus: *Termes* Linnaeus[81].

Mirotermitini Weidner[82], 1956: 99. Type genus: *Mirotermes* Wasmann[83], 1897 [= *Termes* Linnaeus[81], 1758].

Capritermitini Weidner[82], 1956: 100. Type genus: *Capritermes* Wasmann[83], 1897.

Type genus: *Termes* Linnaeus[81], 1758

Included genera (23): *Apsenterotermes* Miller, *Capritermes* Wasmann, *Cavitermes* Emerson, *Cornicapritermes* Emerson, *Cristatitermes* Miller, *Dihoplotermes* Araujo, *Divinotermes* Carrijo & Cancello, *Ekphysotermes* Miller, *Epheloterrmes* Miller, *Hapsidotermes* Miller, *Hesperotermes*

Gay, *Inquilinitermes* Mathews, *Lophotermes* Miller, *Macrognathotermes* Silvestri, *Palmitermes* Hellemans & Roisin, *Paracapritermes* Hill, *Protocapritermes* Holmgren, *Quasitermes* Emerson, *Saxatilitermes* Miller, *Spinitermes* Wasmann, *Termes* Linnaeus, *Tuberculitermes* Holmgren, and *Xylochomitermes* Miller.

Diagnosis: Imago-worker right mandible with RMt$_2$ reduced or absent and posterior margin straight. Left mandible with apical tooth (LAt) longer or slightly shorter than LMt$_{1+2}$. Worker gut with two pairs of Malpighian tubules attached on a nodule connected to the mixed segment. P2 is on the left side of the abdomen (except in *Cornicapritermes*, whose P1 forms a ventral loop and P2 is on the right; M.M. Rocha and T.F. Carrijo, pers. obs.). Soldiers with head subrectangular, a frontal prominence varying in size among genera, and snapping mandibles, except in *Divinotermes* and *Spinitermes*, which exhibit biting/slashing mandibles; and *Tuberculitermes*, which has snapping/slashing mandibles (A. Buček, pers. obs.). Diagnostic UCE loci are listed in Supplementary Data 7. Diagnostic features are given in Supplementary Fig. 18. Additional diagnoses are provided in the systematic sections of Promirotermitinae, Neocapritermitinae, Mirocapritermitinae, and Forficulitermitinae (above).

Remarks: The Termitinae have a pantropical distribution, found in the Afrotropical, Australian, Neotropical, Oceanian and Oriental regions. Termitinae comprises species feeding on diverse substrates, including soil, mounds, wood, and the soil-wood interface.

Discussion

The Rhinotermitidae and Termitinae, as defined before this study, have been recognised as polyphyletic groups since the advent of the molecular phylogenetics era[3,37,38,40]. Our robust phylogenies inferred with UCE data confirm that, unlike all other families and subfamilies of termites, the Rhinotermitidae and Termitinae were non-monophyletic groups in need of a taxonomic revision. Herein, we carried out the needed taxonomic revision and fixed the termite classification. Our comprehensive phylogenetic analyses unambiguously identified four neoisopteran family-level clades diverging alongside the Serritermitidae and Termitidae: the Heterotermitidae (*Coptotermes*, *Heterotermes*, and *Reticulitermes*), Psammotermitidae (*Psammotermes* and *Prorhinotermes*), Termitogetonidae (*Termitogeton*), and Rhinotermitidae (now restricted to *Acorhinotermes*, *Dolichorhinotermes*, *Parrhinotermes*, *Rhinotermes*, and *Schedorhinotermes*). Our analyses also recognised ten subfamily-level clades forming monophyletic groups together with the Cubitermitinae, Engelitermitinae, Nasutitermitinae, and Syntermitinae: *i.e.*, the Amitermitinae, Crepititermitinae, Cylindrotermitinae, Forficulitermitinae, Microcerotermitinae, Mirocapritermitinae, Neocapritermitinae, Promirotermitinae, Protohamitermitinae, and Termitinae (see Table 1). The erection of these new families and subfamilies enriches the termite nomenclature and allows for a predictive classification entirely comprised of monophyletic groups at the supra-generic level.

One potential concern of this newly proposed termite classification is the inflation of the number of family and subfamily names. However, the alternative strategy of synonymizing a number of families and subfamilies has important caveats. Synonymizing the Rhinotermitidae, Serritermitidae, and Termitidae would require downgrading the Rhinotermitidae and Termitidae to subfamily ranks. This would profoundly affect the nomenclature because the terms Rhinotermitidae and Termitidae have been widely used, and both Rhinotermitinae and Termitinae are already valid subfamilies. Such a downgrade would bring unnecessary confusion and undermine our goal to resolve paraphyly in Neoisoptera. Similarly, synonymizing the Cubitermitinae, Engelitermitinae, Nasutitermitinae, Syntermitinae, and Termitinae would strongly affect nomenclature, especially due to the loss of the Nasutitermitinae Hare[84]. The Nasutitermitinae are the largest subfamily of Termitidae with the obvious synapomorphy of soldiers bearing conical nasi, and this name has been widely accepted and used ever since its erection. Therefore, expanding family and subfamily

names largely maintain the stability of the termite classification while also avoiding confusion in the vast termite literature. Our classification preserves the stability of termite nomenclature by maintaining some key families and subfamilies that are featured in the literature, and synonymizing them would have negative impacts on many disciplines.

Despite the above-listed advantages, favouring splitting the formerly polyphyletic Rhinotermitidae and Termitinae over lumping also has consequences. Many genera previously placed in the Rhinotermitidae and Termitinae now belong to different families and subfamilies, requiring updates to databases and specimen collections. The new proposed termite classification will also have impacts outside the scientific community. For example, "Rhinotermitidae" is well known in the pest control industry for containing the two dominant genera with urban pest species, *Coptotermes* and *Reticulitermes*, which now belong to the Heterotermitidae. While preserving the stability of termite nomenclature, our new termite classification will require termitologists at large to adjust their vocabulary.

Increasing the number of families and subfamilies of Neoisoptera is justifiable considering the distribution of species amongst the main termite lineages. Termite diversity is disproportionately biased toward the Neoisoptera and, more specifically, toward the Termitidae, which include approximately 75% of all extant termite species[7]. Thus, the classification of Termitidae has received more attention than that of the smaller families. Similarly, it justifies that the systems of families within Neoisoptera and subfamilies within Termitidae are enriched compared to less speciose lineages. Several new subfamilies of Termitidae are species-poor lineages. While some of these subfamilies are widespread, such as the cylindrotermitine genera *Cephalotermes* and *Cylindrotermes* in the Afrotropical and Neotropical regions, respectively; the Afrotropical Engelitermitinae and Forficulitermitinae are rare monotypic subfamilies[75]. Notably, the recent description of *Engelitermes zambo*, the only representative of Engelitermitinae[20], indicates that additional termitid subfamilies may be erected in the future to accommodate new species that cannot be placed in existing subfamilies.

Uncertainties in our phylogenetic reconstructions and the morphological diversity of the Neoisoptera were the principal challenges to delimiting new families and subfamilies. The exact phylogenetic relationships amongst the families of Neoisoptera and subfamilies of Termitidae are often unclear. Although we used thousands of UCE markers[44], we failed to resolve the phylogenetic relationships amongst some families of Neoisoptera and many subfamilies of Termitidae because the internodes separating subfamilies are very short. This suggests insufficient time for alleles to coalesce, leading to incomplete lineage sorting[85,86]. Although future phylogenetic analyses may resolve some of these relationships, uncertainties will probably remain due to the apparently rapid radiations within the Termitidae. In addition, some of the new subfamilies of Termitidae include species that do not share clear morphological synapomorphies, complicating their delimitation based on morphological characters. Consequently, some new subfamilies are morphologically diverse. To ensure the robustness of the proposed classification of termites, each subfamily we described is supported as a monophyletic group by all our phylogenetic analyses. The placements of *Genuotermes* and *Onkotermes* in the Syntermitinae and Microcerotermitinae, respectively, represent the only two exceptions, as a few analyses placed them outside these subfamilies. Although these placements are favoured in our analyses, we cannot entirely rule out alternative scenarios. We acknowledge that the presently proposed classification is likely to be amended in the future; however, we expect it to serve as a robust backbone toward a definitive classification of termites.

Methods
Biological samples and sequencing
We gathered genome assemblies of 135 termites and three wood-feeding subsocial cockroaches from the genus *Cryptocercus* to reconstruct the phylogenies. We used previously published UCE datasets[44,87], which we supplemented with sequences of 56 samples (see Supplementary Data 1). Our dataset includes representative species from all genera of Rhinotermitidae *sensu lato* and every subfamily of Termitidae, including all the new subfamilies described here. Within the Termitidae, we included representatives of all termitine lineages that arose shortly after the origin of the first Termitinae.

All samples reported in this study were housed in collections, and no new field collection was performed. Specimens from collections were obtained in accordance with local and worldwide regulations at the time of their collection. Specifically, this involved the terms of the following permits: Australia, no sampling permits required; Bolivia, No. MMAyA-VMABCCGDF-DGBAP No. 1052/2013; Brazil, No. IBAMA #144/2010 and SISBIO #40673; Cameroon, No. 000000010/MINRESI/B00/C00/C10/C12 and No. 00000075/MINRESI/B00/C00/C10/C12; Democratic Republic of Congo (DRC), collections permitted under Belgian Science Policy (BELSPO) institutional project COBIMFO (2010–2015), as well as during the Boyekoli-Ebale-Congo Expedition in 2010 (organised by: the University of Kisangani (DRC), the Royal Museum of Central Africa (Tervuren, Belgium), the Royal Belgian Institute of Natural Sciences, the National Botanical Garden of Belgium; supported by: the Belgian Development Cooperation, BELSPO); Ecuador, No. 06-2011-FAU-DPAP-MA; French Guiana, No. TREL1902817S/136; Israel, no permits required; Ivory Coast, permits granted for protected areas (Taï, Marahoué, Comoé, Banco) by Office Ivoirien des Parcs et Réserves; Kenya, No. NACOSTI/P/15/7983/7214; Madagascar, No. 035/19/MEDD/SG/DGF/DSAP/SCB.Re and No. 202-19/MEDD/SG/DIR-EDD.AATS.ANS.AND; Martinique, no permits required; Mexico, permits provided to the late Paul M. Ban in 1996; Panama, No. SEX/A-36-10; Paraguay, permits provided to Rudolf Scheffrahn through the Museo Nacional de Historia Natural del Paraguay in 2012; Peru, Carta No. 592-2014-MINAGRI-DGFFS/DGEFFS; Singapore, No. NP/RP12-063a; Thailand, sampling carried out through the Khao Chong Insect Laboratory; USA, no permits required; Venezuela, permits provided to Rudolf Scheffrahn in 2008.

Samples were either preserved in 80–100% ethanol and stored at room temperature or preserved in RNA-later®, initially stored for up to several weeks at room temperature, and subsequently at temperatures varying between −20 °C and −80 °C. Whole genomic DNA extraction was performed using the DNeasy Blood & Tissue extraction kit (Qiagen). Tissue samples were disrupted in 2 mL microtubes using two 3 mm steel beads and the TissueLyser II (Qiagen). Library preparation was achieved using the NEBNext® UltraTM II FS DNA Library Preparation Kit (New England Biolabs) and the Unique Dual Indexing Kit (New England Biolabs), with reagent volumes reduced to one-fifteenth of recommended volumes. Because the DNA of samples preserved in ~80% ethanol at room temperature is typically highly fragmented, the incubation time of the enzymatic fragmentation step was set to a maximum of five minutes. This duration ensures a proper end repair, 5´ phosphorylation and dA-tailing, but limits any further significant fragmentation. Concentrations of final libraries were measured with a Qubit 3.0 Fluorometer (Invitrogen) using the Qubit™ 1X dsDNA HS Assay Kit (Invitrogen). The fragment size distribution of libraries was assessed with a 4200 TapeStation System (Agilent) using the High Sensitivity D1000 Kit (Agilent). Libraries were pooled in equimolar concentration, and paired-end reads were generated using the NovaSeq 6000 and HiSeq X Illumina platforms at a read length of 150 bp.

Genome assemblies and extraction of UCEs
Raw reads were quality-trimmed using fastp v0.20.1[88] and assembled with metaSPAdes v3.13[89]. We extracted the core UCEs from these draft assemblies with flanking 200 bp at both 5′ and 3′ ends (~600 bp loci) using PHYLUCE v1.6.6[90] and LASTZ[91]. We used the termite-specific bait set targeting 50,616 loci published by Hellemans et al.[44]. The species

identification codes ("File 1: ids_to_species.txt") and UCE dataset produced in this study ("File 2: TER_UCE_DB_CONTRIB_4.fasta.gz") are available on the Dryad Digital Repository, at https://doi.org/10.5061/dryad.02v6wwqbm. This paper represents Contribution #4 to the Termite UCE Database, available at: https://github.com/oist/TER-UCE-DB/.

Alignments and supermatrices

Extracted UCEs were combined in a total of seven supermatrices (see below) used for subsequent phylogenetic analyses. All UCE loci were aligned with MAFFT[92], as implemented in phyluce_align_seqcap_align. Alignments were either trimmed internally using phyluce_align_get_gblocks_trimmed_alignments_from_untrimmed that implements Gblocks[93,94] with default parameters or only edge-trimmed with phyluce_align_seqcap_align. Loci absent in more than 30% of taxa were filtered out using phyluce_align_get_only_loci_with_min_taxa.

We assessed the compositional bias of each locus after both internal- and edge-trimming treatments (3234 and 3233 loci, respectively) to identify low-quality and rogue loci. We computed the relative composition frequency variability (RCFV) and its normalised version (nRCFV) using RCFV_Reader v1[95]. Chi-square tests of nucleotide homogeneity were performed with BaCoCa v1.105[96]. None of the internally trimmed loci significantly deviated from homogeneity, while five edge-trimmed loci did (at the default $\alpha = 0.01$; for details, see Supplementary Data 2, 3). However, the nRCFV values of these five loci were below 0.005, indicating the deviations from base composition homogeneity were marginal. Consequently, we kept all loci in our analyses.

From the internally trimmed alignments, we constructed three supermatrices using phyluce_align_format_nexus_files_for_raxml: the unfiltered, cogenic, and intergenic datasets. The cogenic and intergenic datasets were obtained using the functional annotation of UCEs from the GFF file (NCBI Annotation Release 100) accompanying the draft genome of the archotermopsid *Zootermopsis nevadensis* (GCF_000696155)[97]. The cogenic dataset consisted of merged non-overlapping UCEs (from the pool of the 40,966 singly annotated UCEs) occurring within the same gene.

From the edge-trimmed alignments, we constructed four supermatrices using the loci coding for proteins along their full length. The position of the UCE loci and their strand orientation was determined by mapping *Z. nevadensis* loci (TER-4-UCEDB) against their corresponding genome (accession GCF_000696155) and GFF annotation file (NCBI Annotation Release 100) using BLASTn v2.10.0+ and bedtools v2.29.2[98]. The reading frame and corresponding amino acid sequences were identified and retrieved using the transeq function of EMBOSS v6.6.0[99]. We constructed two datasets by filtering out sequences with stop codons: one retaining all loci and the other retaining only loci displaying fewer than three stop codons. For each dataset, we aligned the protein sequences of each locus with MAFFT v7.305 and back-translated the protein alignments into codon alignments with PAL2-NAL v14[100]. Subsequent analyses were carried out on both the protein and the codon matrices for each dataset (*i.e.*, four supermatrices). All concatenated sequence supermatrices are described in Supplementary Data 4 and provided in the Dryad Digital Repository ("File 3: supermatrices.tar"), at https://doi.org/10.5061/dryad.02v6wwqbm.

Phylogenetic reconstructions

We reconstructed 51 phylogenetic trees using diverse models and two main approaches: (1) maximum-likelihood phylogenetic analyses performed on concatenated sequence data and (2) multi-species coalescence analyses, which infer the species tree by summarising a collection of maximum-likelihood phylogenetic trees constructed for each UCE locus.

A total of 30 maximum-likelihood phylogenetic trees were reconstructed using IQ-TREE v1.6.12[101] on concatenated sequence data

with 1000 ultrafast bootstrap replicates (UFB) to assess branch supports[102]. A summary of the parameters used for all 30 analyses performed in this study is available in Supplementary Data 5. Phylogenetic trees were reconstructed using nucleotide, codon, or protein sequences. We either used the best-fit substitution model selected with the Bayesian Information Criterion using ModelFinder[103] implemented in IQ-TREE or directly specified one of several predefined substitution models. Briefly, we used a GTR + F + I + G4 nucleotide substitution model on five types of nucleotide alignments: unfiltered, cogenic, intergenic, and protein-coding with and without third codon positions. For alignments of protein-coding nucleotide sequences, we used the empirical ECMK07 + FU model and the mechanistic GY2K + F and MG2K + F3X4 codon models[104]. For amino acid alignments, we used the improved general amino acid replacement matrix (LG) LG + F + G4 alone and combined with a C20 mixture of profiles (LG + C20 + F + G)[105,106], the revised Dayhoff matrix (DCMut)[107], and the insect-based Q matrix (Q.insect)[108,109]. The models were either applied to the unpartitioned supermatrix or the loci-partitioned supermatrix by examining the top 10% of partitioning schemes using the fast relaxed clustering approach[110,111]. For each reconstruction, we used RogueNaRok v1.0.1-3[112] to identify potential rogue taxa based on their bootstrap tree sets.

As maximum-likelihood phylogenetic trees reconstructed with concatenated data may fail to properly resolve short internodes[113], we also ran a total of 21 multi-species coalescence reconstructions with ASTRAL-III v5.7.7[114]. ASTRAL was run on gene trees reconstructed independently for each locus with IQ-TREE using the same models and parameters as in the analyses on concatenated sequence data (for details, see Supplementary Data 5). For gene tree reconstructions, we used the option "-czb" to allow polytomies and reduce gene tree biases. To control for poor-quality loci and rogue taxa, we ran all ASTRAL analyses once more after pruning outliers (at quantile 0.05) independently in each gene tree with TreeShrink v1.3.9[115]. Local posterior probabilities (LPPs) estimated from gene tree quartet frequencies[116] were calculated as branch support values for each tree.

All phylogenetic trees reconstructed in this study are provided in the Dryad Digital Repository ("File 4: trees.tar"), at https://doi.org/10.5061/dryad.02v6wwqbm. We used phytools[117] implemented in R v4.0.2[118] to generate 50% majority rule consensus summary trees, independently for analyses performed on concatenated sequence data and for coalescence analyses (with or without pruning by TreeShrink). Branch support values are UFBs and LPPs for concatenation and coalescence analyses, respectively. We also calculated site concordance factors (sCFs) as an alternative branch support metric[50]. sCFs are defined as the percentage of decisive alignment sites supporting a branch. Branches with sCFs > 50% (*i.e.*, supported by a majority of alignment sites) are considered robust. We calculated sCFs on each consensus tree with IQ-TREE using the option "-scf" and the unfiltered supermatrix. Finally, we assessed alternative topologies for unresolved interfamilial nodes using the approximately unbiased (AU) test[119]. The tests were performed with IQ-TREE, using the unfiltered supermatrix as data input and 10,000 resampling estimated log-likelihood (RELL) replicates (option "-zb 10000"). Alternative topologies were tested against the majority rule consensus tree summarising the 30 analyses performed on concatenated sequence data.

Nomenclatural acts

This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) and the associated information can be accessed through a web browser by appending the LSID to the prefix "http://zoobank.org/". The LSIDs for this publication are: urn:lsid:zoobank.org:act:5F7D1841-7543-4914-B552-10318E2224C2; urn:lsid:zoobank.org:act:DEEDCE51-6696-4C97-BB2E-654EF86C8F9F;

urn:lsid:zoobank.org:act:429D8F1D-1D78-44AD-BF91-4AAE9492251F;
urn:lsid:zoobank.org:act:B9567537-33EF-4B4D-992F-34E0C16B8701;
urn:lsid:zoobank.org:act:1F08A9B3-6F94-498C-A8B4-78ABF508FDA6;
urn:lsid:zoobank.org:act:2C4DDA82-D86C-40CA-BCB9-F5CD5AA60E7B.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Samples used in this study are described in Supplementary Data 1. The raw sequence reads generated in this study have been deposited in the NCBI Sequence Read Archive under the BioProject accession code PRJNA1122986. The raw data from prior publications used in this study are available under BioProject accession codes PRJNA560101, PRJNA1122307 and PRJNA1122966; and copys are available under accession codes GCF_000696155, GCF_002891405, GCA_013340265 and GigaDB100057. The raw sequence data can also be accessed using individual accession numbers given in Supplementary Data 1. The UCE data from prior publications used in this study are available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.x0k6djhn0[120] (file: "Supplementary_Data_6_uces_TER_UCE_DB_CON-TRIB_1.fasta"); https://doi.org/10.5061/dryad.tmpg4f53w[121] (file: "TER_UCE_DB_CONTRIB_3.tar.gz"). The source data for this study (UCE sequences, supermatrices, and trees) are available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.02v6wwqbm[122]. This study is registered under the ZooBank LSID: https://zoobank.org/urn:lsid:zoobank.org:pub:B8A8464B-2FB2-4CA2-8330-A907111FD62E.

Code availability

No new custom code is published with this article. The Termite UCE database and associated codes are available at: https://github.com/sihellem/TER-UCE-DB/.

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S.H. and T.B. conceptualised the experiments. S.H. and T.B. wrote the original draft manuscript, with significant input from M.M.R., E.C., and M.S.E. S.H., G.J., Y.R., E.C., M.R., J.Š., R.H.S., and T.B. collected the samples. M.W. and E.K. performed lab experiments and generated data. S.H. analysed the data. All authors (S.H., M.M.R., M.W., J.R.A., D.K.A., A.G.B., A.B., T.F.C., T.C., C.C., J.P.C., R.C., F.D., J.D., P.E., T.A.E., R.H., M.C.H., M.H., G.J., C.J., C.M.K., E.K., J.K., C.Y.L., F.L., H.F.L., N.L., T.L., K.e.M., K.i.M., D.M., N.M., D.E.O., M.P., D.S.D., N.Y.S., G.T., E.V., J.L.W., J.S., R.H.S., E.C., Y.R., M.S.E., and T.B.) edited and accepted the final version of this manuscript.

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