*European Journal of Taxonomy* 1024: 1–197
https://doi.org/10.5852/ejt.2025.1024.3099

europeanjournaloftaxonomy.eu
ISSN 2118-9773
2025 · Josens G. *et al.*

*Received: 27 July 2024* • *Accepted: 18 July 2025* • *Published: 5 November 2025*

*Topic editor: Tony Robillard* • *Section editor: Frédéric Legendre* • *Desk editor: Kristiaan Hoedemakers*

**Monograph**

urn:lsid:zoobank.org:pub:2A22C9AF-0E2D-46D1-A086-6CBE166F0A77

# An integrative revision of the genus *Isognathotermes* (Termitidae: Cubitermitinae) with description of seven new species and four new subspecies

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**Abstract.** Cubitermitinae species whose workers have enteric valves of the *fungifaber* and *finitimus* patterns were previously gathered into the genus *Isognathotermes.* Here, we revise this genus, combining the morphological and anatomical features of all castes, as well as the species' chorological, ecological, and phylogenetic (mitogenome) characteristics in an integrative taxonomic approach. In addition to the genetic signature, the best morphological criteria for generic recognition are found in the workers' EVA (enteric valve architecture) and the spinosity of the fore coxae of the workers, and the best criteria for specific recognition are found in (a) the valve and caecum of the workers, (b) the caecum, dimensions of the head, and curvature of the mandibles of the soldiers, and (c) the dimensions of the head and the relative dimensions of eyes and ocelli of the imagines. After revision, only eight of the 22 known taxa remain valid, 14 known taxa become junior synonyms, and one is considered as incertae sedis; six new morphologically recognizable species, one cryptic species and four new subspecies are described. The mitogenome of 12 out of the 15 valid species have been sequenced. The following described species are considered valid: *I. bulbifrons* (Sjöstedt, 1924), *I. finitimus* (Schmitz, 1916), *I. fungifaber* (Sjöstedt, 1896), *I. minitabundus* (Sjöstedt, 1913), *I. planifrons* (Sjöstedt, 1924), *I. severus* (Silvestri, 1914), *I. ugandensis* (Fuller, 1923) and *I. zenkeri* (Desneux, 1904). The following species are described as new: *I. acristatus* Josens & Deligne sp. nov., *I. modicus* Josens & Deligne sp. nov., *I. magniplanifrons* Josens & Deligne sp. nov., *I. phallicaecalis* Josens & Deligne sp. nov., *I. phalloides* Josens & Deligne

sp. nov., *I. rectimalatus* Josens & Deligne sp. nov., and *I. similifinitimus* Josens & Deligne sp. nov. Four new subspecies of *I. ugandensis* are recognized: *I. ugandensis burundii* Josens & Deligne subsp. nov., *I. ugandensis kenyae* Josens & Deligne subsp. nov., *I. ugandensis malawii* Josens & Deligne subsp. nov., and *I. ugandensis ugandensis* Josens & Deligne subsp. nov. The following species are considered junior synonyms: *I. antennalis* (Sjöstedt, 1924), *I. banksi* (Emerson, 1928), *I. comstocki* (Emerson, 1928), *I. fungifaber* var. *elongata* (Sjöstedt, 1924), *I. gaigei* (Emerson, 1928), *I. gibbifrons* (Sjöstedt, 1924), *I. heghi* (Sjöstedt, 1924), *I. kemneri* (Emerson, 1928), *I. loubetsiensis* (Sjöstedt, 1924), *I. modestior* (Silvestri, 1914), *I. schmidti* (Emerson, 1928), *I. silvestrii* (Sjöstedt, 1925), *I. speciosus* (Sjöstedt, 1924), and *I. subarquatus* (Sjöstedt, 1926). Are considered as incertae sedis: *I. bredoi* (nomen nudum), *I. congoensis* (Emerson, 1928), an "*I.* aff. *planifrons*" (undescribed), and an unknown *Isognathotermes* from Malawi (undescribed). GenBank accessions: see Supp. file 3 and 'Material examined' of each chapter.

**Keywords.** Blattodea, Blattaria, Isoptera, *Cubitermes*, cryptic species, integrative taxonomy, chorology, DNA barcoding, species delimitation.

Josens G., Deligne J., Harry M., Roy V., Akama P.D., Coulibaly T., Dosso K., Goergen G., Hasson M., Kasangij a Kasangij P., Kifukieto C., Le Ru B., Loko L.E.Y., Ndiaye A.B., Roisin Y., Sion N., Šobotnik J., Stiblik P., Kue di Kuenda S., Traoré S., Viage M., Wango S.P., Kaymak E., Bourguignon T. & Hellemans S. 2025. An integrative revision of the genus *Isognathotermes* (Termitidae: Cubitermitinae) with description of seven new species and four new subspecies. *European Journal of Taxonomy* 1024: 1–197. https://doi.org/10.5852/ejt.2025.1024.3099

## Introduction

The emblematic *Cubitermes* Wasmann, 1906 is widespread in Africa, and was composed, in 2013, of 67 taxa (Krishna *et al*. 2013: 1912). In most cases, the original descriptions were rather succinct and insufficient for delimiting the species clearly. So that Emerson (1928: 507) already emphasized on the difficulty of identifying *Cubitermes* species; this difficulty resulted from the morphological proximity among species and from high intraspecific variability, which were both ignored by prior termitologists such as Sjöstedt (1896–1926), Silvestri (1914) or Fuller (1923). Ruelle (1992) reiterated the need to revise the genus *Cubitermes* and drew attention to the fact that many species had been forgotten, i.e., they had been described but not reported since.

More recently, other authors noted a great diversity among members of *Cubitermes*, which suggested it may be composed of several distinct lineages. Bouillon & Vincke (1971) suggested that *Cubitermes* should be split into at least three genera based on their enteric valves. This proposal was subsequently supported by the observation that species of *Cubitermes* can coexist in the same habitat but when this happens, the coexisting species exhibit different enteric valves, probably linked to competition and the food niche (Wango & Josens 2011). Not only the enteric valve but also the proctodeal blind diverticulum or caecum on the paunch of the hindgut has various morphologies, and provides clues to specific recognition (Johnson 1979). This blind caecum has since been found to be a characteristic of the Cubitermitinae subfamily (Krishna *et al*. 2013: 123). In his reference work on the identification of termite workers, Sands (1998) also put forward the diversity of both enteric valve armatures and caecum shapes, but did not suggest splitting the genus *Cubitermes*.

Most *Cubitermes* nests are mushroom-shaped (with some variations) in West and Central Africa, which has been interpreted as a rain protection device (Emerson 1938); in accordance, the nests are generally dome-shaped (uncapped) in drier East Africa. As already mentioned by Williams (1966), the shape of the nests does not provide any identification criterion but rather seems to be influenced by environmental conditions (Wango & Josens 2011).

Faced with the difficulty of distinguishing species by ambiguous morphological diagnoses, Roy *et al*. (2006) showed the value of mitochondrial and nuclear markers for distinguishing sympatric *Cubitermes* species. Recent works subdivided the genus *Cubitermes* into nine species groups on basis of their enteric valve architectures (EVAs; Josens & Deligne 2019); and phylogenetic studies evidenced that *Cubitermes* was paraphyletic with respect to *Apilitermes*, *Crenetermes*, *Megagnathotermes* and *Thoracotermes* (Bourguignon *et al.* 2017; Hellemans *et al.* 2021). Hellemans *et al.* (2021) recognized five clades, in line with the EVAs of the nine groups. These five clades were erected therein into five genera: *Cubitermes* Wasmann, 1906, *Ternicubitermes* Josens & Deligne, 2021, *Isognathotermes* Sjöstedt, 1926, *Nitiditermes* Emerson, 1960, and *Polyspathotermes* Josens & Deligne, 2021.

However, while the boundaries between these five genera are now well-defined, species identification remains arduous. The restored genus *Isognathotermes* grouped species whose workers have enteric valves of the *fungifaber* and *finitimus* patterns (Josens & Deligne 2019) and included, when restored, 15 species (Hellemans *et al.* 2021: table S4), and currently contains 15 valid species found from Gambia to Malawi.

The aims of this article are to revise the genus *Isognathotermes* and to delineate the species by means of an integrative approach, i.e., to describe or re-describe the species based on the morphology and anatomy of imagines, soldiers, and workers, combined, when possible, with molecular and chorologic-ecological data, and to provide an identification key.

## Material and methods

### Abbreviations

#### Museum abbreviations

AMNH = American Museum of Natural History, New York, the United States
IEAP = Instituto di Entomologia Agraria, Portici (Napoli), Italy
MCGD = Museo Civico di Storia Naturale “Giacomo Doria”, Genoa, Italy
MNHN = Muséum national d’Histoire naturelle, Paris, France
MURS = Museo Università di Roma “Sapienza”, Roma, Italy
NHMM = Natuurhistorisch Museum of Maastricht, the Netherlands
NHMUK = Natural History Museum, London, the United Kingdom
NHRM = Naturhistoriska Riksmuseet, Stockholm, Sweden
PPRI = Plant Protection Research Institute, Biosystematics Division, Queenswood, Pretoria, South Africa
RBINS = Royal Belgian Institute of Natural Sciences, Brussels, Belgium
RMCA = Royal Museum for Central Africa, Tervuren, Belgium, including A. Bouillon’s collection
UMMZ = Museum of Zoology, University of Michigan, Ann Arbor

#### Country abbreviations

CAR = Central African Republic
DRC = Democratic Republic of the Congo (Kinshasa)
RCI = Republic of Côte d’Ivoire

#### Morphological abbreviations

aff. = affinis, a taxon that has a similar morphology
C1–C8 = colour abbreviations from C1 (very pale yellow) to C8 (almost dark) (Josens & Deligne 2019: 5, fig. 1)
Cd = deep colour
Cf = faded colour
DJ = labelling marker of the morphological study

| | |
|---|---|
| EVA | = enteric valve architecture |
| IEy*D* | = imago, eye larger diameter (Josens & Deligne 2019: 14, fig. 6b) |
| IEy*d* | = imago, eye lesser diameter (Josens & Deligne 2019: 14, fig. 6b) |
| IEy*D*/IEy*d* | = imago, compound eye elongation index (= eye index in Williams 1966) equals 1 if the eye is circular and increases when it becomes more oval |
| IEyD/IHdW | = imago, oculo-cephalic index, it increases when the compound eye becomes larger relative to the head |
| IHdW | = imago, head width across compound eyes (Josens & Deligne 2019: 14, fig. 6a) |
| IMlAmD | = imago, left mandible apical to first marginal distance (between tips) (similar to WMlAmD, Josens & Deligne 2019: 20, fig. 8b) |
| IMlmmD | = imago, left mandible distance between the first and third marginal tips (similar to WMlmmD, Josens & Deligne 2019: 20, fig. 8b) |
| IMlAmD/IMlmmD | = Imago; left mandibular apico-marginal index (= La/L1 in Sands 1972); it increases when the apical tooth of the left mandible becomes longer with respect to the distance between the first and third marginal teeth |
| IOc*D* | = imago, ocellus larger diameter (Josens & Deligne 2019: 14, fig. 6d) |
| IOc*d* | = imago, ocellus lesser diameter (Josens & Deligne 2019: 14, fig. 6d) |
| IOc*D*/IOc*d* | = imago, ocellus elongation index, equals 1 if the ocellus is circular and increases when it becomes more oval |
| IPcW | = imago, posclypeus width (Josens & Deligne 2019: 14, fig. 6b) |
| IPnW | = imago, pronotum width (Josens & Deligne 2019: 14, fig. 6c) |
| IT3L | = imago, length of the left hind tibia (similar to ST3L, Josens & Deligne 2019: 16, fig. 7i) |
| IWgL | = imago, left fore-wing length to suture, (Josens & Deligne 2019: 14, fig. 6e) |
| PC | = primary cushion of the enteric valve |
| SC | = secondary cushion of the enteric valve |
| SHdC | = soldier, sagitta of head upper concavity (Josens & Deligne 2019: 16, fig. 7b) (equals zero if the upper profile is either straight or slightly convex) |
| 100 * SHdC/SHdL | = soldier, percentage of upper head concavity |
| SHdL | = soldier, head length to the fore margin of the clypeus (Josens & Deligne 2019: 16, fig. 7a) |
| SHdW | = soldier, head width (Josens & Deligne 2019: 16, fig. 7a) |
| SHdL/SHdW | = soldier, head elongation index |
| SMlC | = soldier, left mandible larger curvature (or sagitta of apico-molar arc); greatest distance between the inner edge of the blade and a line tangent to the tip of apical tooth and to the margin of the molar tooth (Josens & Deligne 2019: 16, fig. 7f) |
| SMlc | = soldier, left mandible lesser curvature (or sagitta of apico-marginal arc) between the marginal tooth and the apical tip (Josens & Deligne 2019: 16, fig. 7f) |
| SMlC/SMlc | = soldier, left mandible bi-curvature index, it increases mainly when the molar tooth becomes more prominent |
| SMlc/SMlL | = soldier, left mandible apical curvature index, it increases when the mandible becomes more curved; this is not the same curvature index as in Williams (1966) |
| SMlc/SMrc | = soldier, ratio between the left and right mandible lesser curvatures, the more asymmetrical the mandibles, the greater the deviation from 1 |
| SMldR | = soldier, radius of the circle of the distal mandible quarter (Josens & Deligne 2019: 16, fig. 7h) |
| SMlL | = soldier, left mandible length in ventral view; from apical tip to base of condyle (Josens & Deligne 2019: 16, fig. 7f), this is not the same measure as in Williams (1966) |

SMlL/SHdL = soldier, gnatho-cephalic index, it increases when the mandible becomes longer with respect to head length
SMlpR = soldier, radius of the circle of the proximal mandible half (Josens & Deligne 2019: 16, fig. 7h)
ln(SMlpR) - ln(SMldR) = soldier, (acceleration of the mandible curvature), it increases if the mandible becomes more curved distally with respect to the proximal curvature and it would equal zero if the mandible blade was a section of a circle (same proximal and distal radii)
SMlW = soldier, width of the mandible precisely at mid-distance between the marginal and the apical tips (Josens & Deligne 2019: 16, fig. 7g)
SMlW/SMlL = soldier, left mandible robustness index, it increases if the mandible becomes thicker in relation to its length
SMrC = soldier, right mandible larger curvature (or sagitta of apico-molar arc); greatest distance between the inner edge of the blade and a line tangent to the tip of apical tooth and to the margin of the molar tooth (Josens & Deligne 2019: 16, fig. 7f)
SMrc = soldier, right mandible lesser curvature (or sagitta of apico-marginal arc) between the marginal tooth and the apical tip (Josens & Deligne 2019: 16, fig. 7f)
ST3L = soldier, length of the left hind tibia (Josens & Deligne 2019: 16, fig. 7i)
WHdW = worker, head maximal width (Josens & Deligne 2019: 20, fig. 8a)
WMlAmD = worker, left mandible apical to first marginal distance (between tips) (Josens & Deligne 2019: 20, fig. 8b)
WMlL = worker, functional length of left mandible (Josens & Deligne 2019: 20, fig. 8c)
WT3L = worker, length of the left hind tibia (similar to Josens & Deligne 2019: 16, fig. 7i)
WVP1-bil = worker's valve PC1-bilaterality index=the ratio of WVP1L length over the average length of the two other odd cushions (WVP3L and WVP5L)
WVP-AvL = worker, enteric valve, average length of the primary cushions 1 to 6
WVP-AvW = worker, enteric valve, average width of the primary cushions 1 to 6
WVPOdd-Elg = worker's valve odd PCs elongation index; it is calculated as the average length of the odd cushions (WVP1L, WVP3L and WVP5L) on the average width of the same odd cushions (WVP1W, WVP3W and WVP5W); it measures the narrowness of the odd PCs
WVS-AvL = worker, enteric valve, average length of the secondary cushions 12 to 61
WVS-AvW = worker, enteric valve, average width of the secondary cushions 12 to 61

**Morphology**

A total of 752 samples were studied, 421 in a full study and 331 in a partial study.

**Full study**

Samples were observed with a Zeiss Discovery V12 stereoscopic microscope (magnification 8–100 ×) and photographed with an ICc3 camera (3 million pixels resolution). The photographs were taken in extended focus driven by the AxioVision® 4.8 (Zeiss) software. In most cases, the samples were oriented according to a standardised procedure: the sample was slightly sunk into a bed of fine glass beads (Glaskügelchen by Kremer Pigmente GmbH, 150–210 µm) and orientated so that two or more points were simultaneously in focus in order to make subsequent measurements comparable.

The morphological study is based on three series of standardised photos (one series per caste) supplemented by indices designed to reflect morphology as objectively as possible.

After several Regression Analyses, Principal Component Analyses and Stepwise Variable Selections (in Factorial Discriminative Analyses) with the software R, packages ade4 (Chessel *et al*. 2004), FactoMineR

and klaR, 29 variables and eight indices were selected for the imagines, 36 variables and 16 indices for the soldiers, 50 variables and 14 indices for the workers' morphology (including their EVAs).

Standardisation of photos and coding of variables were fully described and illustrated in Josens & Deligne (2019: 5–22); the same terminologies and abbreviations have also been used for colour, setation, antennae, mandibles, and EVAs. The samples studied following this "full study procedure" received a study code: "DJ NNNN" where 'NNNN' is a four-digit number. Full study was performed until a total of at least 20 samples for a given species was reached; extra material was then studied following a simplified procedure (hereunder).

To produce the figures, the photographs were traced on tracing paper applied to the screen of a computer.

**Partial study** (simplified procedure)

Three photographs of the soldiers were taken: head capsule in dorsal view, head capsule in lateral view and mandibles in ventral view, not detached from head.

These photos allowed to perform a limited series of measurements: SHdC, SHdL, SHdW, SMlc, SMldR, SMlpR, SMlW, and calculate five indices: ln(SMlpR)/ln(SMldR), SHdL/SHdW, SMlc/SMlL, SMlL/SHdL and SMlW/SMlL.

If imagines were present, they were nevertheless studied following the full study procedure. Workers were not photographed but one individual was dissected, and its caecum and enteric valve checked (and frequently photographed).

The samples studied following the partial study procedure received a study code: "DJ XNNN" where 'X' is a letter and 'NNN' a three-digit number.

**Data analyses**

Because of the great intraspecific variability, Principal Component Analysis (PCA) has proved to be a more effective tool for grouping samples by species than other analyses such as Hierarchical Cluster Analysis. The analyses were carried out using the 'ade4' package (Chessel *et al.* 2004) of the R language (R Core Team 2018).

PCAs were performed throughout the study with progressively increasing numbers of samples: some PCAs were carried out on all the available data (752 samples at the end of the study): 278 imagines, 734 soldiers and 400 workers but these figures were often difficult to understand, as shown in Fig. 20.

To increase the discrimination capacity, most of the PCAs were carried out by distinguishing species with a *fungifaber* EVA (178 imagines, 424 soldiers and 221 workers) and species with a *finitimus* EVA (100 imagines, 310 soldiers and 179 workers) as shown in Figs 21–22.

**Chorological and ecological data**

As far as possible, species are characterised by their geographical distribution or chorology: for this we refer to the ecoregions defined for the WWF that include climate, soil and vegetation types (Olson *et al.* 2001; Burgess *et al*. 2006).

However, for some old samples with partial labelling, their chorology had to be deduced or assumed from the collectors' travel records. A few, rare unlabelled samples were excluded from our study because they could not be attributed to any ecoregion.

Where possible, we have checked that the species' geographical range is not fragmented: see "Species delimitation".

The maps were produced with the package 'maps' and 'mapdata' of the R language (R Core Team 2018).

**Molecular data**

**Extraction and sequencing**

For mitogenome analyses, DNA extraction was attempted on 210 specimens, either sourced from museum collections or newly collected samples. (i) For museum material, preserved for a long time in 70–80% alcohol, samples consisted of either full individuals or dissection residuals. They were extracted using a non-destructive DNA extraction protocol for ancient DNA (Gilbert *et al.* 2007; Thomsen *et al.* 2009), with tissues incubating in the digestion buffer for 20 hours. (ii) Additional new material was preserved in either 80% ethanol or RNA-later©. For these samples, DNA extraction was performed on full individuals using the DNeasy Blood & Tissue extraction kit (Qiagen). In total, 104 specimens produced usable sequencing data. Across the 104 new mitogenomes submitted herewith, 91 mitogenomes were composed of at least 14 865 bp, six were between 10 000 and 14 865 bp, and seven were below 10 000 bp (Supp. file 3).

Libraries were prepared using the NEBNextâ Ultra™ II FS DNA Library Preparation Kit (New England Biolabs) and the Unique Dual Indexing Kit (New England Biolabs). The reagent volumes were reduced to one-fifteenth of recommended volumes with 1ng of target DNA input, and the fragmentation/end step was optimized to the minimal 5 min incubation at 37°C to avoid DNA over-fragmentation of old samples. Libraries were pooled in equimolar concentration and paired-end sequenced using the Illumina HiSeq X or Novaseq platforms at a read length of 150 bp.

In addition to next-generation sequencing and to ascertain some species identities, some samples were selected for barcode sequencing of the *COII* mitochondrial gene.

*COII* sequences were obtained as described by Roy *et al*. (2006). Briefly, DNA was extracted using Wilson buffer followed by a salting-out procedure, and *COII* was PCR amplified using the modified A-tLeu and reverse B-tLys primers (Miura *et al*. 2000). Sequence data were obtained using an automatic DNA sequencer (Applied Biosystems, ABI PRISM 310) and analysed with Sequencing Data software (Applied Biosystems).

**Phylogenetic analyses**

For the whole genome sequences, adapters and low-quality bases were trimmed from raw reads using fastp *v*0.20.1 (Chen *et al.* 2018). Trimmed reads were assembled using metaSPAdes *v*3.13 (Nurk *et al.* 2017). Mitochondrial genome scaffolds were identified in metaSPAdes assemblies and annotated using MitoFinder ver. 1.4 (Allio *et al.* 2020). The newly-generated mitogenomes of 98 samples of *Isognathotermes*, one *Cubitermes*, two *Nitiditermes* and three *Ternicubitermes* were deposited in GenBank (for accessions and size completeness: see Supp. file 3 and 'Material examined' of each chapter).

We reconstructed the maximum-likelihood phylogeny of species of *Isognathotermes* using the above-produced 104 mitogenomes, supplemented by 60 previously published mitogenomes encompassing most of the known diversity of termites (Cameron *et al.* 2012; Bourguignon *et al.* 2015, 2016, 2017; Wu *et al.* 2018; Wang *et al.* 2019, 2022, 2023; Hellemans *et al.* 2022a, 2022b; Arora *et al.* 2023; Romero Arias *et al.* 2024).

The 37 mitochondrial genes – i.e., 13 protein-coding, two rRNA, and 22 tRNA genes – were aligned using MAFFT ver. 7.305 (Katoh & Standley 2013). Protein-coding nucleotide sequences were translated

into the corresponding amino acid sequences using the transeq function from EMBOSS ver. 6.6.0 (Rice *et al.* 2000), and protein sequences were aligned with MAFFT. Protein alignments were back-translated into codon alignments using PAL2NAL ver. 14 (Suyama *et al.* 2006). All 37 gene alignments were concatenated using FASconCAT-G_v1.04.pl (Kück & Longo 2014). The concatenated sequence alignment was partitioned in 41 partitions: the combined rRNAs and tRNAs were coded in two separate partitions, while one partition for each of the three codon positions was coded for all 13 protein-coding genes (i.e., three partitions for each gene). Phylogenetic trees were reconstructed in a maximum likelihood framework using IQ-TREE ver. 2.2.2.5 (Minh *et al.* 2020). For reconstruction, partitions were first merged and the top 10% were investigated (-m MFP+MERGE -rcluster-max 2000 -rcluster 10) (Chernomor *et al.* 2016). The best-fit nucleotide substitution model was selected for each partition with the Bayesian Information Criterion using ModelFinder implemented in IQ-TREE (Kalyaanamoorthy *et al.* 2017). Branch supports were assessed with 1000 bootstrap replicates, both with the ultrafast algorithm (UFB) (Hoang *et al.* 2018), and the Shimodaira-Hasegawa approximate likelihood-ratio (SH-aLRT) test (Guindon *et al.* 2010). The complete phylogeny based on mitogenomes is presented in the Supp. file 1.

We also reconstructed a phylogeny of the *COII* gene incorporating additional data from Sanger sequencing or retrieved from GenBank (for details, see supplementary Supp. file 3 and 'Material examined'). Specifically, this reconstruction included 120 *COII* sequences of *Isognathotermes*, including: one newly deposited *COII* barcode (ISO7; see Supp. file 3); previously published *COII* sequences from Roy *et al*. (2006) and Hellemans *et al*. (2021); and *COII* sequenced extracted from mitogenomes used herein. We used 32 *COII* sequences as outgroups for the reconstruction, all extracted from the mitogenomes of the Kalotermitidae, the Stylotermitidae, the *Coptotermes*, the Macrotermitinae, and all Cubitermitinae included in the mitogenome-based phylogeny. This latter reconstruction followed the same procedure as for the phylogeny reconstructed from the full mitogenomes, with one partition per codon position. The complete phylogeny based on *COII* is presented in the Supp. file 2.

In addition to phylogenetic analyses, we used a 2% dissimilarity cutoff at the mitogenome-level for the definition of species boundaries. At the gene (barcode) level, the Kimura-2-parameter (K2P) nucleotide substitution model with a threshold of 2–4% divergence is the most widely used criterion to define interspecific boundaries (Srivathsan & Meier 2012; Dowton *et al.* 2014; Klimov *et al.* 2019). Although its use is widespread, the K2P model is equally frequently criticized (Srivathsan & Meier 2012; Nishimaki & Sato 2019). In addition, as rates are gene-specific, the use of such substitution model is not appropriate for their use on whole mitogenome. Therefore, we opted for the use of pairwise comparison of sequence similarity through BLAST.

**Species delimitation**

As part of an integrative taxonomy, we used several criteria (morphology, anatomy, chorology, ecology and mitogenome) to delimit species and describe new species.

Morphological requirements: the morphological study is based on multiple measurements and indices (37 for imagines, 52 for soldiers, 64 for workers, including 18 on their EVAs). These data series are synthesised using PCAs, which must be consistent between soldiers, workers (and imagines if present). If this is not the case, a heterogeneous sample can be suspected (comprising more than one species, which is not uncommon).

To avoid describing an abnormal sample as a new species, we decided not to describe a new species if we did not have at least two "complete samples" (i.e., composed of imago, soldier and worker) or three "incomplete samples" (e.g., soldier and worker).

Chorological requirements: for each species, we have ensured that its geographical area is not fragmented, i.e., that it is not divided into several zones separated by geographical barriers or by large void spaces; this is of course only feasible when a large number of sampling sites is available (at least 20). If this happens and if it is not possible to sequence the geographically distant samples, they are presented in the "material examined" as "dubious, possibly cryptic species" (see for example *I. fungifaber*).

As suggested in Fig. 32, there is a distribution of species according to their EVA; in fact, the separation is even better than suggested by the figure because on its scale, as dots indicating savannah and forest environments of the same locality are overlaid. Therefore, we paid attention to the principle of competitive exclusion (Hardin 1960), which should limit or even rule out the coexistence of several species of *Isognathotermes* with the same EVA and caecum on the same site. Hence, we assumed that the types of EVA and caecum are linked to the food niche of these geophagous termites (see the general discussion).

Molecular requirements: to distinguish their cryptic species, Roy *et al*. (2006) used a threshold of 1%. To limit the number of species, we herein considered a priori that samples showing more than 2% dissimilarity in their mitogenomes belong to different species. It follows that cryptic species were likely missed. However, in a few specific situations, with sufficient morphological or chorological arguments, samples with less than 2% dissimilarity in their mitogenomes may be considered a posteriori to belong to different species (or subspecies).

## Results

Phylum Arthropoda Latreille, 1829
Class Insecta Linnaeus, 1758
Super-order Polyneoptera Martynov, 1923
Order Blattodea Wattenwyl, 1882
Infraorder Isoptera Brullé, 1832
Nanorder Neoisoptera Engel *et al.*, 2009
Family Termitidae Latreille, 1802
Subfamily Cubitermitinae Weidner, 1956

Genus ***Isognathotermes*** Sjöstedt, 1926
Figs 1–33, distribution map: Fig. 32; Table 1

*Isognathotermes* Sjöstedt, 1926: 214, by original designation.

### Type species

*Eutermes* (*Cubitermes*) *minitabundus* Sjöstedt, 1913.

### Diagnosis

As in the other Cubitermitinae, the worker's, soldier's and imago's guts are characterized by a mixed segment between mid and hind gut; four Malpighian tubules fused at base and by a blind diverticulum, or caecum, on the paunch of the hind gut (Noirot & Kovoor 1958; Noirot 2001) (Figs 2–3).

The genus *Isognathotermes* is best and fully characterized by its worker's EVA which takes two main forms and an intermediate form (workers of no other Cubitermitinae genera show such EVAs.):

- in the *fungifaber* pattern (Figs 4, 6), the odd-numbered primary cushions (slightly longer than the even primary cushions) are frequently narrowed and crested in their downstream parts (the crests, however, are only visible if the PCs are twisted and viewed in profile), in some species, they are only slightly protruding or even not at all in *I. acristatus* sp. nov., the crested and distal parts of the PCs bear long

curved or hooked bristles; the transition from the part with supporting bristles to the bulbous part is relatively gradual; see also Noirot & Kovoor (1958: 458).
- in the *finitimus* pattern (Figs 5–6), the odd primary cushions are more robust, less or not at all narrowed; a rather swollen part (viewed in profile) bears numerous short, stiff, non-curved bristles and the distal part bears some long curved to hooked bristles; the transition from the part with supporting bristles to the bulbous part is relatively abrupt.
- in the intermediate pattern (Fig. 6) the odd-numbered primary cushions have relatively small crests, are not swollen in their downstream part, and bear numerous slightly curved bristles; the distal parts bear some long curved to hooked bristles (it is closer to the *fungifaber* pattern than the *finitimus* pattern and occurs only in species of the *fungifaber* pattern, mainly *I. severus* and *I. ugandensis*).

The secondary cushions are wide with a homogeneous spine scattering.

The worker is also characterized by the shape and spinosity of its front legs: the fore coxa is carinated and bears two to seven spines on the ventral carina (Fig. 7); the fore trochanter bears three to eight spines. Mandibles as in the imagines.

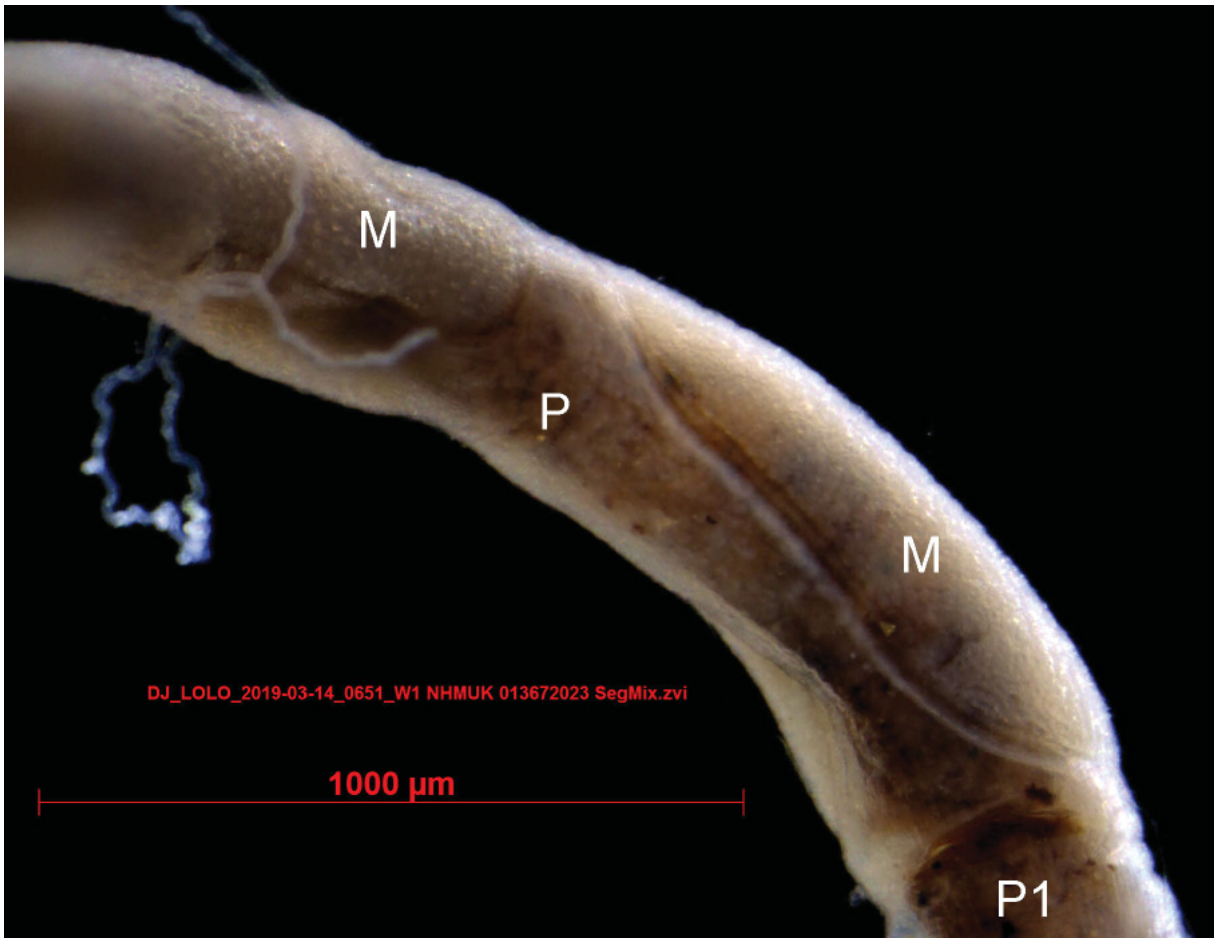


**Fig. 1.** Mixed segment of a worker of *I. fungifaber* (Sjöstedt, 1896) (DJ 0651). Abbreviations: M = mesenteric part of the mixed segment (with Malpighian tubules); P = proctodeal part of the mixed segment; P1 = beginning of ileum.

The soldier is dark-gutted (its gut contains some soil); it has a well-developed frontal gland and a frontal pore (fontanelle) on the frons surrounded by a tuft of setae; it has a deeply bifurcated labrum with straight, convex or, more generally sinuous sides (lyre-shaped labrum), almost always with subtruncated lobes ending in fine, whitish or translucent tips, and bearing three to ten large setae on each lobe; its EVA, however, is not as well characterized as that of worker, especially in the *fungifaber* pattern where it can be confused with a *bilobatodes* or a *muneris* pattern; in the *finitimus* pattern, the soldier's EVA is generally recognizable (Fig. 6).

Its fore trochanter and carinated fore coxa often bear some spines (but less than the worker's). It has a long head (SHdL = 2.18–3.77 mm), a high head elongation index (SHdL/SHdW = 1.22–1.67), and the sabre-like mandibles are always shorter than the head (SMlL/SHdL = 0.66–0.92); antennae of 14–15 articles. All these characters taken together make it possible to recognise the *Isognathotermes* soldiers.

The imago cannot be distinguished easily from other, related Cubitermitinae genera; it is always rather dark (C6–C8), its head bears some large setae overhanging a generally dense mat of short bristles. Its meso- and metanotum generally bear some very fine, pale setae, arranged in a medio-longitudinal strip, generally visible at 40–80× (without any visible small setae in 6.5% of the imagines examined), and frequently with three to four larger setae. The fontanelle is always small; antennae of 16 articles (but shortened in functional queens and kings). Mandibles with apical tooth longer than marginal teeth, three on the left mandible, two on the right. Legs: tibial spurs 3: 2: 2, middle tibia with two extra subapical spines. The enteric valve is weakly developed and can hardly be used for identification (Fig. 6).

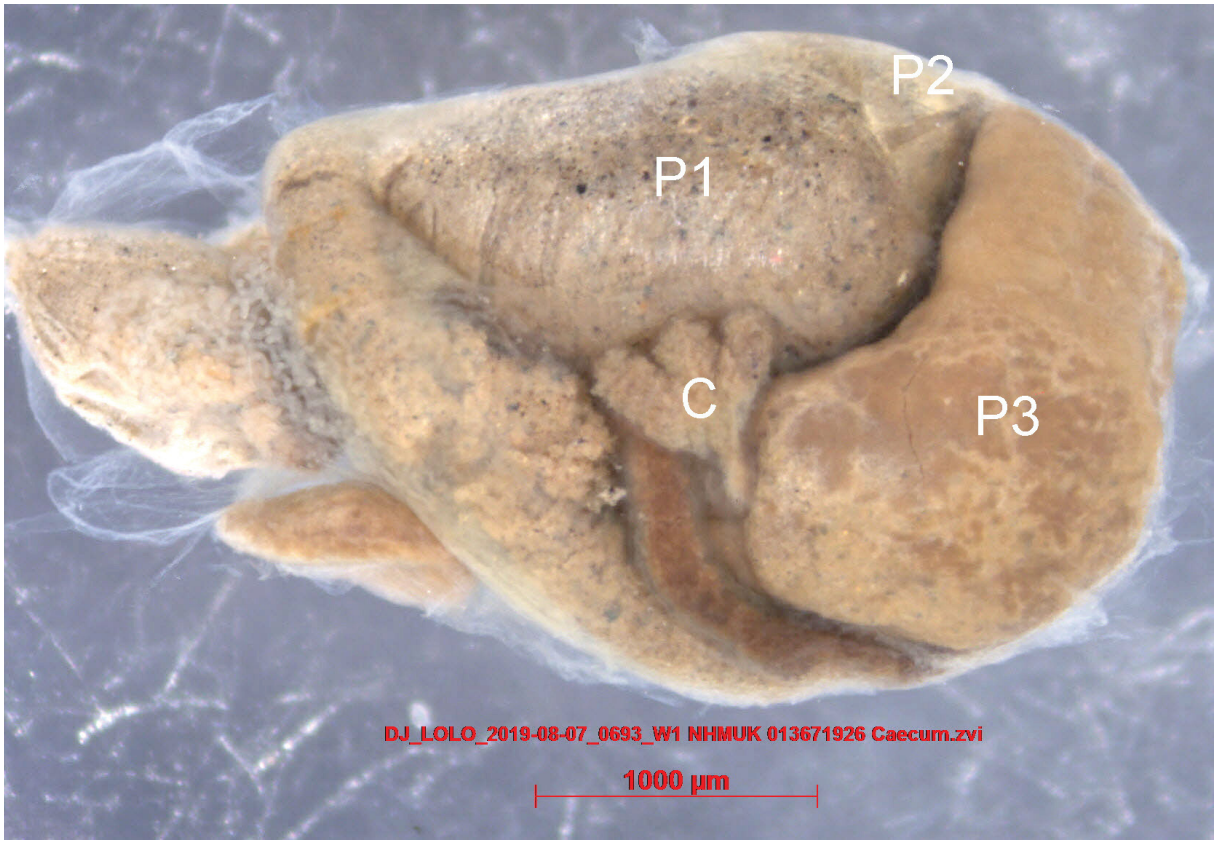


**Fig. 2.** Caecum (or blind diverticulum of the gut) of a worker of *I. minitabundus* (Sjöstedt, 1913) (DJ 0693). Abbreviations: C = caecum (see also Fig. 56), P1 = ileum; P2 = enteric valve; P3 = paunch.

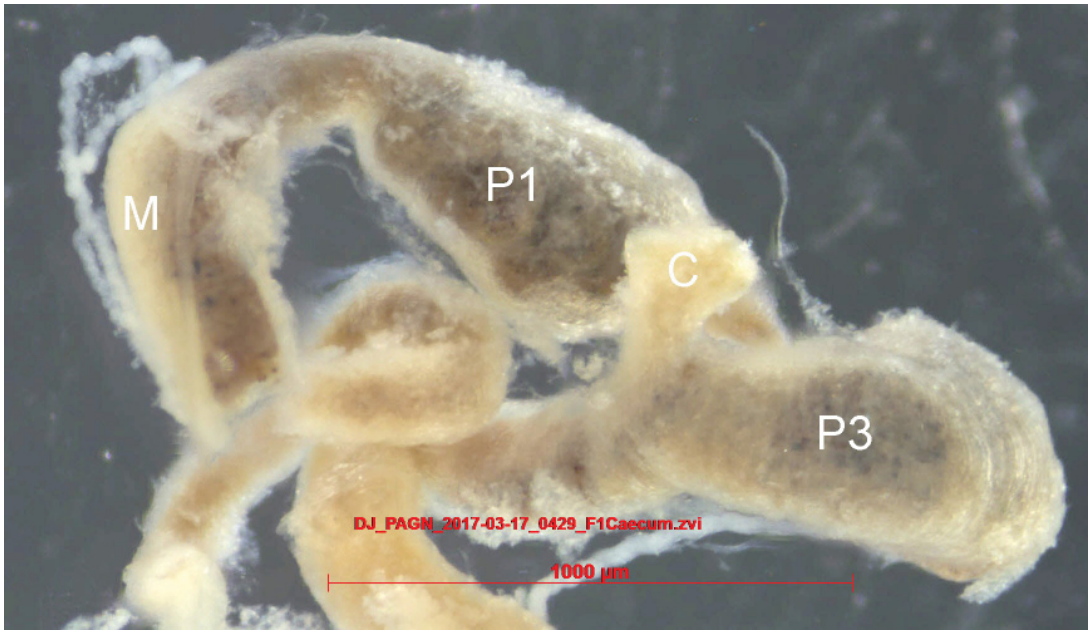


**Fig. 3.** Mixed segment and caecum of an imago of *I. fungifaber* (Sjöstedt, 1896) (DJ 0429). Abbreviations: C = caecum; M = mesenteric part of the mixed segment (with Malpighian tubules); P1 = ileum; P3 = paunch; enteric valve hidden behind the caecum.

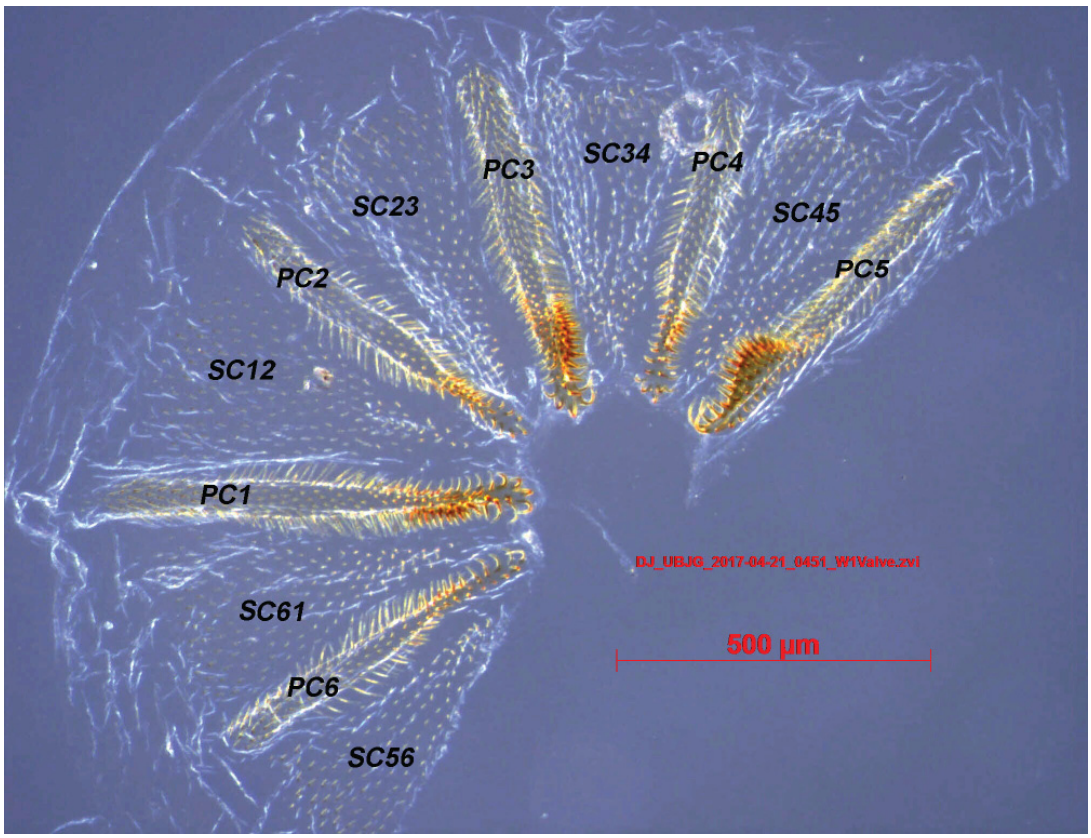


**Fig. 4.** Worker's enteric valve of *I. fungifaber* (Sjöstedt, 1896) (DJ 0451). Note the crested PCs; one of them (PC5) is twisted and shows the long and strong bristles on the crest. Note the slender PCs (in comparison with Fig. 5) and the wide SCs with a homogeneous spine scattering.

**Etymology**

From Greek *ισος* (*isos*, equal, even), *γναθος* (*gnatho*s, mandible), and Latin *termes* (termite), the name *Isognathotermes* probably refers to the type species (see the chapter *I. minitabundus*), either to the resemblance between both mandibles or to the fact that their diameter varies little between both ends.

**Historical review**

The first mention in the literature of a termite that could be an *Isognathotermes* probably dates back to Smeathman (1781) under the name *Termes atrox*: see the historical review of *I. severus*.

This genus was created by Sjöstedt (1926) for a species previously described (soldier only) as *Eutermes* (*Cubitermes*) *minitabundus* by himself in 1913. Indeed, Sjöstedt (1926: 214) considered, in his identification key, that this monotypic genus was significantly different from all other *Cubitermes* species by their soldiers' mandibles which are straight with slightly curved tips. It shared this feature with *Megagnathotermes* but in the latter genus, soldiers have longer mandibles and a less deeply emarginated labrum. In the same work, Sjöstedt (1926: 216) described the imago and worker of *I. minitabundus* which was then the only species of the genus, so these descriptions applied also to the genus itself.

According to Sands (1965: 98) and to Krishna *et al.* (2013: 1858, 1927), "*fide* Emerson card catalog (unpublished)", the imago of *I. minitabundus* had already been described erroneously under the name *Eutermes* (*Trinervitermes*) *carbo* by Sjöstedt (1924a: 42).

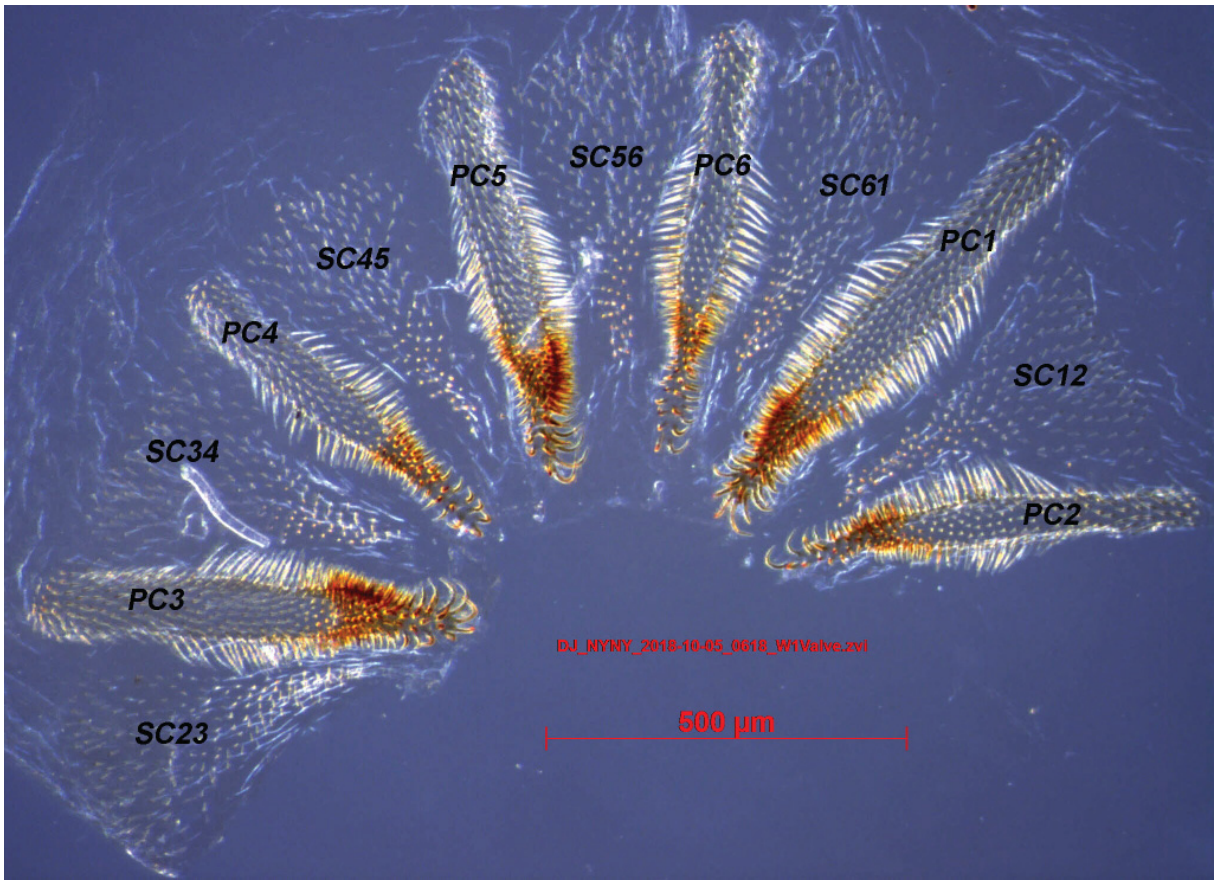


**Fig. 5.** Worker's enteric valve of *I. finitimus* (Schmitz, 1916) (DJ 0618). Note the PCs with a swollen distal part bearing a high density of short bristles (best visible on PC5); the supporting bristles are clearly visible on both sides of every primary cushion. Note the robustness of PCs (in comparison with Fig. 4), and the wide SCs with a homogeneous spine scattering.

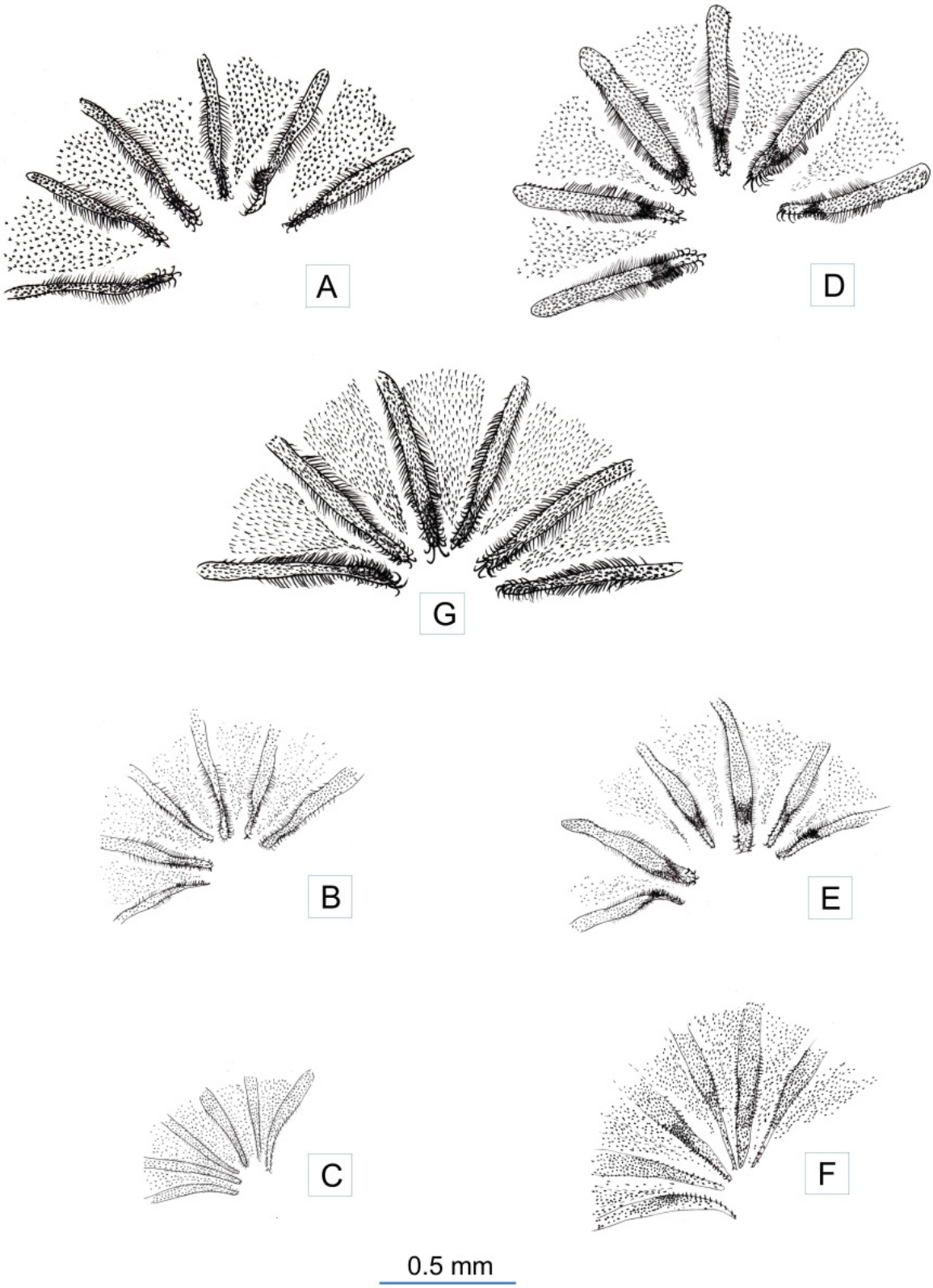


**Fig. 6.** Enteric valves of *I. fungifaber* (Sjöstedt, 1896). **A**. Worker (DJ 0271). **B**. Soldier (DJ 0271). **C**. Imago (DJ 0466), enteric valves of *I. finitimus* (Schmitz, 1916). **D**. Worker (DJ 0286). **E**. Soldier (DJ 0286). **F**. Imago (DJ 0072). **G**. Worker enteric valve of a sample of *I. severus* (Silvestri, 1914) with an intermediate pattern (DJ 0659). All figures to the same scale.

The species was later reverted to the genus *Cubitermes* by Snyder (1949: 161). The genus *Isognathotermes* was recently restored as valid by Hellemans *et al.* (2021: 233) based on a phylogenetic analysis. It now gathers several previous *Cubitermes* species sharing the same kinds of Enteric Valve Architectures (EVAs), i.e., of the *fungifaber* or *finitimus* patterns as defined by Josens & Deligne (2019). Among the genera derived from *Cubitermes* (sensu Wasmann), *Isognathotermes* is probably the most confusing with the most numerous synonymies and misidentifications in museum collections.

The mitogenomes of 12 out of the 15 valid species have been sequenced.

**Species included**

The genus *Isognathotermes* clusters 22 taxa previously housed in the genus *Cubitermes* (sensu Wasmann), namely *C. antennalis* Sjöstedt, 1924; *C. banksi* (Emerson, 1928); *C. bulbifrons* Sjöstedt, 1924; *C. comstocki* (Emerson, 1928); *C. finitimus* Schmitz, 1916; *C. fungifaber* (Sjöstedt, 1896); *C. fungifaber* var. *elongata* Sjöstedt, 1924; *C. gaigei* (Emerson, 1928); *C. gibbifrons* Sjöstedt, 1924; *C. heghi* Sjöstedt, 1924; *C. kemneri* (Emerson, 1928); *C. loubetsiensis* Sjöstedt, 1924; *C. minitabundus* (Sjöstedt, 1913); *C. modestior* Silvestri, 1914; *C. planifrons* Sjöstedt, 1924; *C. schmidti* (Emerson, 1928);


**Fig. 7.** Worker's foreleg of *I. ugandensis* (Fuller, 1923) (DJ 0669). Note the characteristic strong spines on trochanter and coxa (the spines are inserted on a carina).

*C. severus* Silvestri, 1914; *C. silvestrii* Sjöstedt, 1925; *C. speciosus* Sjöstedt, 1924; *C. subarquatus* Sjöstedt, 1926; *C. ugandensis* Fuller, 1923; and *C. zenkeri* (Desneux, 1904).

However, 13 of these 22 species are now considered to be junior synonyms of other species, as explained below. In addition, one species previously housed in the genus *Cubitermes* (sensu Wasmann), namely *C. congoensis* (Emerson 1928) and three possibly new species could not be classified for sure; they are housed in the Incertae sedis chapter.

The genus *Isognathotermes* also includes seven new species: *I. acristatus* sp. nov., *I. magniplanifrons* sp. nov., *I. modicus* sp. nov., *I. phallicaecalis* sp. nov., *I. phalloides* sp. nov., *I. rectimalatus* sp. nov., and *I. similifinitimus* sp. nov.

**Redescription of the genus**

**Imago**

Colour. **Head capsule** well sclerotised, dark, C6–C8, paler (up to C4) in long preserved samples. Fontanelle concolorous or almost so with head capsule. Postclypeus C5–C7 concolorous or somewhat paler (up to two levels) than head capsule. Antennae C4–C6 without any difference between proximal and distal articles. **Thorax**: pronotum C5–C7, somewhat paler than head capsule; meso- and metanotum C5–C7, as pronotum. Legs C3–C5, tibia usually slightly (one level) darker than femur. Wings hyaline with brown to grey tinge (Cf2–Cf4), anterior veins darker. **Abdomen**: tergites C5–C7, as pronotum. Sternites appreciably paler in middle (C3–C5) with both sides darker (C4–C6); posterior sternites darker (C4–C6) than anterior.

Setation. **Head capsule** with some prominent setae, mainly near the eyes, overhanging a generally dense mat of short bristles. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and many shorter ones in middle; meso- and metanotum with some fine, pale setae arranged in a medio-longitudinal strip, mainly on mesonotum and the anterior lobe of metanotum, generally visible at 20–80×, but sometimes without any visible small setae; frequently 1–4 larger setae on metanotum. **Legs** very pilose, furnished (among numerous fine setae) with some large setae becoming sometimes spine-like: 0–18 on the carina of fore coxa and 0–8 on the anterior side of fore coxa; tibia pilose and furnished with 15–30 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 1; Figs 8–12, 23). **Size**: the imagines of the genus *Isognathotermes* (with those of the genus *Polyspathotermes*) are among the largest of those derived from the former genus *Cubitermes* (sensu Wasmann); however, with large overlapping with *Ternicubitermes* and *Nititidermes*. This can be seen in most raw data, exemplified by the head width (Fig. 23); in contrast, indices differ little between genera. **Head capsule** large; fontanelle generally a tiny round or elongate marking (Fig. 8). Compound eyes round to shortly oval (IEy*D*/IEy*d* = 1.00–1.25, Fig. 9). Ocelli round to oval (IOc*D*/IOc*d* = 1.00–1.80). Antennae: 16 articles on alate individuals (one out of 278 alate imagines with 17 articles), always shortened by amputation of 1–4 articles in queens and kings. Labrum: cupola shaped, generally wider than long. **Left mandible** with apical tooth longer and more prominent than first marginal; marginal teeth three in number but second one only suggested by an undulation of edge between first and third marginal teeth (disappearing in worn mandibles); only the apical tooth is acute in unworn specimens; premolar tooth with proximal end obscured or partly obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a

**Table 1.** Genus *Isognathotermes*: ranges of significant measures in the three castes, in alphabetical orders of "Code" column.

| | | Variable * | Code * | *fungifaber* EVA | *finitimus* EVA |
|---|---|---|---|---|---|
| Imagines (n = 283) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.34–0.58 | 0.33–0.48 |
| | | Head: width across the eyes | IHdW | 1.40–1.84 | 1.38–1.78 |
| | | Left mandible: A-m1 distance | IMlAmD | 0.16–0.28 | 0.17–0.30 |
| | | Ocellus: large diameter | IOc*D* | 0.12–0.23 | 0.12–0.21 |
| | | Postclypeus: width | IPcW | 0.65–0.93 | 0.65–0.87 |
| | | Pronotum: maximal width | IPnW | 1.17–1.74 | 1.18–1.72 |
| | | Hind tibia: length | IT3L | 1.45–2.35 | 1.30–2.29 |
| | | Wing: length (n = 127) | IWgL | 10.4–19.5 | 12.2–16.8 |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 0.93–2.06 | 1.05–2.04 |
| Soldiers (n = 737) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.00–0.11 | 0.00–0.12 |
| | | Head: length | SHdL | 2.37–3.72 | 2.18–3.77 |
| | | Head: width | SHdW | 1.58–2.39 | 1.73–2.49 |
| | | Left mandible: lesser sagitta | SMlc | 0.08–0.33 | 0.13–0.36 |
| | | Left mandible: ventral length | SMlL | 1.74–2.99 | 1.55–2.99 |
| | | Hind tibia: length | ST3L | 1.26–1.94 | 1.40–2.01 |
| | Indices | Head elongation index | SHdL/SHdW | 1.22–1.62 | 1.25–1.67 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.03–0.15 | 0.05–0.15 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.51–1.24 | 0.70–1.38 |
| Workers (n = 408) | Raw measures (mm) | Head: width | WHdW | 0.94–1.42 | 1.06–1.43 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.13–0.25 | 0.15–0.22 |
| | | Left mandible: total length | WMlL | 0.47–0.69 | 0.49–0.68 |
| | | Hind tibia: length | WT3L | 1.05–1.49 | 1.12–1.57 |
| | | Valve: PC average length | WVP-AvL | 0.43–0.85 | 0.45–0.77 |
| | | Valve: PC average width | WVP-AvW | 0.04–0.12 | 0.05–0.10 |
| | | Valve: SC average length | WVS-AvL | 0.40–0.73 | 0.36–0.64 |
| | | Valve: SC average width | WVS-AvW | 0.19–0.50 | 0.16–0.41 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 5.57–13.6 | 4.85–11.6 |

* Abbreviations: see definitions in Material and methods.

tiny acute apophysis. **Right mandible** with apical tooth longer and more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel (Fig. 10). **Thorax**: pronotum appreciably wider than long (Fig. 11) and narrower than head width, straight to very weakly sellate with anterior lobe short and very slightly elevated. **Legs**: the fore coxa is flanged ventrally resulting in a more or less sharp edge called here 'carina'. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 2–6 and 7–15 branches respectively (Fig. 12). **Abdomen** of imagines shows 10 fully visible undivided tergites in both sexes. The first sternite is absent or vestigial; fully visible undivided sternites are 8 in male and 6 in female. In the male, the 8 visible undivided sternites are followed by a reduced one divided into two paraprocts; in female the sixth visible sternite (genital plate)


**Fig. 8.** Dorsal view of an imago's head (antennae removed) of *I. minitabundus* (Sjöstedt, 1913) (DJ 0728). The fontanelle is, in this case, somewhat darker than head capsule.


**Fig. 9.** Lateral view of an imago's head (antennae removed) of *I. minitabundus* (Sjöstedt, 1913) (DJ 0728).

is elongated and often covers the three following ones which are divided and reduced, the third having become the two paraprocts. In both male and female each paraproct bears a two-jointed small cercus. **Gut**: The gut of the imago is similar to that of workers with notably a well-defined mixed segment and a caecum (Fig. 3), but the caecum is proportionally less developed.

**Soldier**

Colour. **Head capsule** generally Cd4–Cd6 becoming fader and darker (e.g., Cf5–Cf7) in long preserved samples; frons frequently 1–2 levels darker than back (e.g., C6–C7) sometimes with a sharp contrast giving the impression of a bicolour head; this two-tone colouring has no specific value. Gulamentum concolorous with head or somewhat darker. Antennae and labrum one level paler than head capsule. Mandibles dark (C7–C8) generally with an abrupt clearing on their bases (two levels) which are generally of the same colour as frons. **Thorax**, nota and legs paler than head capsule (C3–C5) somewhat darker in long preserved samples. **Abdomen** grey to red-brown owing to digestive bolus, sometimes with a yellow tinge on tergites.

Setation. **Head capsule** with few scattered fine setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50 × or more). **Labrum** always with 4–9 large setae on each lobe. **Thorax**: pro- and mesonotum with some setae mainly located on fore and hind margins. **Legs**: fore coxa furnished with 0–3 spines on carina and not any (or rarely one) spine on ventral side; trochanter generally with six or seven long lined-up strong setae or spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively; all tibiae furnished with a row of 6–15 spines. **Abdomen**: tergites with few large setae, mainly or only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

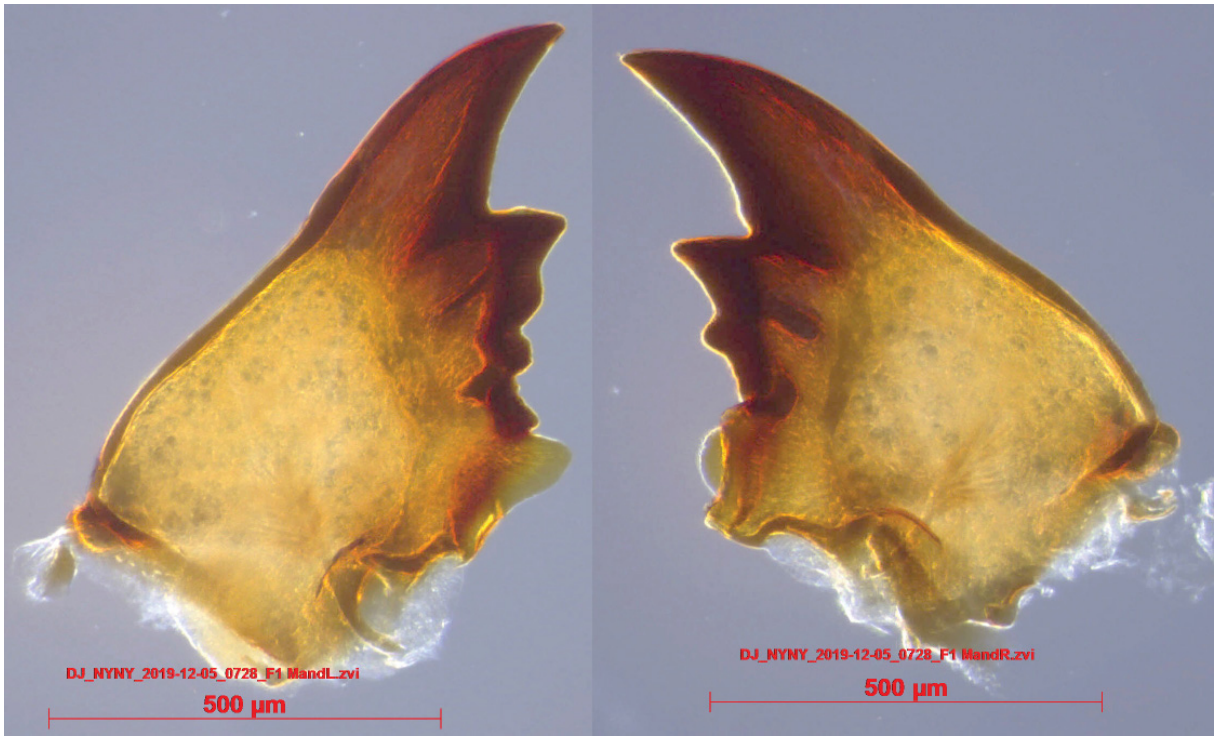


**Fig. 10.** Mandibles of an imago of *I. minitabundus* (Sjöstedt, 1913) (DJ 0728).

Structure (measurements in Table 1; Figs 13–17, 24). **Size**: the soldiers of *Isognathotermes* (with those of *Polyspathotermes*) are among the largest of those derived from the former genus *Cubitermes* (sensu Wasmann); however, with some overlapping with *Ternicubitermes* and *Nitiditermes*. This can be seen in most raw data that vary with genus, exemplified by the head length (Fig. 24); in contrast, most indices differ little between genera. **Head capsule** always clearly sclerotised and appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a more or less strong narrowing near posterior third or fourth (Fig. 13); however, in the soldiers of incipient colonies, lateral sides are slightly convex without any narrowing; posterior side variable: regularly rounded or sometimes with a short straight or even concave part in the middle, or with three short straight or even concave parts. **In profile**: upper profile always more or less concave, also in the case of soldiers from incipient colonies; angle between extended mandibles and frons varies from almost right to 130°; frons with or without any small frontal hump overhanging the fontanelle (Fig. 14). **Gulamentum**: profile generally with a flat posterior part; in ventral view always more or less constricted in its posterior half, with sides of anterior part variable, from smoothly rounded (Fig. 15) to extended into a kind of angular ears. Antennae generally of 15 articles

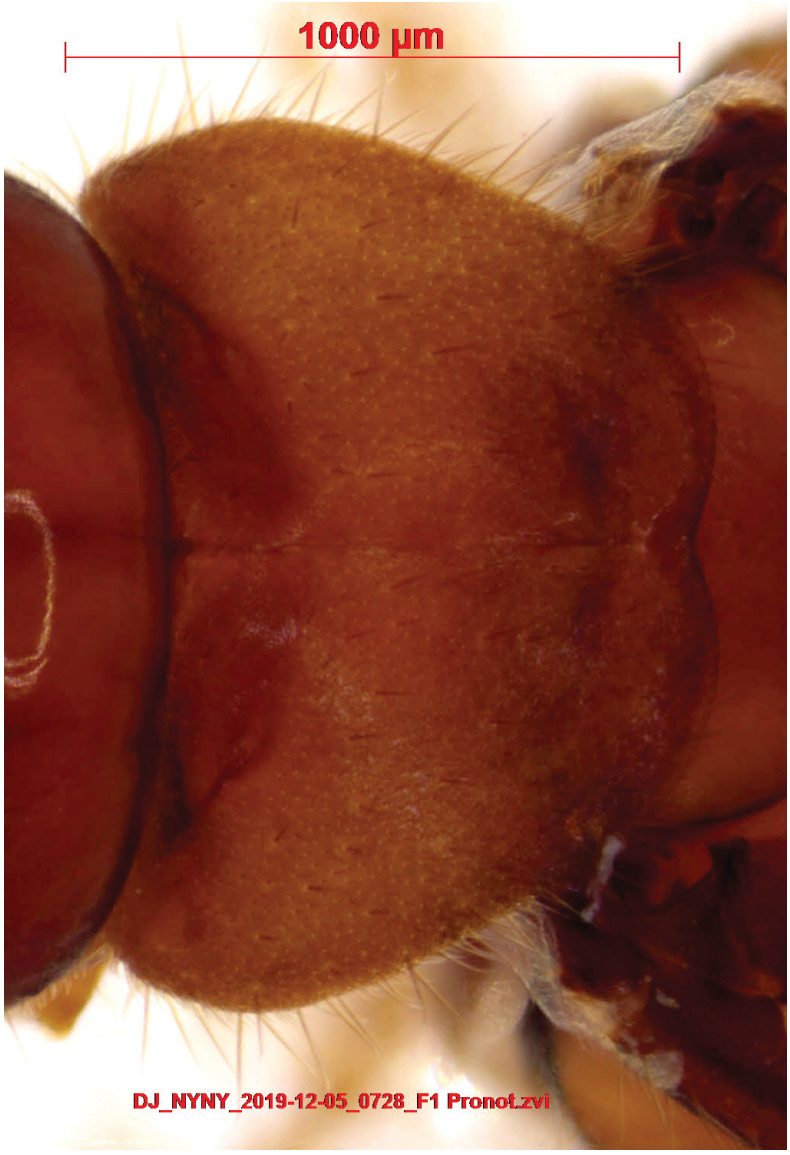


**Fig. 11.** Dorsal view of an imago pronotum of *I. minitabundus* (Sjöstedt, 1913) (DJ 0728).

(14.5 articles in 9%, 14 articles in 6% and only 13 articles in one soldier from an incipient colony). **Labrum**: always deeply bifurcate and generally wider than long, generally (in 82%) with sinuous sides (lyre-shaped labrum) (with convex sides in 11%, or with straight sides in 7%) and almost always with subtruncated lobes ending in fine, whitish or translucent tips; anterior margin concave (Fig. 16). **Mandibles**: sabre-like to almost hooked distally; inner edges smooth with one distinct but generally very small marginal tooth near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible generally slightly more curved than left. **Thorax**: pronotum sellate, narrower than head width, with generally entire anterior and posterior margins (Fig. 17). **Fore coxa** flanged ventrally resulting in a more or less sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions generally showing trilateral symmetry: the odd primary cushions are on average 16% longer


**Fig. 12.** Left anterior wing of an imago of *I. minitabundus* (Sjöstedt, 1913) (DJ 0728).


**Fig. 13.** Dorsal view of a soldier's head (antennae and labrum removed) of *I. finitimus* (Schmitz, 1916) (DJ 0739). Note a slight narrowing near posterior fourth of the head capsule. In this case, the head capsule seems to be bicolorous.

than the even cushions; the odd cushions generally without any crest or with crests weakly developed; in the species with *finitimus* EVAs the pilosity becomes abruptly very dense showing the place where a crest would be expected (in comparison with the worker's EVA); secondary cushions wide at the upstream end narrowing noticeably downstream with a homogeneous spine scattering. **Caecum** rather small, visible in


**Fig. 14.** Lateral view of a soldier's head (antennae and labrum removed) of *I. finitimus* (Schmitz, 1916) (DJ 0739). Note, in this case, a weak dorsal bulge (= upper profile weakly concave) and not any forward frontal hump.


**Fig. 15.** Ventral view of a soldier's head of *I. finitimus* (Schmitz, 1916) (DJ 0739). In this case, the sides of anterior part of gulamentum are smoothly rounded.

ventral view, near centre of abdomen, either shortly lobed (in most species) or developed as a finger-like process that is sometimes capped or swollen distally.

**Worker**

Colour. **Head capsule** pale (C1–C3) turning grey in long preserved samples. Antennae: proximal articles pale (C2–C3), distal articles always 1–2 levels darker (C4–C5). **Thorax**, nota and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect, scattered setae. Labrum with few, robust, scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: nota with scattered setae. **Legs**: fore coxa always carinated, bearing one fine seta and furnished with 3–7 spines on carina (only 2 spines in two out of 400 samples) and 0–4 spines on ventral side; fore trochanter with 5–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs, and 0, 2, 0 subapical spurs respectively and a row of spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

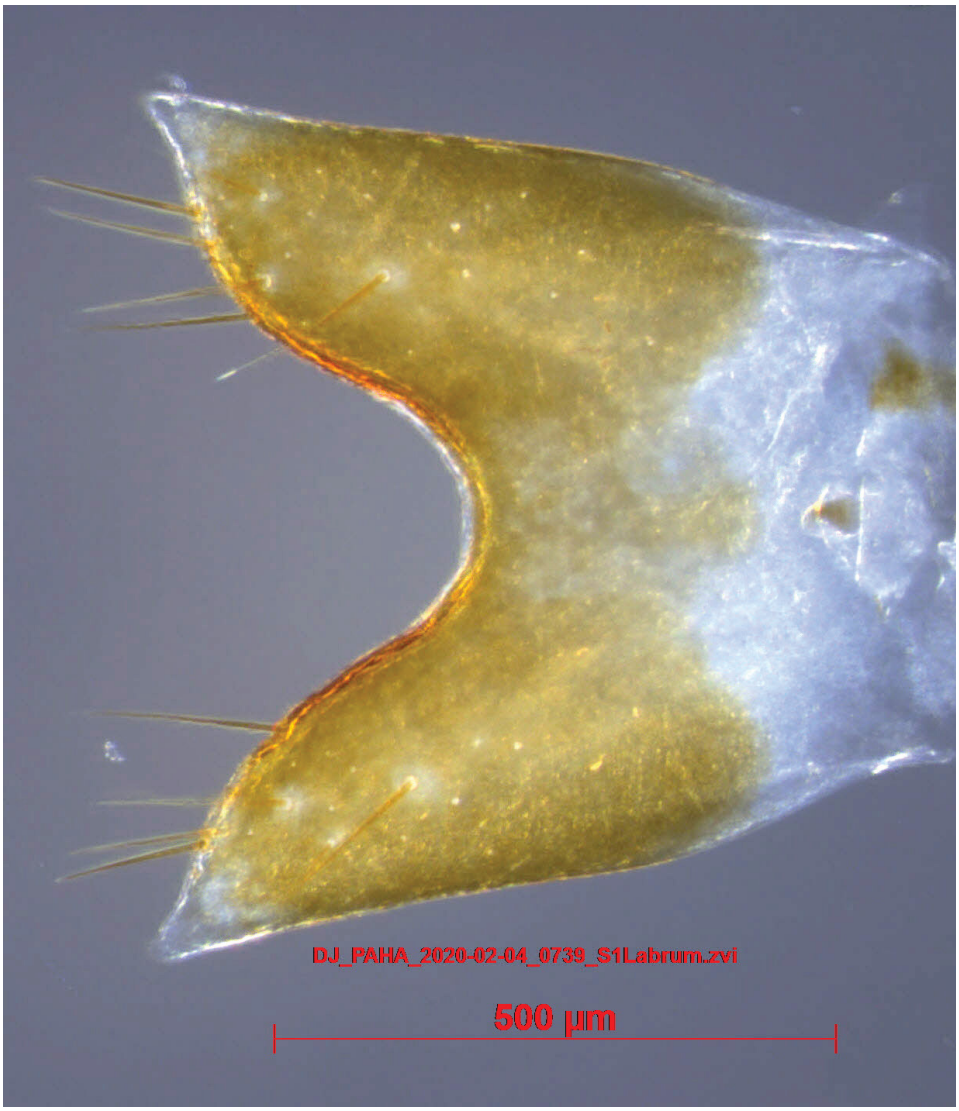


**Fig. 16.** Labrum of a soldier of *I. finitimus* (Schmitz, 1916) (DJ 0739). Note the characteristic lyre shape and the subtruncated lobes, ending in whitish, almost translucent tips.

Structure (measurements in Table 1; Figs 18–19, 25). **Size**: the workers of *Isognathotermes* (with those of *Polyspathotermes*) are among the largest of those derived from the former genus *Cubitermes* (sensu Wasmann); however, with large overlapping with *Ternicubitermes* and *Nitiditermes*. This can be seen in most raw data that vary with genus, exemplified by the hind tibia lengths (Fig. 25); in contrast, indices differ very little between genera. **Head capsule** weakly sclerotised (except mandibles) (Fig. 18). Antennae 15 articles, more rarely 14.5 or 14, and only 13 in a worker from an incipient colony. Labrum: cupola shaped, generally wider than long. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal well developed, second marginal faint (visible as an undulated edge but disappearing in worn mandibles), third marginal with a blunt tip; premolar tooth with its proximal end partly generally hidden under molar prominence; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis (Fig. 19). **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal well developed with a sharp tip when fresh; second marginal smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel (Fig. 19). **Thorax**: pronotum sellate. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in posterior half of abdomen. The **enteric valve** with either a *fungifaber* or a *finitimus* EVA or an intermediate EVA (but in one species, *I. acristatus* sp. nov., with a *muneris* EVA), always with a triradial symmetry; the odd PCs, in their downstream part, either bear crests that are as high as or higher


**Fig. 17.** Pro- and mesonotum of a soldier of *I. finitimus* (Schmitz, 1916) (DJ 0739).

than they are wide, with long and strong bristles (*fungifaber* EVA, Fig. 4) or bear at that place a higher density of rather short bristles on a globular bulge (*finitimus* EVA, Fig. 5); supporting bristles are generally numerous: 13–38 on each side of the odd PCs (with an exception in *I. acristatus*); secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum rather small, visible in ventral view, near centre of abdomen, frequently with two or three small lobes or developed as a finger-like process that is sometimes capped or swollen distally.

**Morphologic analysis**

The worker's valve remains the best criterion to recognise the genus *Isognathotermes*, with the exception of *I. acristatus* sp. nov. whose valve is similar to the *Ternicubitermes* pattern. Additionally, the spinosity of workers' fore coxae characterises well the genus *Isognathotermes* (including *I. acristatus*), although this feature is shared with *Polyspathotermes* and some species of *Nitiditermes*.

While the soldier caste allows the best separation between species, several soldier characteristics need to be brought together to delimit the *Isognathotermes* genus (see diagnosis).

The imagines provide few discriminating criteria and are sometimes difficult to distinguish from other Cubitermitinae imagines. As a notable exception, however, four subspecies of *I. ugandensis*, practically indistinguishable from the soldiers, could be evidenced from the imagines' overall dimensions, as well both eyes and ocelli relative dimensions.

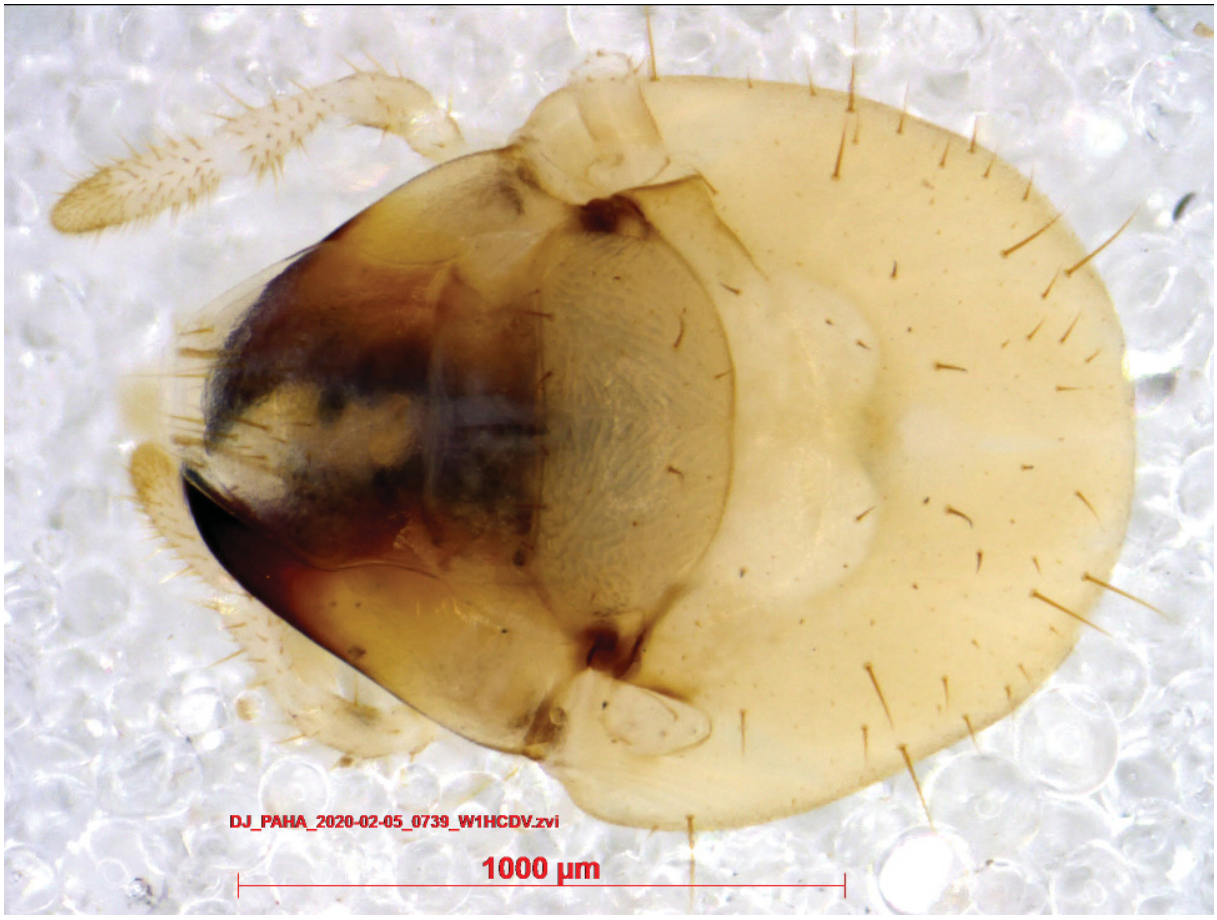


**Fig. 18.** Dorsal view of a worker's head (antennae removed) of *I. finitimus* (Schmitz, 1916) (DJ 0739).

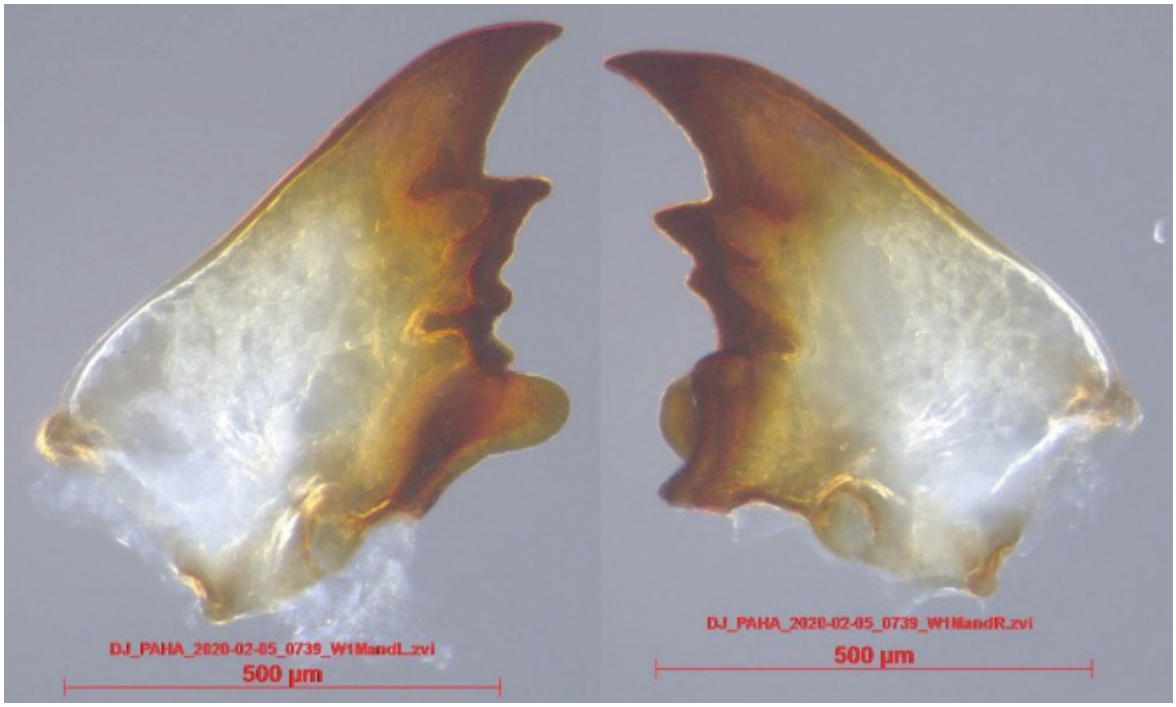


**Fig. 19.** Left and right unworn mandibles of a worker of *I. finitimus* (Schmitz, 1916) (DJ 0739).

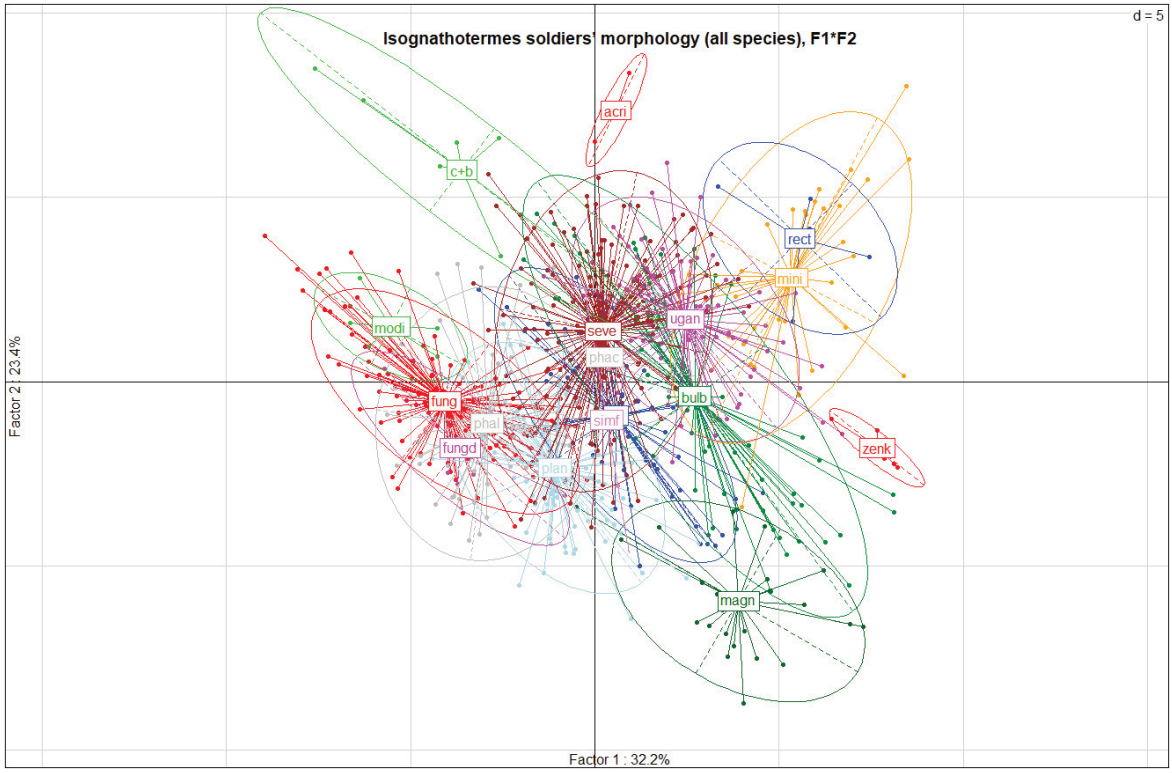


**Fig. 20.** PCA on soldier's morphology involving all *Isognathotermes* species. The first axis is linked with size, the second with mandible curvature. Species with a *fungifaber* EVA are shown in warm colours, those with a *finitimus* EVA are shown in cool colours; note the superposition of both groups. Meaning of labels as in Fig. 21 and Fig. 22.

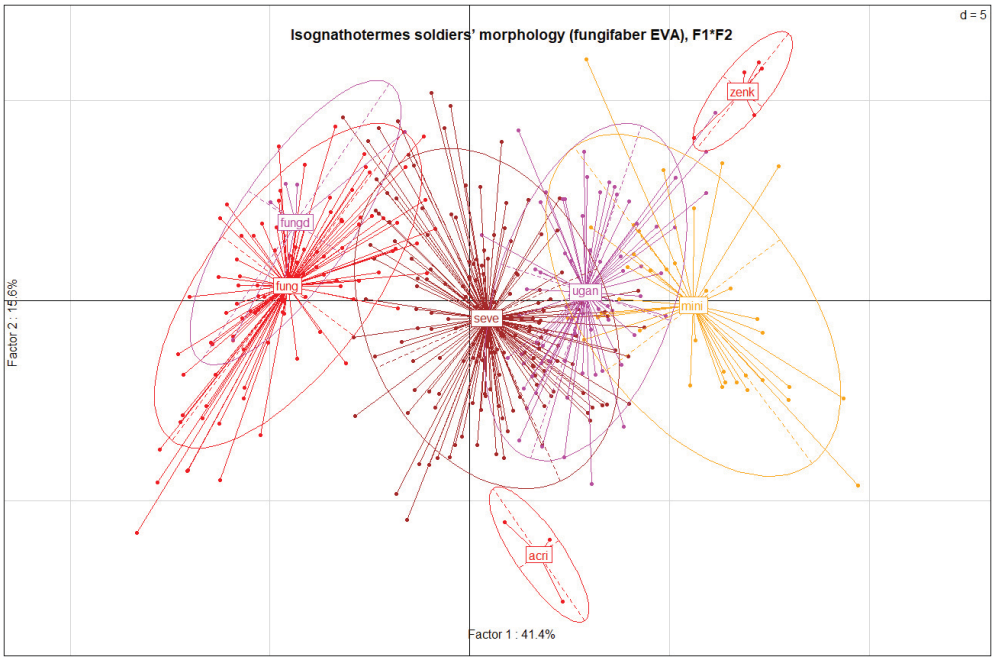


**Fig. 21.** PCA on soldier's morphology involving only the *Isognathotermes* species with a *fungifaber*-type EVA. The first axis is linked to size, the second to mandible curvature and robustness. acri = *I. acristatus* sp. nov.; fung = *I. fungifaber*; fungd = "dubious *I. fungifaber*"; mini = *I. minitabundus*; seve = *I. severus*; ugan = *I. ugandensis*; zenk = *I. zenkeri*. Compared with Fig. 20, the graph is easier to read but there are still a number of significant overlaps.

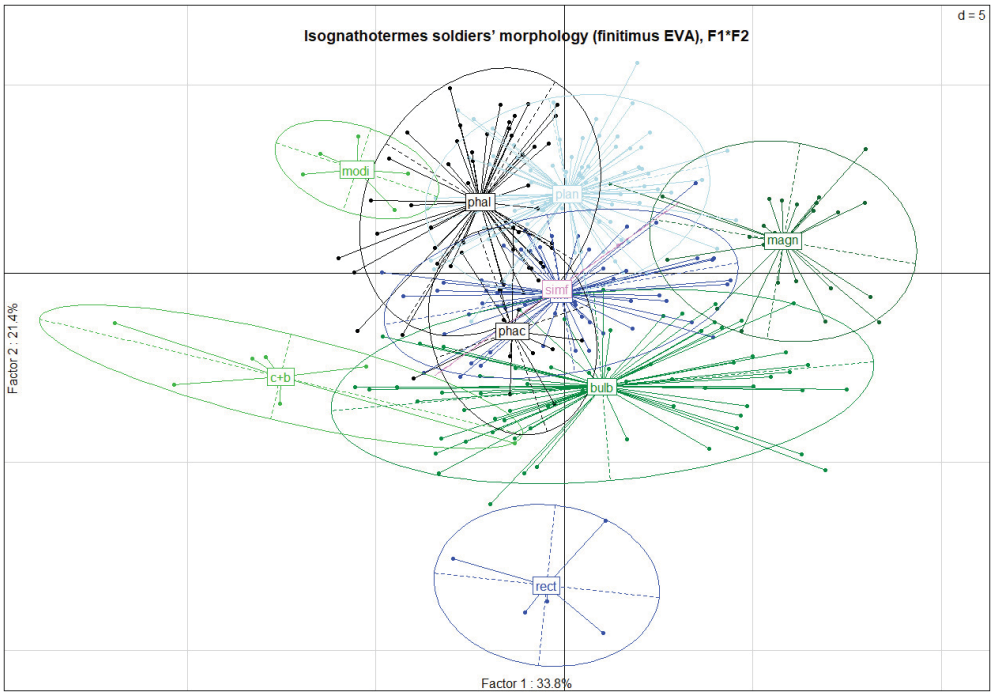


**Fig. 22.** PCA on soldier's morphology involving only the *Isognathotermes* species with a *finitimus*-type EVA; the first axis is linked to size, the second to mandible curvature. bulb = *I. bulbifrons*; c+b = *I. congoensis* + incipient/young colonies of *I. bulbifrons*; fini (this label hidden under the simf label) = *I. finitimus*; magn = *I. magniplanifrons* sp. nov.; modi = *I. modicus* sp. nov.; phac = *I. phallicaecalis* sp. nov.; phal = *I. phalloides* sp. nov.; plan = *I. planifrons*; rect = *I. rectimalatus* sp. nov.; simf = *I. similifinitimus* sp. nov. Compared with Fig. 20, the graph is easier to read but there are still many overlaps, mainly with *I. finitimus* (blue ellipse in the middle).

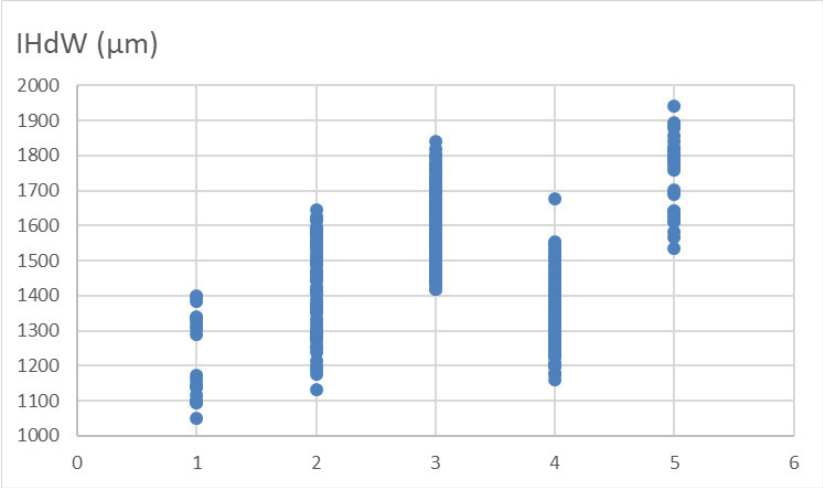


**Fig. 23.** Comparison of the imagines' head widths (in µm) of the genera derived from *Cubitermes* (sensu Wasmann): 1 = *Cubitermes* (sensu Hellemans *et al*. 2021); 2 = *Ternicubitermes*; 3 = *Isognathotermes*; 4 = *Nitiditermes*; 5 = *Polyspathotermes*.

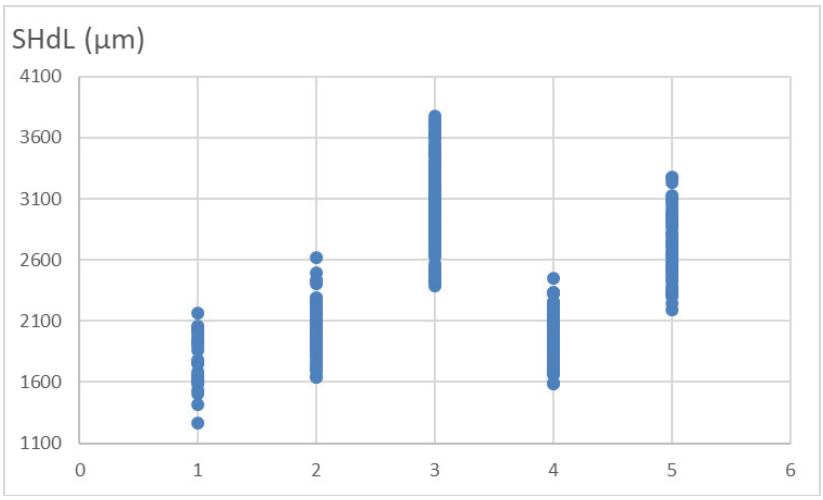


**Fig. 24.** Comparison of the soldiers' head lengths (in µm) of the genera derived from *Cubitermes* (sensu Wasmann 1906): same abscissa as in Fig. 23.

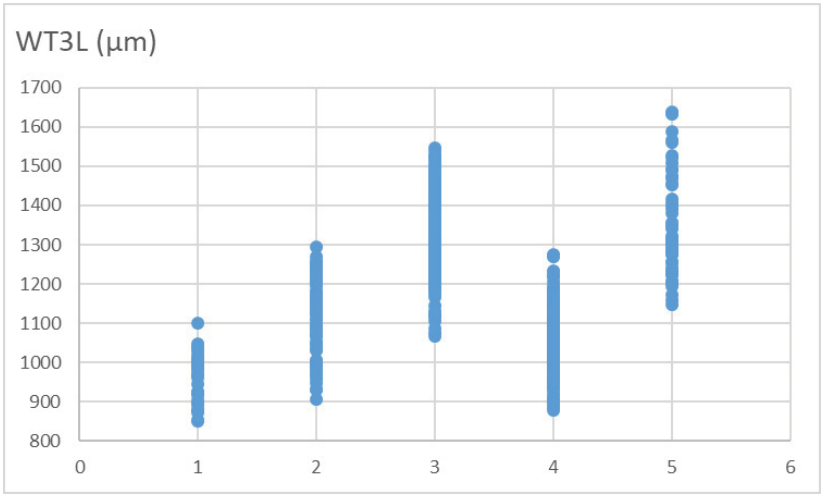


**Fig. 25.** Comparison of the workers' hind tibia lengths (in µm) of the genera derived from *Cubitermes* (sensu Wasmann 1906): same abscissa as in Fig. 23.

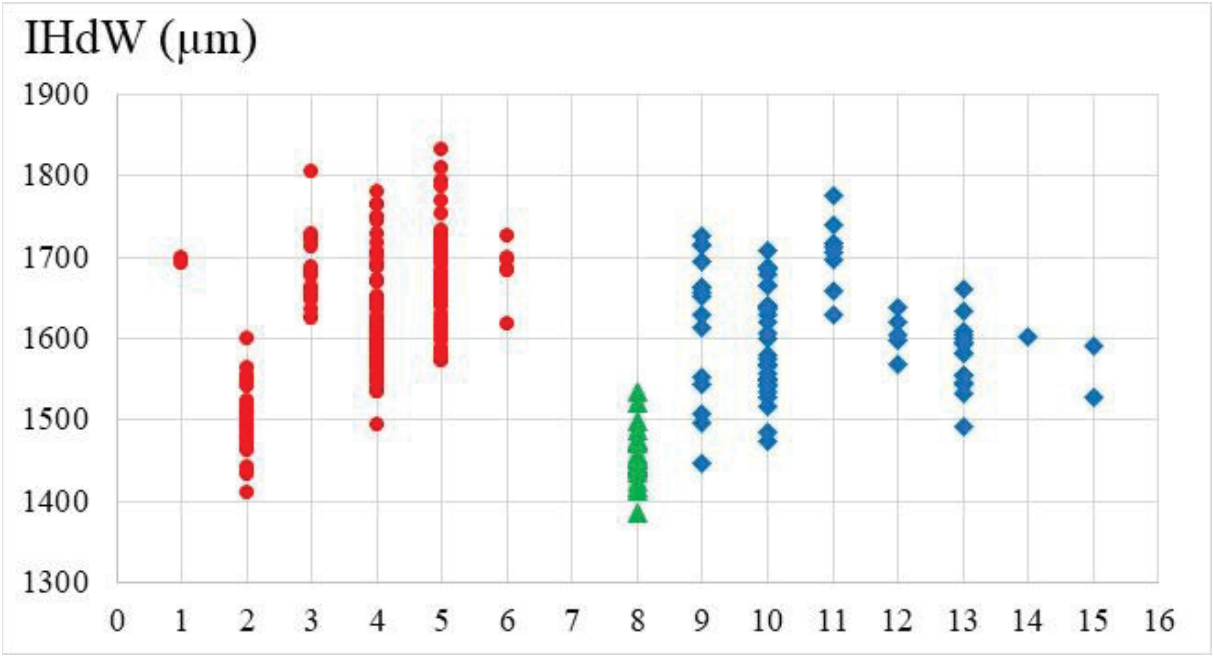


**Fig. 26.** Comparison of imagines' head widths (in µm) in the genus *Isognathotermes* Sjöstedt, 1926. Red circles = species with a *fungifaber* EVA; green triangles = species with a *finitimus* EVA and a phalloid caecum; blue diamond shapes = species with a *finitimus* EVA and a small lobed caecum. 1 = *I. acristatus* sp. nov.; 2 = *I. fungifaber*; 3 = *I. minitabundus*; 4 = *I. severus*; 5 = *I. ugandensis*; 6 = *I. zenkeri*; 7 = *I. phallicaecalis* sp. nov. (imago not available); 8 = *I. phalloides* sp. nov.; 9 = *I. bulbifrons*; 10 = *I. finitimus*; 11 = *I. magniplanifrons* sp. nov.; 12= *I. modicus* sp. nov.; 13 = *I. planifrons*; 14 = *I. rectimalatus* sp. nov.; 15 = *I. similifinitimus* sp. nov.

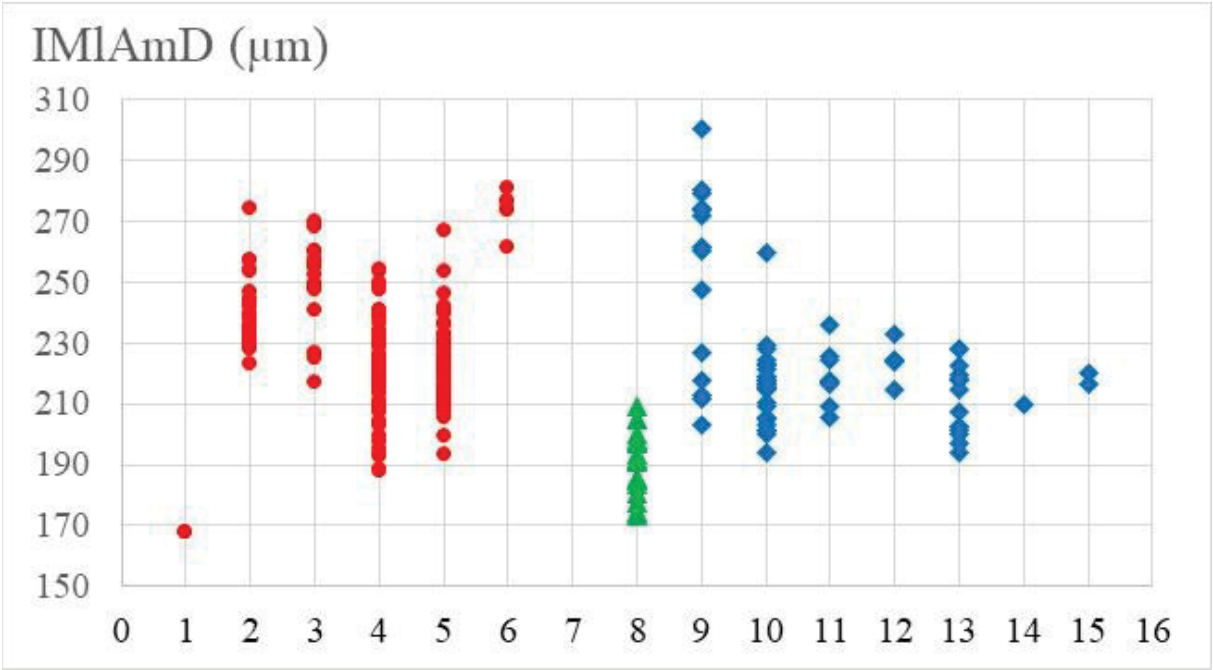


**Fig. 27.** Comparison of imagines' left apico-marginal distances (in µm) in the genus *Isognathotermes* Sjöstedt, 1926; same symbols and same abscissa as in Fig. 26.

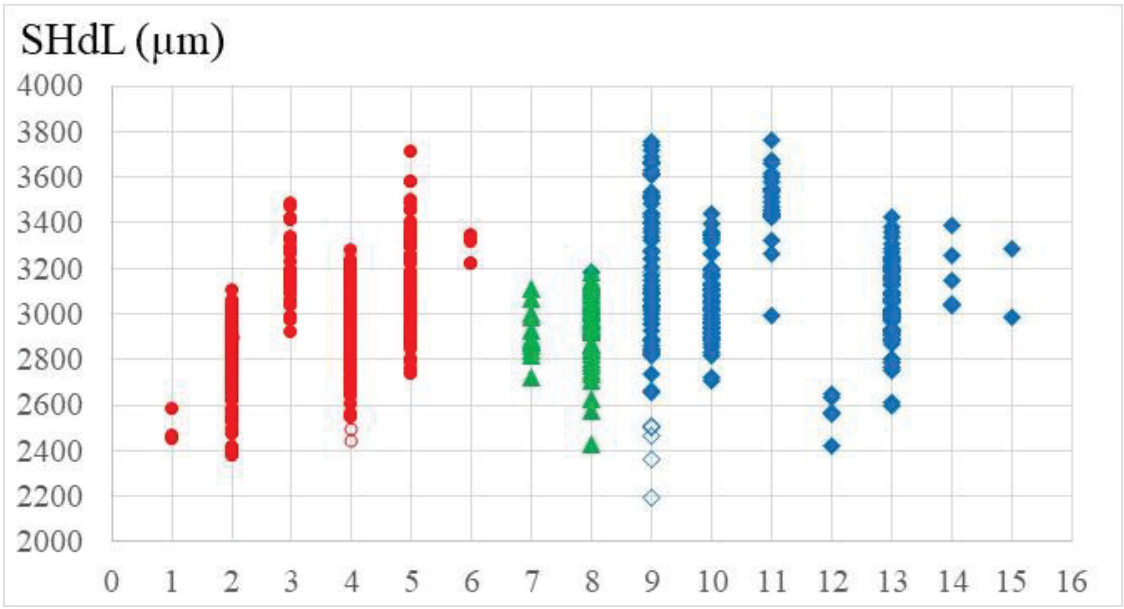


**Fig. 28.** Comparison of soldiers' head lengths (in µm) in the genus *Isognathotermes* Sjöstedt, 1926. Red circles = species with a *fungifaber* EVA; green triangles = species with a *finitimus* EVA and a phalloid caecum; blue diamond shapes = species with a *finitimus* EVA and a small lobed caecum. 1 = *I. acristatus* sp. nov.; 2 = *I. fungifaber*; 3 = *I. minitabundus*; 4 = *I. severus*; 5 = *I. ugandensis*; 6 = *I. zenkeri*; 7 = *I. phallicaecalis* sp. nov.; 8 = *I. phalloides* sp. nov.; 9 = *I. bulbifrons*; 10 = *I. finitimus*; 11 = *I. magniplanifrons* sp. nov.; 12 = *I. modicus* sp. nov.; 13 = *I. planifrons*; 14= *I. rectimalatus* sp. nov.; 15 = *I. similifinitimus* sp. nov.; empty red circles = *I. modestior* (regarded as synonymous with *I. severus*); empty blue diamond shapes = incipient or young colonies of *I. bulbifrons* + *I. congoensis* (considered a possible synonym of *I. bulbifrons*).

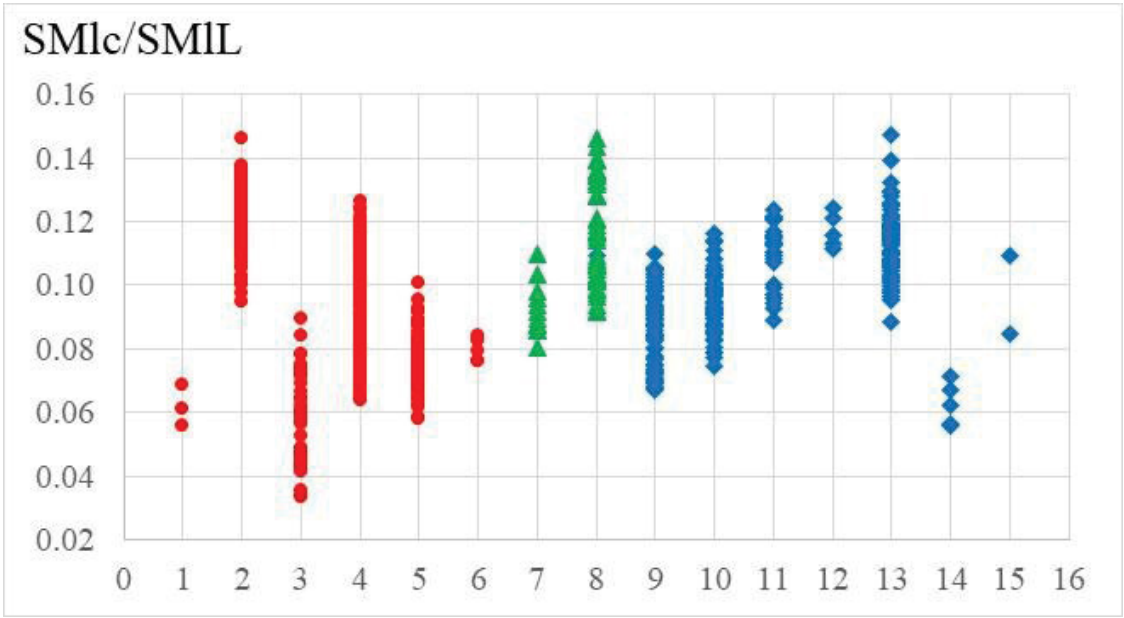


**Fig. 29.** Comparison of soldiers' left mandible apical curvature indices in the genus *Isognathotermes* Sjöstedt, 1926; same symbols and same abscissa as in Fig. 28 but *I. modestior* (regarded as synonymous with *I. severus*) mixed with other *I. severus* and very young colonies of *I. bulbifrons* + *I. congoensis* (considered a possible synonym of *I. bulbifrons*) mixed with other *I. bulbifrons*.

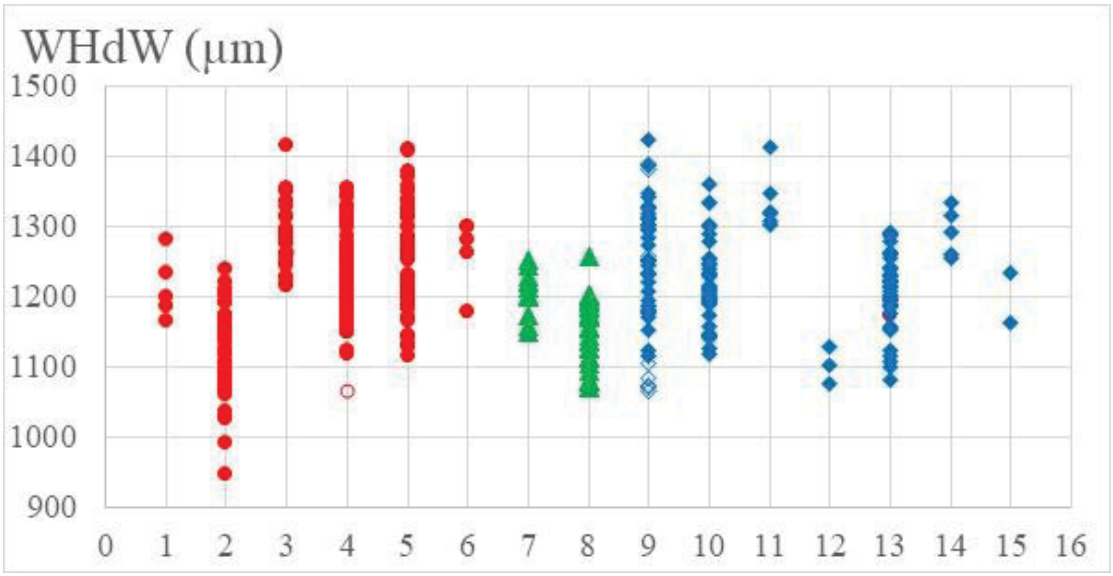


**Fig. 30.** Comparison of workers' head widths (in µm) in the genus *Isognathotermes* Sjöstedt, 1926. Red circles = species with a *fungifaber* EVA; green triangles = species with a *finitimus* EVA and a phalloid caecum; blue diamond shapes = species with a *finitimus* EVA and a small lobed caecum. 1 = *I. acristatus* sp. nov.; 2 = *I. fungifaber*; 3 = *I. minitabundus*; 4 = *I. severus*; 5 = *I. ugandensis*; 6 = *I. zenkeri*; 7 = *I. phallicaecalis* sp. nov.; 8 = *I. phalloides* sp. nov.; 9 = *I. bulbifrons*; 10 = *I. finitimus*; 11 = *I. magniplanifrons* sp. nov.; 12 = *I. modicus* sp. nov.; 13 = *I. planifrons*; 14= *I. rectimalatus* sp. nov.; 15 = *I. similifinitimus* sp. nov.; empty red circles = *I. modestior* (regarded as synonymous with *I. severus*); empty blue diamond shapes = incipient or young colonies of *I. bulbifrons* + *I. congoensis* (considered a possible synonym of *I. bulbifrons*).

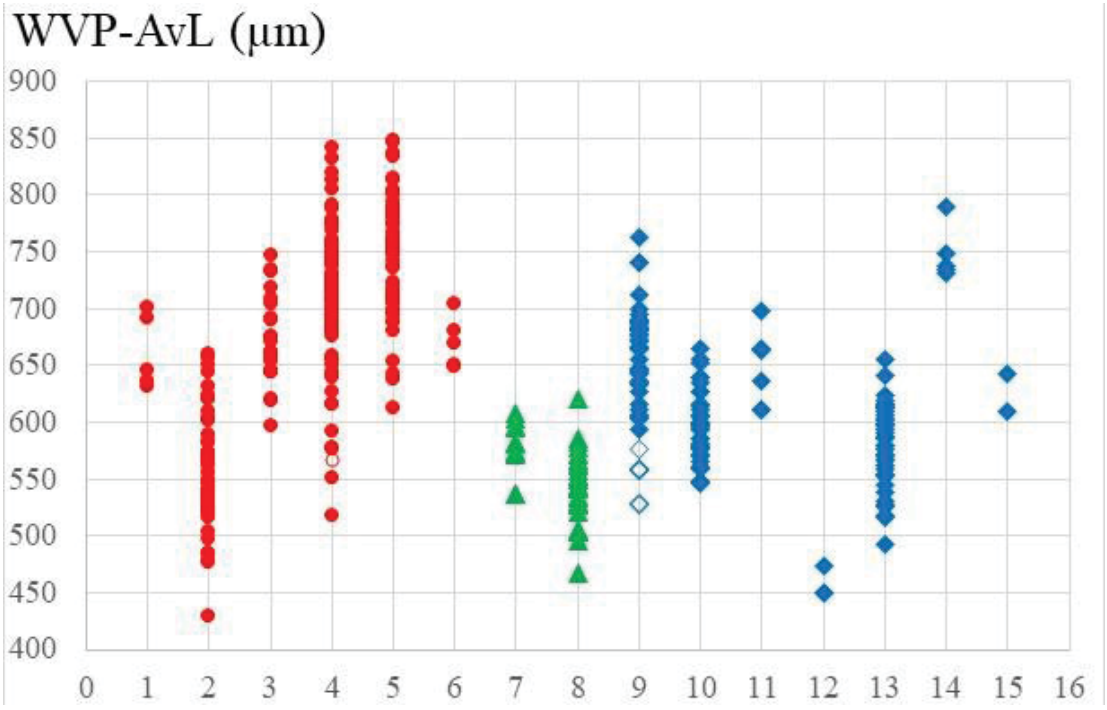


**Fig. 31.** Comparison of workers' average lengths (in µm) of the enteric valve primary cushions (PCs) in the genus *Isognathotermes* Sjöstedt, 1926; same symbols and same abscissa as in Fig. 30.

Ideally, therefore, all three castes should be available for proper identification, bearing in mind that *Isognathotermes* termite mounds, especially older ones, often contain several species and can lead to misidentification.

An initial distinction between *finitimus*–type and *fungifaber*–type EVAs is essential: a Principal Component Analysis (PCA) on the soldiers' morphology involving all the species seems indeed confusing (Fig. 20). However, applying a PCA separately to species with a *fungifaber*–type EVA (Fig. 21) and those with a *finitimus*–type EVA (Fig. 22) results in better (though not yet complete) separation of the species. Nevertheless, it is important to note that creating sub–genera based on EVA types is not feasible because they do not delineate two distinct clades.

Colour does not provide any diagnostic criterion: it depends on both the age of the individual at the time of capture and the time spent in the alcohol before being studied.

**Chorology-ecology**

This genus has been collected in forests and savannahs of West, Central, and East Africa, from Gambia to Kenya and from Angola to Malawi (Fig. 32). The species with a *finitimus* EVA are almost restricted to forested areas of central Africa while the species with a *fungifaber* EVA or an intermediate EVA can be found in forests and savannahs and is therefore present in a much larger area, from west to east equatorial Africa. There are only a few localities where species with *finitimus* and *fungifaber* EVAs coexist (Fig. 32). All species are soil feeders.

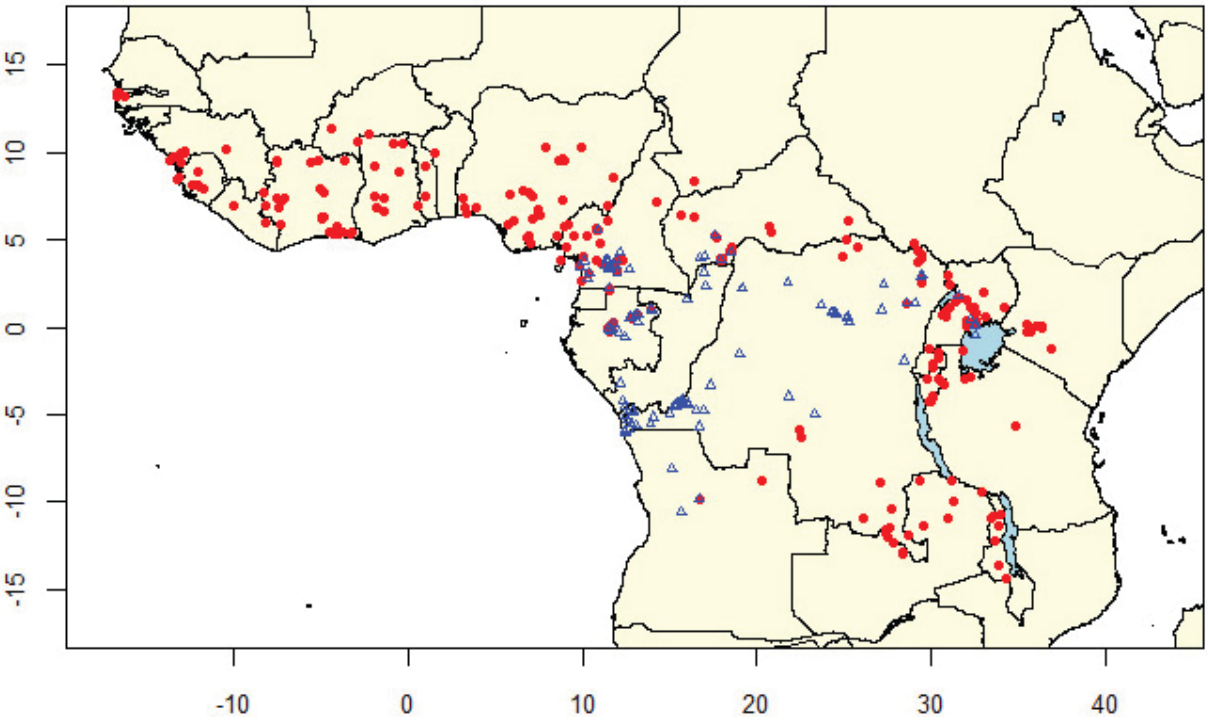


**Fig. 32.** Distribution map of the genus *Isognathotermes* Sjöstedt, 1926: species with a *fungifaber* or an intermediate EVA (red dots), species with a *finitimus* EVA (blue triangles). Note that very few localities host species from both groups together.

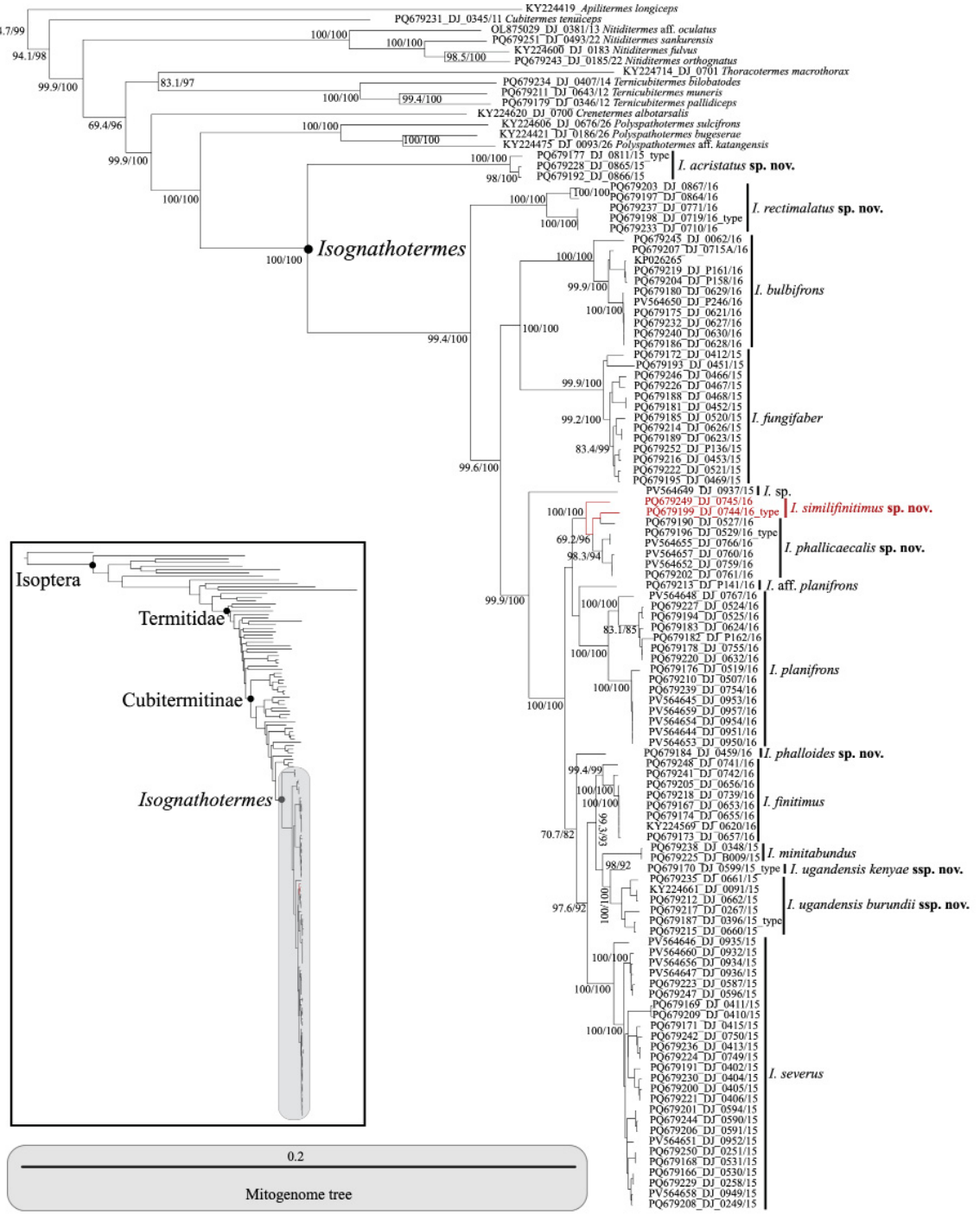


**Fig. 33.** Phylogenetic relationships between species of *Isognathotermes* Sjöstedt, 1926. The tree was reconstructed with IQ-TREE from complete mitogenomes with 41 partitions (see methods). Node support values are Shimodaira-Hasegawa approximate likelihood-ratio/Ultrafast bootstrap (SH-aLRT/UFB). Intra-specific support values on short edges were omitted for clarity. Numbers after the slash in the study code indicate the type of enteric valve (Josens & Deligne 2019): /11 = *bilobatus* pattern; /12 = *muneris* pattern; /13 = *oculatus* pattern; /14 = *bilobatodes* pattern; /15 = *fungifaber* pattern; /16 = *finitimus* pattern; /22 = *sankurensis* pattern; /23 = *oblectatus* pattern; /26 = *sulcifrons* pattern. The mention "type" in the label indicates specimens sequenced from the type series. Red edges and labels indicate the intricate paraphylies of *I. similifinitimus* sp. nov. and *I. phallicaecalis* sp. nov. The complete reconstruction is presented in Supp. file 1.

**Phylogenetic analyses**

Our phylogenetic tree integrates the mitogenomes of 101 samples from the genus *Isognathotermes* (Fig. 33). Mitogenome similarities between all members of *Isognathotermes* are larger than 91.23% (Table ST2). These analyses revealed that the analysed samples belonged to 12 lineages (out of the 15 morphological valid species reported herein), excluding the unidentified species represented by the samples DJ P141 and DJ 0937. All species were monophyletic, with the exception of the intricate paraphylies of *I. similifinitimus* sp. nov. and *I. phallicaecalis* sp. nov. Note that our exclusive use of (maternally-inherited) mitogenomes may have limited our ability to fully resolve the evolutionary relationships among species of *Isognathotermes*.

The 12 species could further be subdivided into five main clades. The first four clades are monospecific, all supported by SHalrt > 99 and UFB = 100, and respectively composed of: the species (i) *I. acristatus* sp. nov.; (ii) *I. rectimalatus* sp. nov.; (iii) *I. bulbifrons*; and (iv) *I. fungifaber*. The fifth clade combines the eight remaining species: *I. severus*, *I. minitabundus*, *I. ugandensis*, *I. finitimus*, *I. phallicaecalis* sp. nov., *I. phalloides* sp. nov., *I. planifrons*, and *I. similifinitimus* sp. nov., While the relationships among species of the first four clades are highly supported (SHalrt > 99 and UFB = 100), the relationships between species of the fifth clade are unresolved.

Interestingly, the clades evidenced from the mitogenomic tree did not perfectly match EVA patterns. While clades I and IV are limited to the *fungifaber* EVA, and clades II and III to the *finitimus* EVA; the last unresolved clade V groups species exhibiting both EVAs.

Additionally, we reconstructed a phylogenetic tree based on the *COII* gene (Supp. file 2) to study the placements of samples from Roy *et al*. (2006) and Hellemans *et al*. (2021) in the herein presented larger sampling of *Isognathotermes*. The *COII* tree included 120 samples of *Isognathotermes*, and recovered similar patterns as the mitogenome-based tree including the paraphyly of *I. similifinitimus* sp. nov. and *I. phallicaecalis* sp. nov. In addition, both *I. phalloides* (DJ 0459) and *I.* aff. *planifrons* (DJ P141) were inserted within *I. severus*. We specifically detail our reanalyses of samples within *I. fungifaber* and *I. planifrons* in their respective sections.

**Identification key**

*Isognathotermes* species show very high intraspecific variability: Figs 26–31 clearly show the extent to which the measurements of different species overlap. In the absence of molecular data, the identification of *Isognathotermes* species thus remains difficult and it was not possible to produce an accurate key based on a single caste. We also remind the reader that several species may live together in the same termite mound, thereby complexifying the identification task. As few selected measures are rarely sufficient to recognise a species, a multidimensional approach (PCA) has been used in this study; however, such multidimensional approach cannot be easily incorporated into a dichotomous key.

The dissection of a worker is essential to recognise its enteric valve and caecum types; precise measurements of soldiers' head and mandible length and curvature (in ventral view) are required as well as geographic origin.

The identification key begins with the genera derived from *Cubitermes* sensu Wasmann (items 1–4) and then gives the species of *Isognathotermes* (items 5–18). Incipient colonies (one or two soldiers with some workers and a non-physogastric queen) are excluded from the key. Abbreviations: see the chapter Material and methods.

1. Worker and soldier: conical fore coxae bearing some fine, soft setae but not any spines or spine-like setae. Imagines: conical fore coxae bearing many soft setae ..... 2
– Worker and soldier: carinated fore coxae bearing some spines or spine-like setae (rarely none in the soldier). Imagines: carinated fore coxae bearing some spine-like setae among many other soft setae ..... 3

2. PCs of the workers valve bearing no more than 3–6 supporting bristles on each side; SCs generally with a heterogeneous scattering of spines (the spines are lacking in some irregular spots). This criterion also applies, albeit less clearly, to soldiers ..... ***Cubitermes*** Wasmann, 1906 (sensu Hellemans *et al.* 2021)
– PCs of the worker's valve bearing 10–30 supporting bristles on each side; SCs with either a homogeneous scattering of the spines, or with a heterogeneous scattering tending towards the shape of a spearhead ..... ***Ternicubitermes*** Josens & Deligne, 2021

3. Worker and soldier EVAs: SCs narrow (not wider or only slightly wider than the PCs). Generally, two PCs ending in a sclerified spatula but, in some samples from West Africa, not any spatula and, in this case, PC1 much longer than the others (WVP1-bil = 1.42–1.62). Soldiers on average smaller: SHdL = 1.55–2.45 mm ..... ***Nititermes*** Emerson, 1960
– Worker and soldier: SCs clearly wider than the PCs; PC1 equal to or somewhat longer than the others (WVP1-bil = 1.00–1.26). Soldiers on average larger: SHdL = 2.05–3.80 mm ..... 4

4. Soldier: triangular or finger-shaped labrum lobes. Worker and soldier EVAs: three to six PCs bearing a sclerified spatula (only sketched in some soldiers)..... ***Polyspathotermes*** Josens & Deligne, 2021
– Soldier: lyre-shaped labrum or with triangular lobes. Worker and soldier EVAs: PCs not spatulated (or sometimes with soft, not sclerified spatulas) ..... 5 ***Isognathotermes*** Sjöstedt, 1926

5. Worker's EVA: odd PCs distally narrowed and crested and bearing strong, long bristles: *fungifaber* EVA, Figs 4, 6, sometimes an intermediate EVA, Fig. 6) but one species, *I. acristatus* sp. nov., with a *bilobatodes* EVA) ..... 6
– Worker's EVA: odd PCs distally barely narrowed, rather swollen and bearing numerous strong, short setae: *finitimus* EVA (Figs 5–6) .....11

6. Sample from regions south or east of the Congolian forests; soldier's left mandible on average less curved (SMlc = 0.08–0.24 mm); asymmetrical curvature of the mandibles: the right is generally more curved than the left (SMlc/SMrc = 0.51–1.03) ..... 7
– Sample from West Africa or regions north of the Congolian forests; soldier's left mandible on average more curved (SMlc = 0.14–0.33 mm); curvature of the mandibles less asymmetrical, SMlc/SMrc = 0.79–1.24) ..... 9

7. Smaller soldier (SHdL = 2.44–2.59 mm); worker's valve with almost non-existent crests on the odd PCs (*bilobatodes* EVA); sample from Angola ..... ***I. acristatus*** Josens & Deligne sp. nov.
– Larger soldier (SHdL = 2.91–3.72 mm); worker's valve with well-developed crests on the odd PCs; sample from a more eastern country ..... 8

8. Two species very difficult to distinguish without sequencing. Sample from East Africa (from Uganda to Northern Zambia: Fig. 49). Four subspecies, only identifiable from imagines, see chapter *I. ugandensis* ..... ***I. ugandensis*** (Fuller, 1923)
– Sample from the DRC (Kasaï–Katanga) or Northern Zambia (Fig. 49)..... ***I. minitabundus*** (Sjöstedt,1913)

9. Soldier with longer mandibles (SMlL = 2.75–2.99 mm in ventral view); sample from Cameroon ..... ***I. zenkeri*** (Desneux, 1904)
– Soldier with shorter mandibles (SMlL = 1.74–2.58 mm) ..... 10

10. Two species sometimes difficult to distinguish without sequencing. On average, smaller soldier (SHdL = 2.37–3.11 mm, ST3L = 1.26–1.67 mm), smaller worker (WHdW = 0.94–1.25 mm), imago of the same size; sample of evergreen forests from southern RCI to Gabon (Fig. 45) ..... ..... ***I. fungifaber*** (Sjöstedt,1896)
– On average, larger soldier (SHdL = 2.43–3.29 mm, ST3L = 1.52–1.93 mm), larger worker (WHdW = 1.06–1.26 mm), imago of the same size; sample from various ecosystems (savannah, orchard, woodland, forest gallery or secondary forest, or from the evergreen forest in RCI near the border with Liberia or from the Lobaye province, CAR); large geographical range across Africa from Gambia to CAR (Figs 45, 49)..... ***I. severus*** (Silvestri, 1914)

11. Soldier's and worker's caecum extended forward in a finger-like process, sometimes swollen, or capped distally (phalloid caecum, Figs 55–56) ..... 12
– Soldier's and worker's caecum rather small, generally with 2–5 short lobes (Fig. 2) sometimes a small amorphous button..... 13

12. Mandibles, on average, less curved SMlc = 0.18–0.26 mm, sample from the evergreen Congolian forest (Congo Republic, Cameroon) ..... ***I. phallicaecalis*** Josens & Deligne sp. nov.
– Mandibles, on average, more curved SMlc = 0.19–0.33 mm, sample from gallery forests in the south-west and west of the DRC of from northern Angola ..... ***I. phalloides*** Josens & Deligne sp. nov.

13. Smaller species (SHdL = 2.42–2.66 mm) from Gabon ..... ***I. modicus*** Josens & Deligne sp. nov.
– Larger species (SHdL = 2.65–3.77 mm) ..... 14

14. Worker's left mandible with a larger apico-marginal distance (WMlAmD = 0.20–0.21 mm), soldier's mandibles, especially the right one, very slightly curved (SMrc = 0.13–0.19 mm, SMrC = 0.20–0.25 mm); sample from Angola ..... ***I. rectimalatus*** Josens & Deligne sp. nov.
– Worker's left mandible generally with a smaller apico-marginal distance (WMlAmD = 0.15–0.22 mm); soldier's mandibles generally more curved (SMrc = 0.16–0.38 mm, SMrC = 0.24–0.49 mm); sample from elsewhere ..... 15

15. Larger species (SHdL = 2.98–3.77 mm) from Haut-Uele or Kivu, DRC ..... ..... ***I. magniplanifrons*** Josens & Deligne sp. nov.
– Generally smaller species (SHdL = 2.60–3.76 mm) from elsewhere ..... 16

16. Soldier's head generally more heavily humped (SHdC = 0.01–0.12 mm); worker's valve with longer secondary cushions (WVS-AvL = 0.47–0.62 mm) ..... ***I. bulbifrons*** (Sjöstedt,1924)
– Soldier's head generally more slightly humped (SHdC = 0.01–0.08 mm); worker's valve with shorter secondary cushions (WVS-AvL = 0.38–0.56 mm) ..... 17

17. Soldier's mandibles somewhat more curved (SMlc = 0.19–0.35 mm); indistinguishable workers and imagines; sample from forests of western-central Africa (Cameroon, CAR, Gabon, Congo and Kongo-Central, DRC, Fig. 47) ..... ***I. planifrons*** (Sjöstedt,1924)
– Soldier's mandibles somewhat less curved (SMlc = 0.16–0.31 mm); indistinguishable workers and imagines; sample from continental forests of central Africa ..... 18

18. Two species indistinguishable without sequencing; sample from the continental forests of Central Africa (CAR, DRC, Uganda, Fig. 38) ..... ***I. finitimus*** (Schmitz, 1915)
– Cryptic species; only one site known to date, south of Kisangani, DRC (Fig. 47) ..... ..... ***I. similifinitimus*** Josens & Deligne sp. nov.

## *Valid species and subspecies*

***Isognathotermes acristatus*** Josens & Deligne sp. nov.
urn:lsid:zoobank.org:act:D984D1ED-5165-427D-9F6F-3AA7D263967C
Figs 26–34, distribution map: Fig. 47; Table 2

### Diagnosis

This species is rather atypical in the genus *Isognathotermes*; the worker is small sized and characterised by its odd PCs without crests but furnished with strong setae at the place where crests would be expected (Fig. 34); it could therefore be confused with a species of *Ternicubitermes* (*bilobatodes* EVA). The PCs carry a low number (5–10) of supporting bristles; it could therefore also be confused with a species of *Cubitermes* (sensu Hellemans *et al.* 2021). However, it has carinated fore coxae bearing 3–4 strong spines (the workers of *Ternicubitermes* and *Cubitermes* have unarmed conical coxae). It is also characterised by a high PC elongation index: WVPOdd-Elg = 9.79–13.6.

The soldier is small sized in the genus *Isognathotermes* and can be recognised by its very weakly curved mandibles (even less curved than those of *I. rectimalatus* sp. nov.): SMlc = 0.11–0.16 mm.

The imago is medium sized in the genus *Isognathotermes* and can hardly be distinguished from *I. severus* or *I. ugandensis ugandensis*. It has larger ocelli than *I. ugandensis* (IOc*D* = 0.20–0.22 mm).

To date, this species is only known from Angola.

### Etymology

The epithet *acristatus*, from Greek α (without) and Latin *cristatus* (crested) refers to the quasi absence of crests on the odd PCs of the enteric valve, even in the worker caste.

### Material examined

Four samples from two locations.

#### Holotype

ANGOLA • soldier; Mussende; 10°33.17′ S, 15°39.492′ E; 25 Oct. 2021; M. Hasson leg.; study code: DJ 0811; GenBank no PQ679177 (mitogenome); BE RMCA INS.Iso.059148.

#### Paratypes

ANGOLA • soldier, worker, ♂ (alate), ♀ (queen); same data as for holotype; BE RMCA INS.Iso.059149.

### Other material examined

ANGOLA • soldier, worker; Cangandala N.P.; 9°49.33′ S, 16°40′ E; 1 Mar. 2019; M. Viage leg.; study code: DJ 0865; GenBank no PQ679228 (mitogenome); BE RMCA INS.Iso.059145 • soldier, worker; Cangandala N.P.; 9°49.33′ S, 16°40′ E; 1 Mar. 2019; M. Viage leg.; study code: DJ 0866; GenBank no PQ679192 (mitogenome); BE RMCA INS.Iso.059147 • soldier, worker; Cangandala N.P.; 9°49.33′ S, 16°40′ E; 1 Mar. 2019; M. Viage leg.; study code: DJ 0868; BE RMCA INS.Iso.059146.

**Historical review**

Specimens of this species were recently collected by two of us (MV & MiH) in Angola; the imago, the soldier, and the worker are described here.

**Description**

**Imago**

Colour. **Head capsule**: well sclerotised and dark (C6); fontanelle slightly (one level) paler. Postclypeus concolorous with head capsule. Antennae C4–C5. **Thorax**: pronotum concolorous with head capsule; meso- and metanotum C4 slightly paler than head. Legs tibia C5 slightly paler than femur C4. **Abdomen**: tergites C5. Sternites appreciably paler in middle (C3) with both sides darker (C5) posterior sternites darker (C4–C5) than anterior.

Setation. **Head capsule**, with some prominent setae set amongst a high density of short, fine setae forming a dense mat. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and shorter ones in middle; meso- and metanotum with some fine, pale setae, arranged in a medio-longitudinal strip, visible at 80×, with some large setae on posterior lobe. **Legs** very pilose, furnished (among numerous fine setae) with 9–10 stronger setae on the carina of fore coxa and 3–4 on the ventral side of fore coxa and 8–9 on trochanter; tibia pilose, fore, mid, and hind tibia furnished with 15–30 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 2, Fig. 34). **Size**: the imagines of *I. acristatus* sp. nov. are medium sized in the genus *Isognathotermes* (Fig. 26). **Head capsule**: compound eyes shortly oval; ocelli rather large (IOcD > 0.20 mm) oval, removed from eyes by a distance equal to 0.8–0.9 ocellus small diameter; fontanelle generally a tiny round or elongate marking. Antennae: 16 articles, shortened to 13 by amputation in queen. Labrum: cupola shaped, wider than long. **Left mandible** with apical tooth small sized in the genus (Fig. 27) and more prominent than first marginal; marginal teeth three in number but second one only suggested by an undulation of edge between first and third marginal teeth; only the apical tooth is acute in unworn specimen; premolar tooth unobstructed and clearly visible in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth always more prominent than first marginal; marginal teeth two in number; second marginal tooth with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut** not studied.

**Soldier**

Colour. **Head capsule** C4–C6. Antennae and labrum concolorous or somewhat paler than head capsule. Mandibles dark (C6–C8) with an abrupt clearing on their bases (two levels) which is generally the same colour as frons. **Thorax** and legs paler than head capsule (C2–C4). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Labrum** with 4–5 large setae on each lobe. **Thorax**: pro- and mesonotum with a small number of setae mainly located on margins. **Legs**: fore coxa with at least one fine seta and 2–6 spines or strong setae on

carina and not any spine on ventral side; trochanter generally with some strong lined-up setae; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively (the latter sometimes weakly developed) and a row of 6–15 spines along their shaft. **Abdomen**: tergites with some large setae, mainly or only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 2, Fig. 34). **Size**: the soldiers of *I. acristatus* sp. nov. is among the small soldiers in the genus *Isognathotermes* (Fig. 28). **Head capsule**: always clearly sclerotised; appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a very slight narrowing near posterior third or fourth; from antennal sockets sides converge towards bases of mandibles; posterior side regularly convex. Slightly to strongly concave **upper profile**; angle between extended mandibles and frons obtuse; frons with a small bump that overhangs the fontanelle. Gulamentum in ventral view constricted in its posterior half, with sides of anterior part smoothly rounded to extended into a kind of angular ears. Antennae: of 14–15 articles. **Labrum**: deeply bifurcate and wider than long, with almost straight sides; rounded lobes without translucent tips; anterior margin concave. **Mandibles**: sabre-like; inner edges smooth with one distinct but small marginal tooth, near molar tooth on each

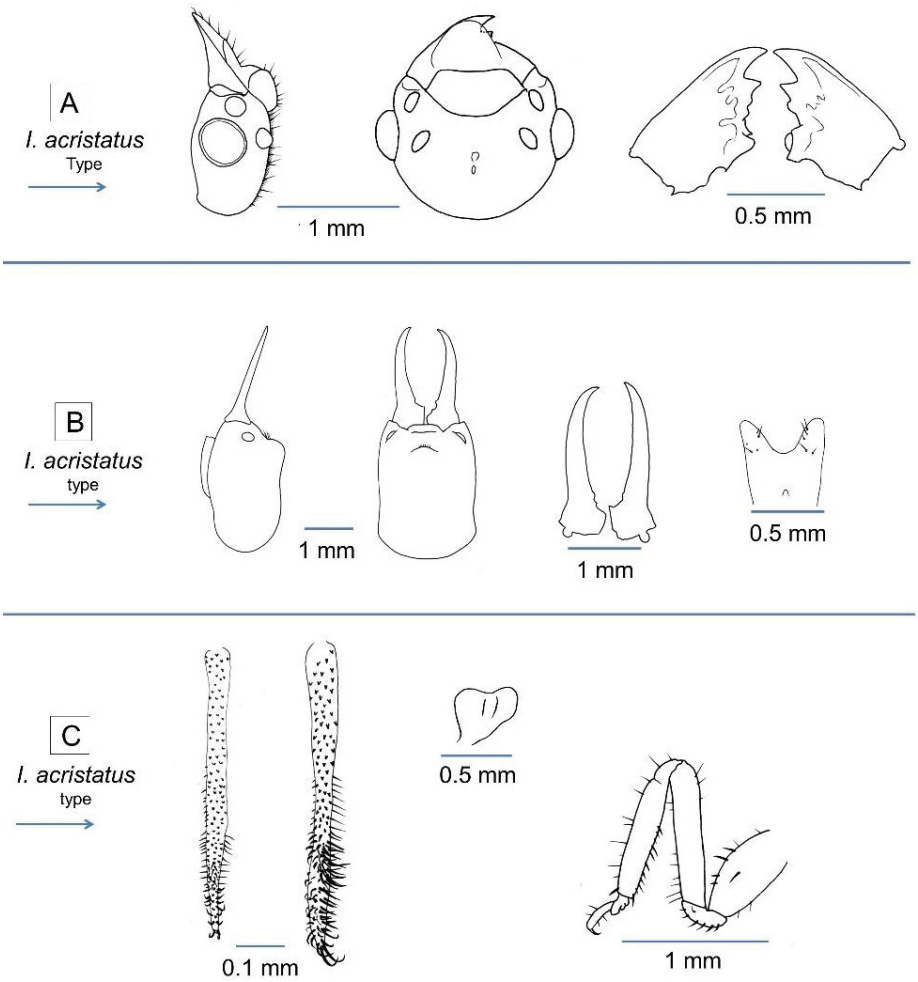


**Fig. 34.** *Isognathotermes acristatus* Josens & Deligne sp. nov.: imago, soldier, and worker. **A**. Lateral and dorsal views of an alate male's head capsule from the *I. acristatus* type colony (DJ 0811), and dorsal view of this imago's mandibles. **B**. Lateral and dorsal views of a soldier's head capsule from the type colony, ventral view of its mandibles, and dorsal view of its labrum. **C**. PC1s of soldier's and worker's enteric valves from the type colony, caecum and foreleg of this worker.

**Table 2.** *Isognathotermes acristatus* Josens & Deligne sp. nov.: ranges of significant measures in the three castes, in alphabetical orders of the "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 2) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.42–0.46 | 0.44 |
| | | Head: width across the eyes | IHdW | 1.69–1.71 | 1.70 |
| | | Left mandible: A-m1 distance | IMlAmD | 0.16–0.17 | 0.17 |
| | | Ocellus: large diameter | IOc*D* | 0.20–0.22 | 0.21 |
| | | Postclypeus: width | IPcW | 0.83–0.85 | 0.84 |
| | | Pronotum: maximal width | IPnW | 1.37–1.43 | 1.40 |
| | | Hind tibia: length | IT3L | 1.84–2.02 | 1.94 |
| | | Wing: length (n = 1) | IWgL | 17.2 | 17.2 |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 0.93–1.01 | 0.97 |
| Soldiers (n = 4) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.04–0.08 | 0.07 |
| | | Head: length | SHdL | 2.44–2.59 | 2.58 |
| | | Head: width | SHdW | 1.78–1.94 | 1.93 |
| | | Left mandible: lesser sagitta | SMlc | 0.11–0.16 | 0.13 |
| | | Left mandible: ventral length | SMlL | 2.15–2.22 | 2.18 |
| | | Hind tibia: length | ST3L | 1.50–1.62 | 1.62 |
| | Indices | Head elongation index | SHdL/SHdW | 1.32–1.38 | 1.34 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.06–0.07 | 0.06 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.65–0.76 | 0.76 |
| Workers (n = 5) | Raw measures (mm) | Head: width | WHdW | 1.16–1.29 | 1.24 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.13–0.17 | 0.14 |
| | | Left mandible: total length | WMlL | 0.53–0.58 | 0.56 |
| | | Hind tibia: length | WT3L | 1.22–1.31 | 1.30 |
| | | Valve: PC average length | WVP-AvL | 0.63–0.70 | 0.65 |
| | | Valve: PC average width | WVP-AvW | 0.05–0.07 | 0.06 |
| | | Valve: SC average length | WVS-AvL | 0.49–0.64 | 0.50 |
| | | Valve: SC average width | WVS-AvW | 0.29–0.33 | 0.29 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 9.79–13.6 | 12.7 |

* Abbreviations: see definitions in Material and methods.

mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. **Mandibles** very slightly curved, among the least curved in the genus. Right mandible slightly more curved than left. **Thorax**: pronotum sellate, as wide as 52 to 56% of head width, with straight anterior and posterior margins. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in second half of abdomen. **Caecum** rather small, best seen in ventral view, near centre of abdomen, three- to four-lobed. Arrangement of enteric valve cushions showing trilateral symmetry, the odd cushions narrow and longer than the even ones (as in the *muneris* EVA).

**Worker**

Colour. **Head capsule** pale (C2–C3). Antennae: proximal articles pale (C2), distal articles two levels darker (C4). **Thorax**, nota, and legs pale (C2–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect, scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50 × or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa carinated, bearing one fine seta and furnished with 3–4 spines on carina and 1–3 on ventral side; fore trochanter with 6 lined up spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of 7–15 spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 2, Fig. 34). **Size**: the workers of *I. acristatus* sp. nov. are medium sized in the genus *Isognathotermes*.(Fig. 30). **Head capsule**: weakly sclerotised (except mandibles). Antennae: 14–14.5 articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed but shorter than in most other species; marginal teeth three in number, first marginal well developed but with a blunt tip even when fresh, second marginal faint (visible as an undulated edge and disappearing in worn mandibles), third marginal with a blunt tip; premolar tooth unobstructed and clearly visible in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal well developed with a sharp tip when fresh; second marginal smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as about 63% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions of the *muneris* pattern with triradial symmetry: the odd PCs, in their downstream part, are narrow and bear strong, bent setae; supporting bristles are few: 5–10 on each side of the odd PCs; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum rather small, visible in ventral view, near centre of abdomen, shortly lobed (3–4 small lobes).

**Chorology-ecology**

This species is only known from Angola, its geographic distribution (Fig. 47) is linked with the Angolan Miombo woodland ecoregion.

**Molecular data**

Mitogenomes of *I. acristatus* sp. nov. (three samples) exhibit less than 1% dissimilarity with each other (Supp. file 4: GenBank accessions: see supplementary Supp. file 3 and 'Material examined'), and much more with other species. The species *acristatus* is found sister–group to all other *Isognathotermes* species (Fig. 33); its atypical EVA -very simple and comparable to the EVA of *Cubitermes* or *Ternicubitermes*- may represent the ancestral state of this genus' EVA.

***Isognathotermes bulbifrons*** (Sjöstedt, 1924)
Figs 26–31, 33, 35–37, distribution map: Fig. 38; Table 3

*Cubitermes bulbifrons* Sjöstedt, 1924b: 256 (soldier only).
*Cubitermes heghi* Sjöstedt, 1924b: 255.
*Cubitermes gibbifrons* Sjöstedt, 1924b: 255. **Syn. nov**.
*Mirotermes* (*Cubitermes*) *kemneri* Emerson, 1928: 509, fig. 54. **Syn. nov**.

*Cubitermes bulbifrons* – Sjöstedt 1926: 247–248 (all castes). — Snyder 1949: 157. — Ruelle 1975: 7. — Krishna *et al.* 2013: 1916–1917. — Josens & Deligne 2019: 60–61.
*Cubitermes heghi* – Sjöstedt 1926: 249, pl 9 fig. k. — Ruelle 1992: 500.

*Mirotermes* (*Cubitermes*) *heghi* – Emerson 1928: 511–513, fig. 56.
*Mirotermes* (*Cubitermes*) *congoensis* – Emerson 1928: 519–520, fig. 61, as possible synonym?
*Cubitermes* sp. affinis *subarquatus* "spC" – Roy *et al.* 2006: 4–5. **Syn. nov**.
*Isognathotermes bulbifrons* – Hellemans *et al.* 2021: 233.

**Diagnosis**

The individuals of this species come in two forms, one medium sized (previously called *I. gibbifrons*) and a large one (previously called *I. bulbifrons*) (Fig. 72); these two species are here synonymised on the basis of chorological-ecological data and the sequencing of their mitogenomes.

The worker has a *finitimus* EVA (Fig. 5) and is among the medium sized to the largest workers of the genus *Isognathotermes* (Fig. 30; WHdW = 1.11–1.43 mm) it can hardly be distinguished from the workers of other species which have the same kind of EVA.

The soldier has generally a recognizable *finitimus* EVA; it is among the medium to the largest sized soldiers of the *Isognathotermes* species with a *finitimus* EVA (SHdL = 2.65–3.76 mm; Figs 28–29), with less curved mandibles (SMlc = 0.14–0.31 mm) than *I. magniplanifrons* sp. nov. As it is suggested by its name, its head is bulbous: the upper profile is moderately to strongly concave (SHdC = 0.01–0.12 mm), on average, clearly more than that of *I. magniplanifrons* (but this is shared with *I. severus*, *I. minitabundus*, and *I. ugandensis* which have *fungifaber* EVAs).

The imago is among the medium to the largest sized imagines in the genus *Isognathotermes* with a *finitimus* EVA, (IHdW = 1.44–1.73 mm); the larger ones can be confused with the imago of *I. magniplanifrons* sp. nov. Its mandibular apico-marginal distance is clearly larger (IMlAmD = 0.20–0.30 mm) than in any other *Isognathotermes* species with a *finitimus* EVA (Fig. 27). Some samples could be confused with *I. finitimus* (same size, mandibles of *I. bulbifrons* less curved than in *I. finitimus*) or with *I. phallicaecalis* sp. nov. that has a different caecum.

This species is also defined by its ecology: all known samples come from forested regions up to about 300 km from the Atlantic coast (Fig. 38).

**Etymology**

The name *bulbifrons* from the Latin *bulbus* (onion) and *frons* (forehead) refers to the fact that the frons of the soldier viewed from the side is distinctly bulbous, as Sjöstedt pointed out in the original description.

**Material examined**

Sixty-five samples from 23 locations (and four incipient or young colonies from one location). Of the 55 old museum samples examined, three were initially labelled as *Cubitermes bulbifrons*, five as *C. gibbifrons*, 14 as *C. heghi*, one as *C. kemneri*, two as *C. subarquatus*, one as *C fungifaber*, 17 as *Cubitermes* sp., and five as *Cubitermes* 2, and seven were not identified. Of the four incipient or young colonies, two were labelled as *C. gaigei* and two as *C. heghi*. This species also includes six samples of *C.* aff. *subarquatus* "spC" (in Roy *et al.* 2006).

**Paratypes of *Cubitermes bulbifrons* Sjöstedt, 1924**
DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker; Mukimbungu; 5°8.5′ S, 14°2.3′ E; ca 1904; K.E. Laman leg.; study code: DJ 0298; initially *C. bulbifrons*; AMNH.

**Syntypes of *Cubitermes gibbifrons* Sjöstedt, 1924**
DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker; Mukimbungu; 5°8.5′ S, 14°2.3′ E; ca 1904; K.E. Laman leg.; study code: DJ 0280; initially *C. gibbifrons*; NHMM.

**Paratypes from type colony of *Cubitermes heghi* Sjöstedt, 1924**
DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker; Mukimbungu; 5°8.5′ S, 14°2.3′ E; ca 1904; K.E. Laman leg.; study code: DJ 0290; initially *C. heghi* → *C. bulbifrons*; AMNH.

**Paratypes from type colony of *Mirotermes* (*Cubitermes*) *kemneri* Emerson, 1928**
CAMEROON • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0297; initially *C. kemneri*; AMNH.

**Other material examined**

ANGOLA • soldier, worker; Quimucanda; 8°5.14′ S, 15°7.43′ E; 27 Nov. 2024; J. Šobotnik leg.; study code: DJ 0970; BE RMCA INS.Iso.059892.

CAMEROON • soldier, worker, ♀ (queen); Edea; 3°29′ N, 9°50′ E; [no date, around 1912]; from J. Bequaert collection; study code: DJ 0610; initially *C. bulbifrons*; AMNH • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0109; initially *C. heghi* in RMCA; BE RMCA INS.Iso.059152 • soldier, worker, ♀ (alate); Mbalmayo; 3°31′ N, 11°30′ E; 17 Oct. 1962; G. Becker leg.; study code: DJ 0723; initially *C. heghi*; NHMUK • soldier; Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ U120; initially *C. heghi*; NHMUK 13671911 • soldier; Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ U122; initially *C. heghi*; NHMUK 13671907 • soldier, worker, ♀ (alate); Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ 0727; initially *C. heghi*; NHMUK • soldier, worker, ♀ (queen); Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ 0725; initially *C. heghi*; NHMUK • soldier, worker, ♂ (king), ♀ (queen); Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ 0726; initially *C. heghi*; NHMUK • soldier, ♀ (queen); Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ U104; initially *C. gaigei*; NHMUK 13671901 • soldier, ♀ (queen); Edea; 3°48′ N, 10°8′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ U109; initially *C. gaigei*; NHMUK 13671899 • soldier, worker; Kala; 3°51′ N, 11°22′ E; 27 Apr. 1992; A. Dejean leg.; study code: DJ 0063; initially *C. subarquatus* in RMCA; BE RMCA INS.Iso.059154 • soldier, worker; Nkolbisson (Yaoundé); 3°52.25′ N, 11°27.25′ E; 20 Jun. 1992; A. Dejean leg.; study code: DJ 0062; GenBank no PQ679245 (mitogenome); initially *C. subarquatus* in RMCA; BE RMCA INS.Iso.059153 • soldier, worker; Akok; 2°47′ N, 10°17′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ 0714; initially *C. bulbifrons*; NHMUK 13671835 • soldier, worker; Bilik; 3°31′ N, 11°17′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ 0706; initially *C. heghi*; NHMUK 13671839 • soldier; Ebogo; 3°31′ N, 11°30′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U094; initially *C. heghi*; NHMUK 13671838 • soldier; Ebogo; 3°31′ N, 11°30′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U095; initially *C. heghi*; NHMUK 13671842 • soldier; Eboufek; 3°31′ N, 11°30′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U098; initially *C. heghi*; NHMUK 13671843 • soldier, worker, ♀ (queen); Eboufek; 3°30′ N, 11°53′ E; ca 1995; P. Eggleton *et al*. leg.; study code: DJ 0715; GenBank no PQ679207 (mitogenome); initially *C. heghi*; NHMUK 13671836 • soldier, worker; Mbalmayo; 3°31′ N, 11°30′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ 0713; initially *C. heghi*; NHMUK 13671837 • soldier, worker; Mbalmayo; 3°31′ N, 11°30′ E; Apr. 1996; P. Eggleton *et al.* leg.; study code: DJ 0712; initially *C. heghi*; NHMUK 13671840 • soldier, worker; Mbalmayo; 3°25.1′ N, 11°27.1′ E; 17 Apr. 2015; J. Šobotnik leg.; study code: DJ 0253; BE RMCA INS.Iso.059151 • soldier; Ejokou; 3°20′ N, 11°27′ E; 12 Mar. 2018; J. Šobotnik leg.; study code: DJ 0968; BE_RMCA_INS. Iso.059947.

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker; Luali; 5°6′ S, 12°29′ E; 26 Aug. 1912; J. Bequaert leg.; study code: DJ 0058; initially *C. fungifaber* in RMCA; BE RMCA INS.Iso.059234 • soldier, worker; Luali; 5°6′ S, 12°29′ E; 26 Aug. 1913; J. Bequaert leg.; study code: DJ 0614; initially *C. gibbifrons*; AMNH • soldier; Sona Pangu; 5°30′ S, 13°55′ E; 9 Apr. 1948; A. Emerson leg.; study code: DJ U117; initially *C. gibbifrons*; NHMUK 13671905 • soldier, worker, ♂ (king), ♀ (queen); Sona Pangu; 5°30′ S, 13°55′ E; 9 Apr. 1948; A. Emerson leg.; study code: DJ 0615; initially *C. gibbifrons*; AMNH • soldier, worker; Luki; 5°39′ S, 13°4′ E; 19 Apr. 1965; A. Bouillon leg.; study code: DJ 0890;

initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059229 • soldier; Luki; 5°39′ S, 13°4′ E; 20 Sep. 1965; G. Mathot leg.; study code: DJ B280; initially *Cubitermes* sp. in RMCA; BE RMCA INS. Iso.059218 • soldier; Luki; 5°39′ S, 13°4′ E; 20 Sep. 1965; G. Mathot leg.; study code: DJ B281; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059219 • soldier; Luki; 5°39′ S, 13°4′ E; 20 Sep. 1965; G. Mathot leg.; study code: DJ B284; initially *Cubitermes* 2 in RMCA; BE RMCA INS.Iso.059222 • soldier; Luki; 5°39′ S, 13°4′ E; 20 Sep. 1965; G. Mathot leg.; study code: DJ B288; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059224 • soldier; Luki; 5°39′ S, 13°4′ E; 20 Sep. 1965; G. Mathot leg.; study code: DJ B289; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059216 • soldier, worker; Luki; 5°39′ S, 13°4′ E; 20 Sep. 1965; A. Bouillon (?) leg.; study code: DJ 0176; BE RMCA INS. Iso.059225 • soldier, worker; Luki; 5°39′ S, 13°4′ E; 20 Sep. 1965; G. Mathot leg.; study code: DJ 0888; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059226 • soldier, worker; Luki; 5°39′ S, 13°4′ E; 20 Sep. 1965; G. Mathot leg.; study code: DJ 0889; initially *Cubitermes* sp. in RMCA; BE RMCA INS. Iso.059227 • soldier, worker, ♀ (queen); Luki; 5°39′ S, 13°4′ E; 20 Sep. 1965; G. Mathot leg.; study code: DJ 0915; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059231 • soldier, worker, ♀ (queen); Luki; 5°39′ S, 13°4′ E; 20 Sep. 1965; G. Mathot leg.; study code: DJ 0916; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059232 • soldier; Mbamba Kilenda; 4°55′ S, 15°30′ E; 19 Oct. 1966; C. Nkakala leg.; study code: DJ B311; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059150 • soldier; Luki; 5°39′ S, 13°4′ E; 1 Apr. 1971; A. Bouillon leg.; study code: DJ B278; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059214 • soldier; Luki; 5°39′ S, 13°4′ E; 1 Apr. 1971; A. Bouillon leg.; study code: DJ B279; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059215 • soldier, worker, ♂ (king); Kai Tshianga; 5°51.5′ S, 12°42′ E; 2 Apr. 1971; A. Bouillon leg.; study code: DJ 0917; initially *Cubitermes* 2 in RMCA; BE RMCA INS.Iso.059233 • soldier; Kai-Tshianga; 5°52′ S, 12°42′ E; 2 Apr. 1971; A. Bouillon leg.; study code: DJ B305; initially *Cubitermes* 2 in RMCA; BE RMCA INS.Iso.059217 • soldier; Kai-Tshianga; 5°52′ S, 12°42′ E; 2 Apr. 1971; A. Bouillon leg.; study code: DJ B306; initially *Cubitermes* 2 in RMCA; BE RMCA INS.Iso.059220 • soldier; Kai-Tshianga; 5°52′ S, 12°42′ E; 2 Apr. 1971; A. Bouillon leg.; study code: DJ B307; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059223 • soldier, worker; Kai-Tshianga; 5°52′ S, 12°42′ E; 2 Apr. 1971; A. Bouillon leg.; study code: DJ 0892; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059228 • soldier; Kiemi; 5°32′ S, 12°49′ E; 2 Apr. 1971; A. Bouillon leg.; study code: DJ B310; initially *Cubitermes* 2 in RMCA; BE RMCA INS.Iso.059221 • soldier, worker; Kiemi; 5°16′ S, 12°34′ E; 2 Apr. 1971; A. Bouillon leg.; study code: DJ 0893; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059230.

GABON • soldier; Mekambo; 1°0.4′ N, 13°56′ E; Jan. 1957; P.-P. Grassé and C. Noirot leg.; study code: DJ P158; GenBank no PQ679204 (mitogenome); MNHN EP9829 • soldier; Piste du Bouéni; 0°20′ N, 13°11′ E; Jan. 1957; P.-P. Grassé and C. Noirot leg.; study code: DJ P170; MNHN EP9831 • soldier; route Makokou–Booué; 0°35′ N, 12°45′ E; Jan. 1957; P.-P. Grassé and C. Noirot leg.; study code: DJ P161; GenBank no PQ679219 (mitogenome); MNHN EP9830 • soldier; Piste du Bouéni; 0°44′ N, 13°12′ E; Jan. 1957; P.-P. Grassé and C. Noirot leg.; study code: DJ P160; MNHN EP9881 • soldier; Piste du Bouéni, km 53; 0°44′ N, 13°12′ E; Jan. 1957; P.-P. Grassé and C. Noirot leg.; study code: DJ P165; MNHN EP9882 • soldier, worker; Route Makokou–Mekambo; 0°41′ N, 13°2′ E; 24 Mar. 1962; J. Pasteels leg.; study code: DJ 0722; initially *C. heghi*; NHMUK • soldier, worker; Simintang; 0°34′ N, 12°42′ E; 16 Apr. 1962; J. Deligne leg.; study code: DJ 0721; initially *C. heghi*; NHMUK • soldier; Forêt des Abeilles; 0°19′ S, 12°7′ E; 1995; C. Bordereau (?) leg.; study code: DJ P215; MNHN EP9828 • soldier; La Lopé N.P.; 0°15′ S, 11°35′ E; 7 Mar. 1998; M. Harry leg.; study code: DJ P246; GenBank no PV564650 (mitogenome); MNHN EP9883 • soldier, worker; La Lopé N.P.; 0°15′ S, 11°35′ E; 9 Mar. 1998; M. Harry leg.; study code: DJ 0621; GenBank nos DQ246543 (*COII*) DQ246533 (*ITS2*) PQ679175 (mitogenome); initially *C.* aff. *subarquatus* "spC" (cf. Roy *et al.* 2006); MNHN EP9834 • worker; La Lopé N.P.; 0°12.7′ S, 11°33.5′ E; 9 Mar. 1998; M. Harry leg.; study code: DJ 0627; GenBank nos DQ127304 (*COII*), DQ246537 (*ITS2*), PQ679232 (mitogenome); initially *C.* aff. *subarquatus* "spC" (cf. Roy *et al.* 2006); MNHN EP9835 • soldier, worker; La Lopé N.P.; 0°15′ S, 11°35′ E; 9 Mar. 1998; M. Harry leg.; study code: DJ 0628; GenBank nos DQ127303 (*COII*), DQ246531 (*ITS2*), PQ679186

(mitogenome); initially *C.* aff. *subarquatus* "spC" (cf. Roy *et al.* 2006); MNHN EP9836 • soldier, worker; La Lopé N.P.; 0°16.7′ S, 11°33′ E; 9 Mar. 1998; M. Harry leg.; study code: DJ 0922; MNHN EP9832 • soldier, worker; La Lopé N.P.; 0°16.7′ S, 11°33′ E; 11 Mar. 1998; M. Harry leg.; study code: DJ 0629; GenBank nos DQ127307 (*COII*), DQ246534 (*ITS2*), PQ679180 (mitogenome); initially *C.* aff. *subarquatus* "spC" (cf. Roy *et al.* 2006); MNHN EP9837 • soldier, worker; La Lopé N.P.; 0°12.7′ S, 11°33.5′ E; 13 Mar. 1998; M. Harry leg.; study code: DJ 0630; GenBank nos DQ246544 (*COII*), DQ246535 (*ITS2*), PQ679240 (mitogenome); initially *C.* aff. *subarquatus* "spC" (cf. Roy *et al.* 2006); MNHN EP9838 • soldier, worker; La Lopé N.P.; 0°12.7′ S, 11°33.5′ E; 13 Mar. 1998; M. Harry leg.; study code: DJ 0631; GenBank nos DQ127306 (*COII*), DQ246536 (*ITS2*); initially *C.* aff. *subarquatus* "spC" (cf. Roy *et al.* 2006); MNHN EP9839 • soldier, ♂ (king); La Lopé N.P.; 0°15′ S, 11°35′ E; 16 Mar. 1998; M. Harry leg.; study code: DJ P239; MNHN EP9833.

**Historical review**

The soldier alone was first described shortly as *Cubitermes bulbifrons* by Sjöstedt (1924b: 256) on a sample from Mukimbungu, DRC; all castes were subsequently described in Sjöstedt (1926: 247–248) on a sample from Gabon. In the same papers, Sjöstedt (1924b: 255) described shortly the soldier of *Cubitermes heghi*, whose soldier and worker he described with more details (1926: 249) on a sample from Mukimbungu, DRC. He considered both species as very similar, *C. bulbifrons* being somewhat larger than *C. heghi*. Sjöstedt (1926: 221–226) included both species in a key of the *Cubitermes* soldiers and inserted them in a "*bulbifrons*-Gruppe" of species with an upwards humped frons. He also included *C. bulbifrons* in a key of the imagines (Sjöstedt 1926: 218–220).

Snyder (1949: 157) catalogued *Cubitermes bulbifrons* and *C. heghi* in the sub-family Termitinae.

Ruelle (1975: 7) established *C. heghi* as a junior synonym of *C. bulbifrons*; however, Ruelle (1992: 500), changed his mind and established *C. bulbifrons* as a junior synonym of *C. heghi* for a reason of page priority. Krishna *et al.* (2013: 1916) housed *Cubitermes bulbifrons* in the sub-family Cubitermitinae; espousing the view of Ruelle (1975) but contesting the reversal of precedence proposed by Ruelle (1992), they therefore considered this species as the senior synonym of *C. heghi*. Synonymy of the two species is compatible with their enteric valve morphology, as both species belong to the same *finitimus* valve group (Josens & Deligne 2019: 42–44).

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

*Cubitermes* aff. *subarquatus* "spC", mentioned by Roy *et al.* (2006) in La Lopé National Parc, Gabon was considered a cryptic species on a genetical base. Hellemans *et al.* (2021: 231) placed it in the restored genus *Isognathotermes* and maintained its cryptic status. But with the recent sequencing of several samples of *I. bulbifrons* (not available in 2021), it turned out that *C.* aff. *subarquatus* "spC" must become a junior synonym of *I. bulbifrons*.

*Mirotermes* (*Cubitermes*) *kemneri* was described by Emerson (1928: 509); this species was synonymized with *C. zenkeri* by Ruelle (1975: 8; 1992: 501). However, the EVAs do not support this synonymy (Josens & Deligne 2019: 42–44, 62). *Cubitermes kemneri* is proposed, here, as a junior synonym of *I. bulbifrons*.

Despite the difference in size, recent sequencing of the mitogenomes confirmed synonymy of *I. gibbifrons* with *I. bulbifrons*, a synonymy that had been suspected by the fact that several samples of *I. bulbifrons* and *I. gibbifrons* had been found in the same locations.

The NHMUK collection contains two samples from incipient colonies (DJ 0725 and DJ 0726) and two samples of very young colonies (DJ U104 and DJ U109) that were collected at Edea, Cameroon, by N.M.

Collins; they are identified as *I. bulbifrons* based on their queens (not at all physogastric but wingless and with shortened antennae). If the soldiers had been used instead, the resulting identification would have be '*I. congoensis'*. It is indeed well known (Noirot 1955; Mathot 1964; and personal (G.J., J.D.) observations) that the first soldiers and workers produced by young colonies are significantly smaller than the soldiers and workers of mature colonies. In the PCA (Fig. 22), the ellipse labelled "c+b" pools *I. congoensis* and the young societies of *I. bulbifrons*: it shows a strong difference of size (x-axis) from mature colonies (labelled 'bulb'); moreover, it is stretched because it is made up on the one hand of the two incipient colonies plus the two *I. congoensis* samples (the four points furthest to the left = smallest individuals) and, on the other hand, of the two very young colonies (slightly larger individuals). Therefore, the samples identified as *I. congoensis* (the imagines of them being unknown), might also be incipient colonies of *I. bulbifrons*, hence their location in the chapter Incertae sedis.

**Redescription**

**Imago**

The description provided by Emerson (1928: 511–513) under the name *Mirotermes* (*Cubitermes*) *heghi* concerned in fact *Cubitermes* (now *Polyspathotermes*) *sulcifrons.* The imago of *P. heghi* has indeed a much smaller fontanelle and, among the species of the former *Cubitermes* genus of West Africa, only imagines of *P. sulcifrons* show a fontanelle as large as that described and figured by Emerson (Josens & Deligne 2019: 62). Further, the imago of *Cubitermes kemneri* was never described, so the imago of *I. bulbifrons* was only described to-date by Sjöstedt (1926: 247–248) based on alates and queen from Gabon (not examined).

Colour. **Head capsule**: well sclerotised, dark, C6–C7; fontanelle concolorous or almost so with head capsule. Postclypeus C5–C6 slightly paler (one level) than head capsule. Antennae C5–C6 without any difference between proximal and distal articles. **Thorax**: pronotum C6–C7, as head capsule; meso- and metanotum C6–C7, as pronotum. Legs C4–C5, tibia usually slightly (one level) darker than femur. Wings hyaline with brown to grey tinge (Cf3–Cf4), anterior veins darker. **Abdomen**: tergites C6–C7. Sternites appreciably paler in middle (C3–C4) with both sides darker (C4–C6); posterior sternites darker (C4–C6) than anterior.

Setation. **Head capsule** with some prominent setae, mainly near the eyes, and a higher density of shorter, finer setae everywhere. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at magnification 50 × or more). **Thorax**: pronotum with prominent setae mainly on margins and many shorter ones in middle; meso- and metanotum with some fine, pale setae, arranged in a medio-longitudinal strip, generally visible at 20–40 ×; sometimes three to four larger setae on metanotum. **Legs** very pilose, furnished (among numerous fine setae) with some fine spines: 6–11 on the carina of fore coxa and 1–3 on the ventral side; tibia pilose; fore, mid, and hind tibia furnished with 30–40 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 3; Figs 26–27, 35). **Size**: the imagines of *I. bulbifrons* are, on average, rather variable (Fig. 26); some individuals (with *I. zenkeri*), have the largest apical teeth and the largest apico-marginal distances (IMlAmD = 0.20–0.30 mm (Fig. 27). **Head capsule**: compound eyes nearly round; fontanelle generally a tiny elongate marking; ocelli nearly round to oval removed from eyes by a distance about equal to 0.7 to 1.3 ocellus small diameter. Antennae: 16 articles on alate individuals, always shortened by amputation by one to three articles in queens and kings. Labrum: cupola shaped. **Left mandible** with apical tooth, on average, longer than in most other species of the genus and always longer and more prominent than first marginal; marginal teeth three in number but second one only suggested by a slight undulation of edge between first and third marginal teeth; only the apical

tooth is acute in unworn specimens; premolar tooth with proximal end obscured or partly obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth always longer and more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and slightly narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a sharp carina. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 2–3 and 10–11 branches, respectively.

**Soldier**

Colour. **Head capsule** generally Cd4–Cd6 becoming fader and darker (e.g., Cf5–Cf7) in long preserved samples; there is frequently a gradient from a darker frons to a paler back (e.g., C6 → C4). Gulamentum concolorous with or somewhat darker than head. Antennae and labrum somewhat paler (one to two levels) than head capsule. Mandibles dark (C7–C8) generally with an abrupt clearing on their bases (two palette levels) which is generally the same colour as frons. **Thorax**, nota and legs paler than head capsule

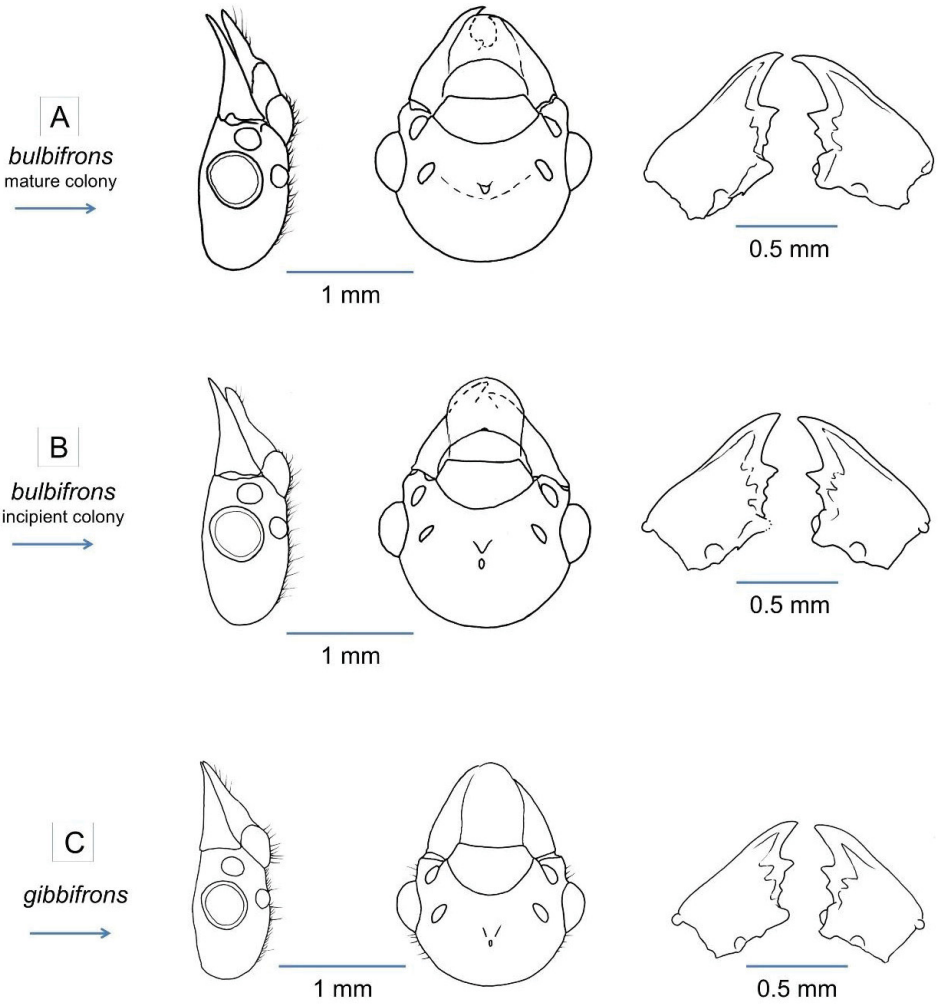


**Fig. 35.** *Isognathotermes bulbifrons* (Sjöstedt, 1924) and junior synonym species: imagines. Lateral and dorsal views of an imago's head capsule, and dorsal view of this imago's mandibles. **A**. Physogastric queen of a mature colony (DJ 0727). **B**. Non-physogastric queen of an incipient colony (DJ 0725). **C**. King from a non-type colony of *Cubitermes gibbifrons* (DJ 0615). The type samples did not contain any imago.

**Table 3.** *Isognathotermes bulbifrons* (Sjöstedt, 1924): ranges of significant measures in the three castes, in alphabetical orders of the "Code" column. The four incipient or young colonies are excluded from the measurements.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 15) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.33–0.47 | NA |
| | | Head: width across the eyes | IHdW | 1.44–1.73 | NA |
| | | Left mandible: A-m1 distance | IMlAmD | 0.20–0.30 | NA |
| | | Ocellus: large diameter | IOc*D* | 0.14–0.20 | NA |
| | | Postclypeus: width | IPcW | 0.71–0.87 | NA |
| | | Pronotum: maximal width | IPnW | 1.30–1.72 | NA |
| | | Hind tibia: length | IT3L | 1.66–2.04 | NA |
| | | Wing: length (n= 2) | IWgL | 14.1–16.8 | NA |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.25–2.04 | NA |
| Soldiers (n = 64) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.01–0.12 | 0.09 |
| | | Head: length | SHdL | 2.65–3.76 | 3.36 |
| | | Head: width | SHdW | 1.82–2.45 | 2.23 |
| | | Left mandible: lesser sagitta | SMlc | 0.14–0.31 | 0.26 |
| | | Left mandible: ventral length | SMlL | 2.12–2.87 | 2.49 |
| | | Hind tibia: length | ST3L | 1.51–2.01 | 1.85 |
| | Indices | Head elongation index | SHdL/SHdW | 1.36–1.67 | 1.50 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.06–0.11 | 0.10 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.70–1.20 | 0.95 |
| Workers (n = 40) | Raw measures (mm) | Head: width | WHdW | 1.11–1.43 | 1.34 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.16–0.22 | 0.21 |
| | | Left mandible: total length | WMlL | 0.54–0.67 | 0.63 |
| | | Hind tibia: length | WT3L | 1.24–1.55 | 1.51 |
| | | Valve: PC average length | WVP-AvL | 0.56–0.77 | 0.69 |
| | | Valve: PC average width | WVP-AvW | 0.06–0.10 | 0.09 |
| | | Valve: SC average length | WVS-AvL | 0.47–0.62 | 0.53 |
| | | Valve: SC average width | WVS-AvW | 0.21–0.33 | 0.25 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 6.49–10.3 | 7.27 |

* Abbreviations: see definitions in Material and methods.

(C3–C5) somewhat darker in long preserved samples. **Abdomen** grey to red-brown owing to digestive bolus, sometimes with a yellow tinge on tergites.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of hair-like setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Labrum** always with 5–9 large setae on each lobe. **Thorax**: pro- and mesonotum with some setae located mainly on margins. **Legs**: fore coxa furnished with 0–3 spines on carina and not any one on ventral side; trochanter generally with some long lined-up setae, sometimes with four to seven spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively; all

tibiae furnished with a row of 6–15 spines. **Abdomen**: tergites with some large setae, mainly or only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 3; Figs 28–29, 36). **Size**: the soldiers of *I. bulbifrons* are rather variable, the largest of them are (with those of *I. magniplanifrons*) the largest of the genus *Isognathotermes*; this is best seen in the length of the soldiers' heads (Fig. 28). **Head capsule**: always clearly sclerotised and appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a narrowing near posterior third or fourth (however, in the soldiers of incipient or very young colonies, lateral sides are slightly convex without any narrowing); from antennal sockets sides converge more or less clearly towards bases of mandibles; posterior side variable. **In profile**: upper profile always clearly concave, even in soldiers from incipient colonies; frons with a small frontal hump (rarely with no hump) overhanging the fontanelle, even in soldiers from incipient colonies. Gulamentum in ventral view always more or less constricted in its posterior half, with sides of anterior part softly curved or forming an acute widening or even a kind of ear on each side; generally, with a flat posterior part from side view. Antennae: of 15, sometimes 14.5, articles (only 13 articles in one soldier from an incipient colony). **Labrum**: always deeply bifurcate and wider than long, with sides generally lyre-shaped, rarely straight; lobes angular, with fine, whitish or translucent tips; anterior margin concave. **Mandibles**: sabre-like, almost hooked distally; inner edges smooth with one distinct but generally very small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible generally slightly more curved than left. **Thorax**: pronotum sellate, as wide as 52–68% of head width, with generally entire anterior and posterior margins. **Fore coxa** flanged ventrally resulting in a carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions showing trilateral symmetry: the odd cushions are on average 17% longer than the even cushions, generally without any hump or with humps weakly developed, however, the pilosity becoming abruptly very dense shows the place where a hump is expected (Fig. 6); secondary cushions wide at the upstream end narrowing noticeably downstream with a homogeneous spine scattering. **Caecum** always rather small, best seen in ventral view, near centre of abdomen, lobed (two or three small lobes).

**Worker**

Colour. **Head capsule** pale (C1–C3) turning grey in long preserved samples. Antennae: proximal articles pale (C2–C3), distal articles always one to two levels darker (C4–C5). **Thorax**, nota and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50 × or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa always carinated, bearing one fine seta and furnished with 3–4 spines on carina and 1–3 on ventral side; fore trochanter with 5–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 3; Figs 30–31, 37). **Size**: the workers of *I. bulbifrons* are among the medium sized to the largest of the genus *Isognathotermes* (with large overlapping on several other species: Fig. 30). **Head capsule**: weakly sclerotised (except mandibles). Antennae: generally 14.5 articles, 14 in workers from incipient colonies. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal well developed but

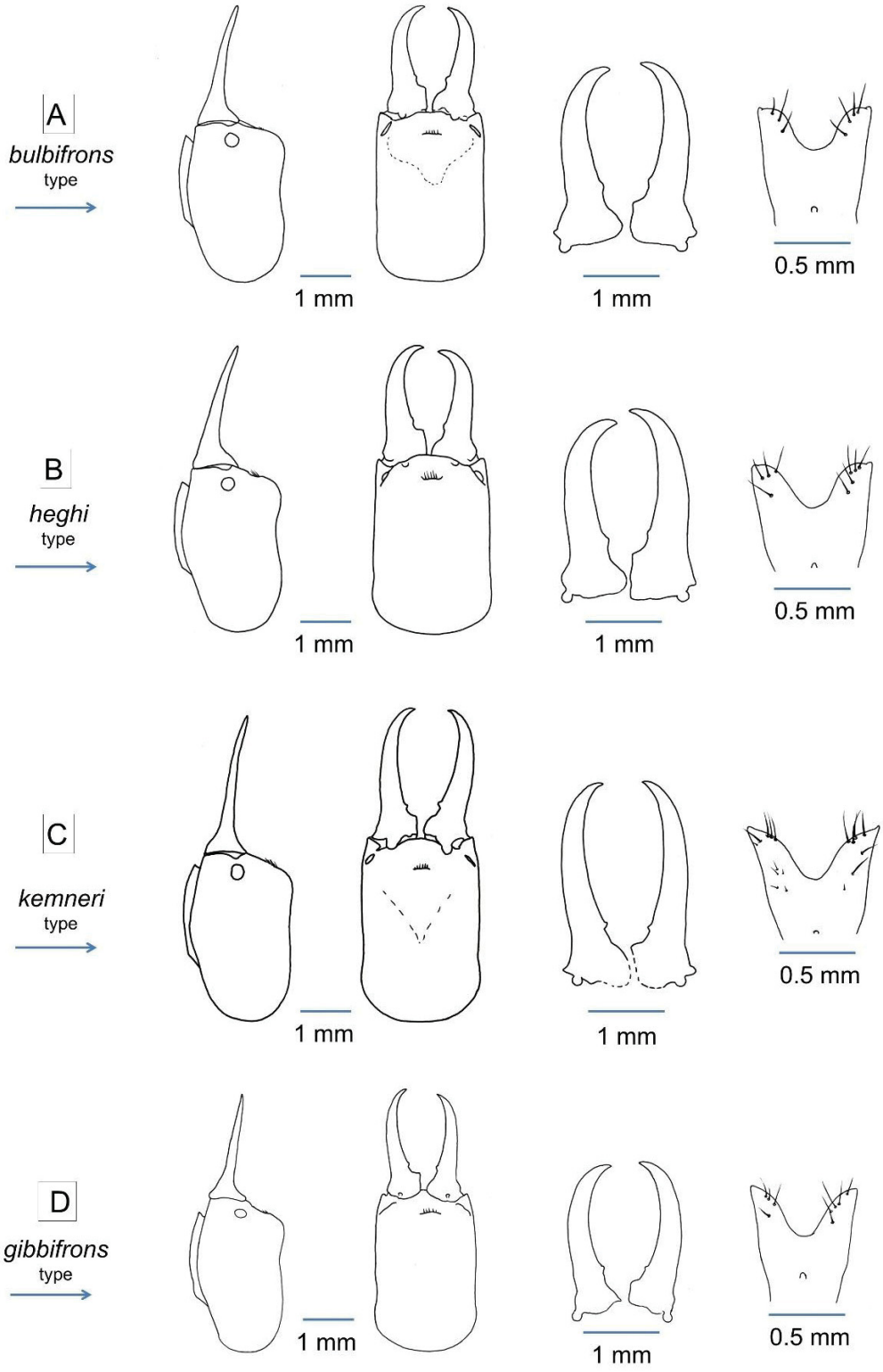


**Fig. 36** (continued on next page). *Isognathotermes bulbifrons* (Sjöstedt, 1924) and junior synonym species: soldiers. Lateral and dorsal views of a soldier's head capsule, ventral view of its mandibles, and dorsal view of its labrum. **A**. From type colony of *Cubitermes bulbifrons* Sjöstedt, 1924 (DJ 0298). **B**. From type colony of *Cubitermes heghi* Sjöstedt, 1924 (DJ 0290). **C**. From type colony of *Mirotermes* (*Cubitermes*) *kemneri* Emerson, 1928 (DJ 0297). **D**. From type colony of *Cubitermes gibbifrons* Sjöstedt, 1924 (DJ 0280).

with a blunt tip even when fresh, second marginal faint (visible as an undulated edge but disappearing in worn mandibles), third marginal with a blunt tip; premolar tooth with its proximal end generally hidden under molar prominence; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal well developed with a sharp tip when fresh; second marginal smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 64 to 78% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions of the *finitimus* pattern with triradial symmetry: the odd PCs, in their downstream part, are wide and bear at that place a high density of rather short bristles on a globular bulge; supporting bristles are generally numerous: 22–38 on each side of the odd PCs; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum always rather small, visible in ventral view, near centre of abdomen, shortly lobed (three, rarely two or four, small lobes, sometimes only sketched).

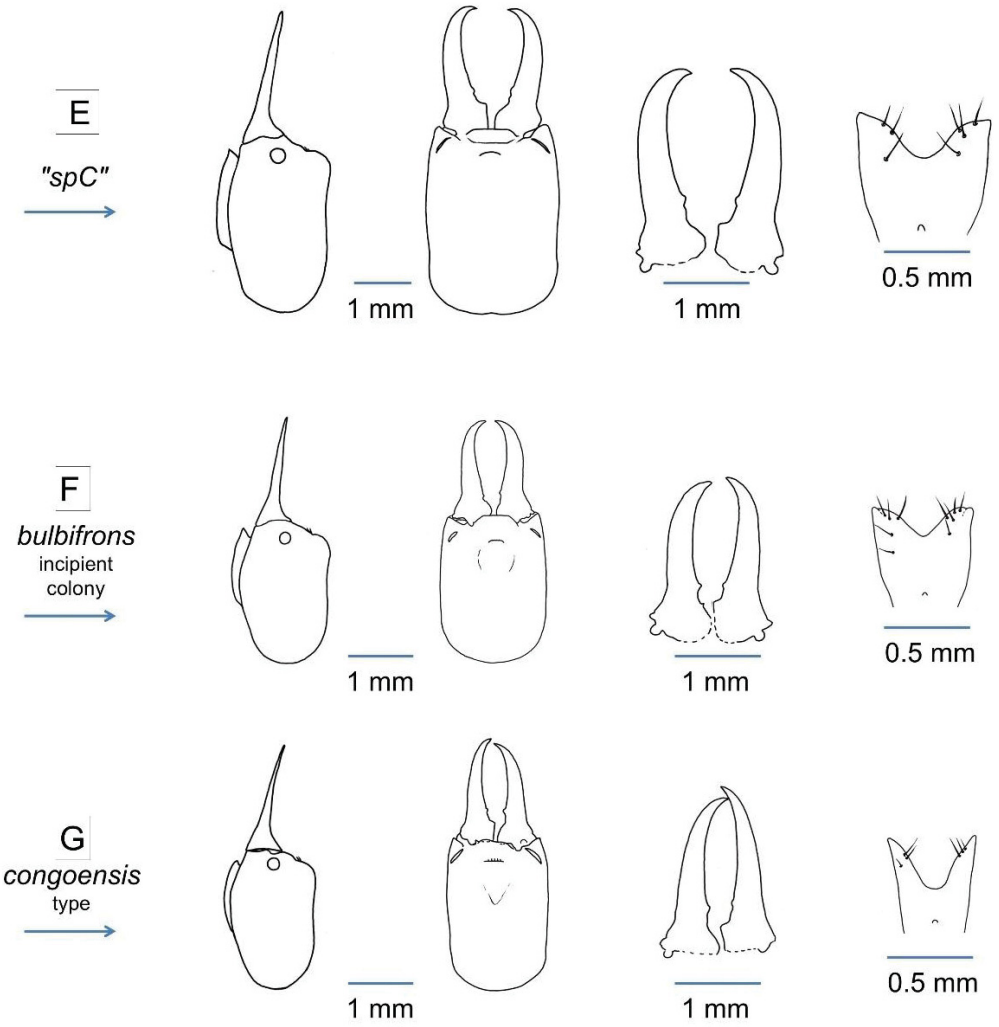


**Fig. 36** (continued). **E**. From "*C.* aff. *subarquatus* spC" (DJ 0621). **F**. From an incipient colony of *I. bulbifrons* (DJ 0725). **G**. From type colony of *Mirotermes* (*Cubitermes*) *congoensis* Emerson, 1928 (DJ 0299), probably also an incipient colony of *I. bulbifrons* (Sjöstedt, 1924) (labrum somewhat distorted by dessication).

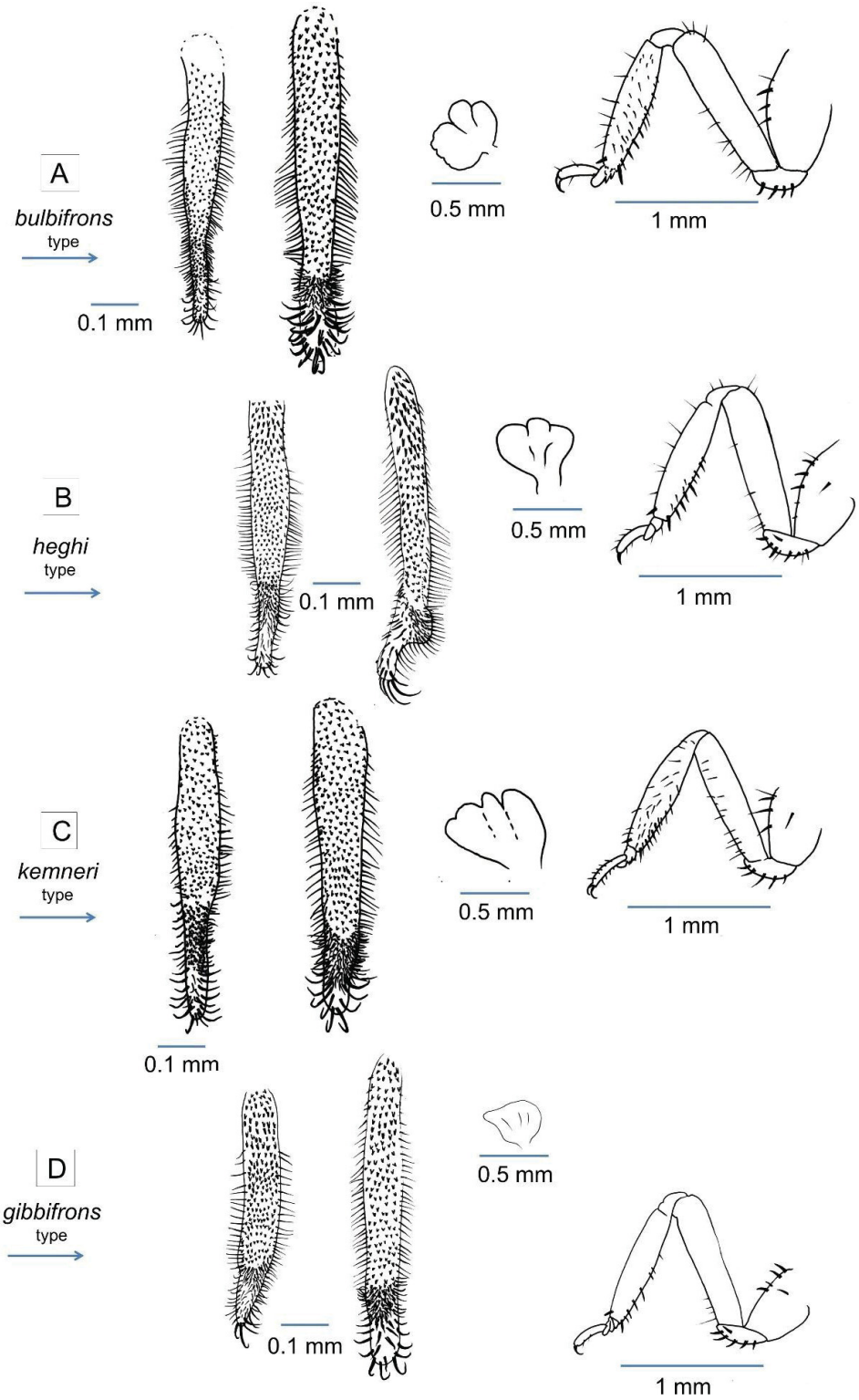


**Fig. 37** (continued on next page). *Isognathotermes bulbifrons* (Sjöstedt, 1924) and junior synonym species: soldiers and workers. PC1s of soldier's and worker's enteric valves, worker's caecum and foreleg. **A**. From type colony of *Cubitermes bulbifrons* Sjöstedt, 1924 (DJ 0298). **B**. From type colony of *Cubitermes heghi* Sjöstedt, 1924 (DJ 0290), the downstream end of worker's PC1 is twisted. **C**. From type colony of *Mirotermes* (*Cubitermes*) *kemneri* Emerson, 1928 (DJ 0299). **D**. From type colony of *Cubitermes gibbifrons* Sjöstedt, 1924 (DJ 0280).

**Chorology-ecology**

This species has been collected in the northwestern Congolian lowland forest and the Atlantic equatorial coastal forest ecoregions (Cameroon, Gabon, DRC and Angola) up to about 300 km from the Atlantic coast (Fig. 38).

**Molecular data**

The species *I. bulbifrons* corresponds to the *Cubitermes* "spC" in Roy *et al.* 2006 and Hellemans *et al.* 2021, proposed on basis of the *COII* gene. Our present sampling includes full mitogenomes from Gabonese samples previously published under the appellation "*Cubitermes* aff. *subarquatus* spC" by Roy *et al.* (2006), which we herein formally assign to *I. bulbifrons.*

Ten mitogenomes of *I. bulbifrons* collected from Gabon and Cameroon are published alongside this work (GenBank accessions: see Supp. file 3 and 'Material examined'). Overall, mitogenomes exhibit less than

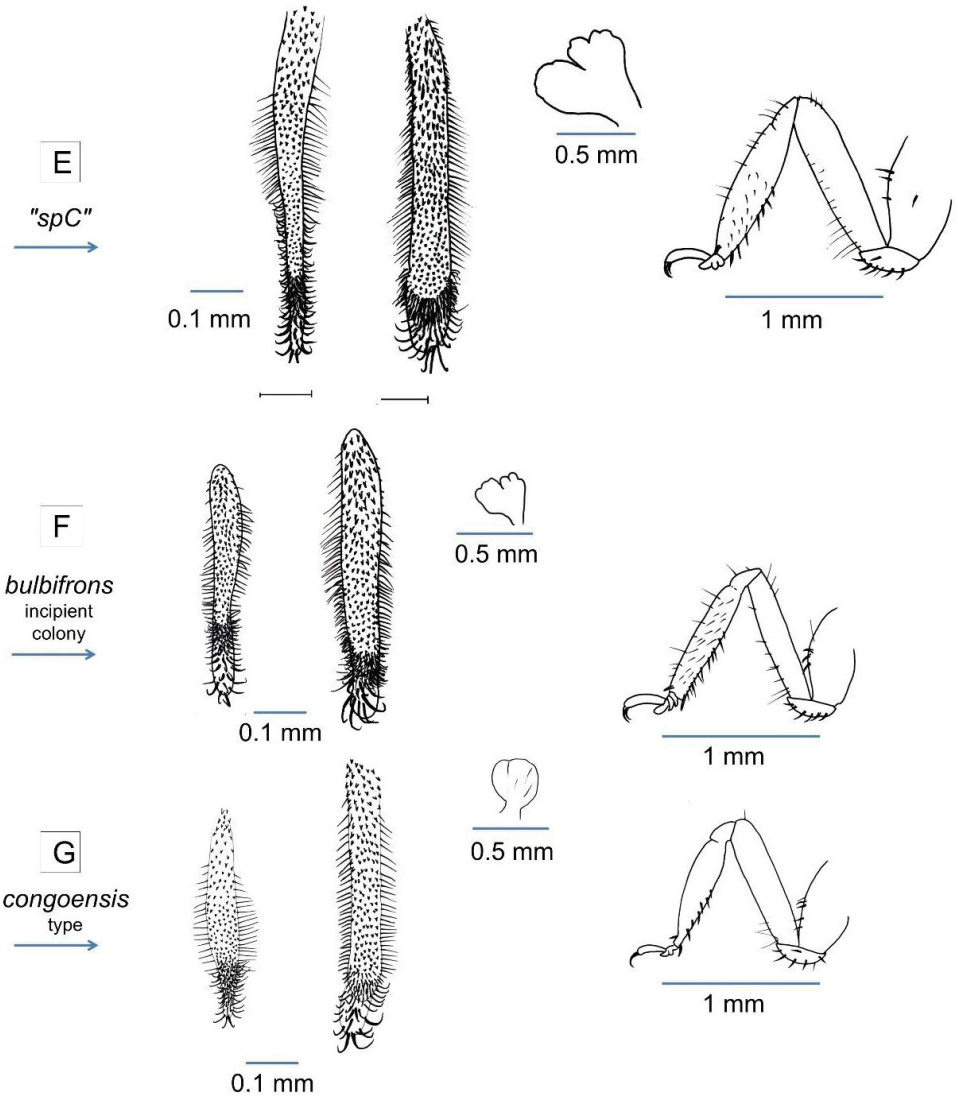


**Fig. 37** (continued). **E**. From "*Cubitermes* aff. *subarquatus* spC" (DJ 0621). **F**. From an incipient colony of *I. bulbifrons* (Sjöstedt, 1924) (DJ 0726). **G**. From type colony of *Mirotermes* (*Cubitermes*) *congoensis* Emerson, 1928 (DJ 0299 & 0484), which is, probably, also an incipient colony of *I. bulbifrons*.

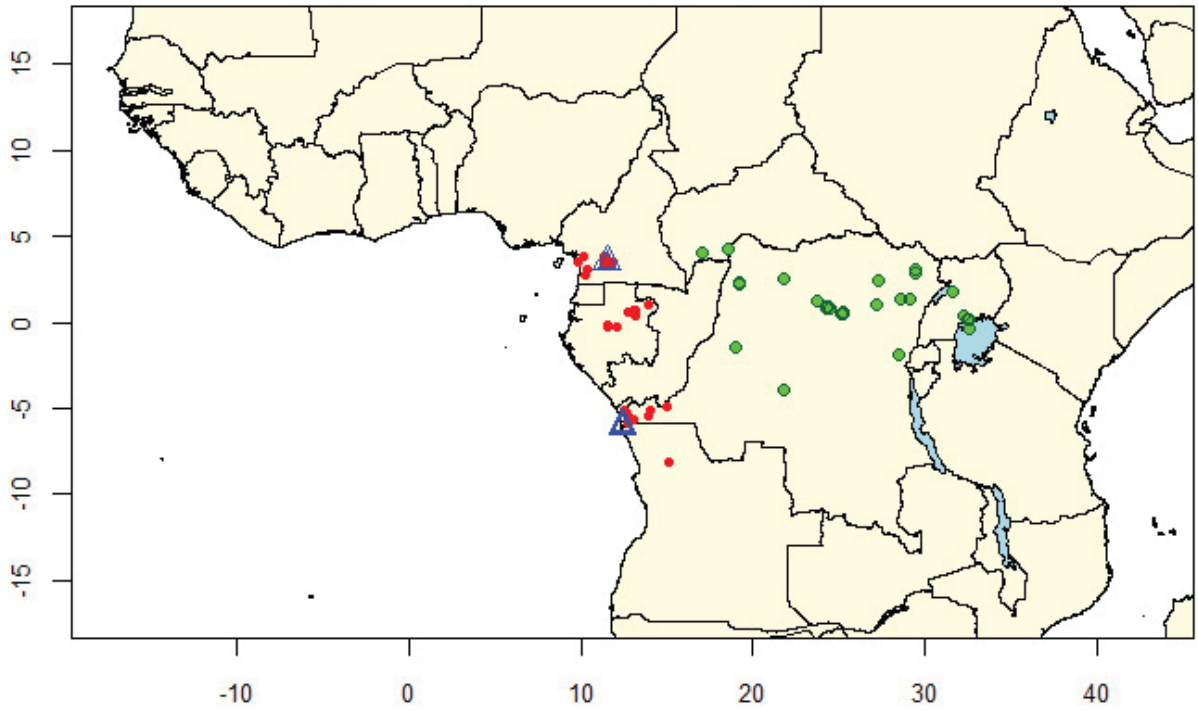


**Fig. 38.** Distribution map of *Isognathotermes bulbifrons* (Sjöstedt, 1924) (red dots), *I. finitimus* (Schmitz, 1916) (green dots), and *I. congoensis* (Emerson, 1928) (blue triangles).

2% dissimilarity with each other (Supp. file 4 with the samples DJ 0621 and DJ P158 being the most dissimilar). Of the ten samples sequenced, nine belonged to the large form of *I. bulbifrons* and only one (DJ P246) to the former *I. gibbifrons* (the medium-sized form of *I. bulbifrons*).

### ***Isognathotermes finitimus*** (Schmitz, 1916)

Figs 5, 13–20, 22, 26–33, 39–41, distribution map: Fig. 38; Table 4

*Cubitermes finitimus* Schmitz, 1916: 120–124, figs 1–2.
*Cubitermes speciosus* Sjöstedt, 1924b: 256. **Syn. nov**.
*Mirotermes* (*Cubitermes*) *subarquatus* Emerson, 1928: 510–511, pl. XXIX fig. 55.

*Cubitermes finitimus* – Sjöstedt 1926: 221–226. — Snyder 1949: 159. — Bouillon & Vincke 1971: 269. — Krishna *et al.* 2013: 1920. — Josens & Deligne 2019: 60–61, figs 11, 16.
*Cubitermes subarquatus* – Krishna *et al.* 2013: 1938.
*Isognathotermes finitimus* – Hellemans *et al.* 2021: 231–233.

**Diagnosis**

As already pointed out by H. Schmitz (1916), a soldier or an imago alone does not allow a confident identification. Indeed, this species is difficult to identify from its morphology since it is in a medium position in the genus *Isognathotermes* (blue ellipse in the middle of Fig. 22).

It is obviously easier to identify this species from its mitogenome: *I. finitimus* makes a clade well apart from the *planifrons* clade (Hellemans *et al.* 2021: 231).

If molecular data are not available, the best recognition is reached by a combination of worker's EVA, soldiers' mandibles, and geographical origin.

The worker has a *finitimus* EVA and is among the medium-sized workers of the genus *Isognathotermes* (Fig. 30).

The soldier is also medium sized in the genus *Isognathotermes* (Fig. 28; SHdL = 2.70–3.45 mm), and its EVA can generally be recognized as a *finitimus* EVA. The forehead has little, or no prominence, and the upper profile is only slightly concave. In comparison with *I. planifrons*, it has, on average, a higher acceleration of the mandible curvature: ln(SMlpR) - ln(SMldR) = 1.28–2.42 (0.89–2.28 in *I. planifrons*), that means: mandibles less curved at the base and more so at the tip. In *I. planifrons*, the soldier has on average slightly more curved mandibles.

The imago is also medium sized (Fig. 26) in the genus *Isognathotermes* (IHdW = 1.47–1.71 mm).

This medium-sized species can be confused with several other species with a *finitimus* EVA: *I. planifrons* and *I. bulbifrons* (*I. phalloides* sp. nov. and *I. phallicaecalis* sp. nov. have also similar sizes and morphologies but they can be distinguished easily by their caecum).

*Isognathotermes finitimus* can also be characterized by its ecology and chorology: it has always been found in continental forests east of longitude 15°E (but the *I. finitimus* and *I. planifrons* areas overlap in the south-west of CAR (Figs 38, 47); other species with a *finitimus* EVA can be found in this area: *I. magniplanifrons* sp. nov. with distinctly larger soldiers or *I. phallicaecalis* sp. nov. and *I. phalloides* sp. nov. with a characteristic, different caecum.

**Etymology**

The epithet *finitimus* from the Latin *finitimus* (bordering, close to) doubtless refers to the proximity of *C. finitimus* with both *C. fungifaber* and *C. zenkeri*, discussed at length by Schmitz in the original description.

**Material examined**

Sixty samples from 24 locations. Of the 35 old museum samples examined, nine samples were initially labelled as *Cubitermes finitimus*, four as *C. fungifaber*, one as *C. fungifaber* var. *elongata*, one as *C. loubetsiensis*, six as *C. minitabundus*, 11 as *C. speciosus*, two as *C. subarquatus*, and one as *Cubitermes* sp.

**Syntype of *Cubitermes finitimus* Schmitz, 1916**

DEMOCRATIC REPUBLIC OF THE CONGO • ♀ (queen); Stanleyville [= Kisangani]; 0°31′ N, 25°12′ E; before 1904; H. Kohl leg.; study code: DJ 0291; initially *C. finitimus* → *C. fungifaber*; AMNH.

**Syntypes of *Cubitermes speciosus* Sjöstedt, 1924**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker, ♀ (queen); Moto; 2°54.47′ N, 29°24.85′ E; 1923; L. Burgeon leg.; study code: DJ 0061; initially *C. speciosus* in RMCA; BE RMCA INS.Iso.059178.

Krishna *et al.* (2013: 1937) mention that other syntype samples are deposited in AMNH and PPRI, not examined.

**Syntypes of *Cubitermes subarquatus* Sjöstedt, 1926**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, ♂ (alate); Stanleyville [= Kisangani]; 0°31′ N, 25°12′ E; before 1904; H. Kohl leg.; study code: DJ 0803; initially *C. subarquatus* → *C. finitimus*; AMNH, IZC 00321262.

This latter label (DJ 0803) has been amended: on the one hand Emerson (1928: 510–511) mentioned for this sample: "Lubila River, Belgian Congo: Lang-Chapin Coll., Sept. 20, 1919" but in his introduction he wrote: "the collection was made by Mr. Herbert Lang and Mr. James P. Chapin during the American Museum Congo expedition, 1909–1915,…": this period does not include the collecting date of September 1919. On the other hand, the photo of the nest (plate XXIX) is dated "September 20, 1909", which is consistent with the dates of the Lang-Chapin expedition. In agreement with Sjöstedt (1926: 244), we changed the label to: "Stanleyville [= Kisangani], H. Kohl coll. [Date unknown, probably before 1904]".

Krishna *et al.* (2013: 1938) mention that another syntype sample is deposited in PPRI, not examined.

**Other material examined**

CENTRAL AFRICAN REPUBLIC • soldier, worker; Lobaye rain forest; 4°5′ N, 17°0′ E; 1975; G. Becker leg.; study code: DJ 0680; initially *C. speciosus*; NHMUK 13671988 • soldier; near Bangui; 4°16′ N, 18°31′ E; 1975; G. Becker leg.; study code: DJ 0679; initially *C. speciosus*; NHMUK 13671989.

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, ♀ (alate); Sankuru; 3°57′ S, 21°48′ E; [no date]; unknown leg.; study code: DJ 0279; initially *C. fungifaber* var. *elongata*; AMNH • soldier, worker, ♀ (queen); unclear data: "Lubila R."; 1°0′ N, 27°10′ E; 20 Sept. 1919 or Stanleyville [= Kisangani]; 0°31′ N, 25°12′ E; before 1904; H. Kohl leg.; study code: DJ 0295; initially *C. subarquatus* → *C. finitimus*; AMNH • soldier, worker; Irumu–Avakubi road; 1°21′ N, 29°6′ E; Oct. 1906; unknown leg.; study code: DJ 0677; initially *C. subarquatus*; NHMUK 13671992 • soldier, worker; Medje; 2°25′ N, 27°18′ E; Jun. 1914; Lang-Chapin leg.; study code: DJ 0122; initially *C. loubetsiensis* in RMCA; BE RMCA INS.Iso.059177 • soldier, ♀ (queen); Medje; 2°25′ N, 27°18′ E; Jun. 1914; Lang Chapin leg.; study code: DJ N125; initially *C. fungifaber*; AMNH • soldier, worker; Medje; 2°25′ N, 27°18′ E; Jul. 1914; Lang-Chapin leg.; study code: DJ 0612; initially *C. finitimus*; AMNH • soldier, worker; unclear location "Lubila R."; [1°0′ N, 27°10′ E ?]; 20 Sep. 1919; Lang-Chapin leg.; study code: DJ 0064; initially *C. subarquatus* in RMCA; BE RMCA INS.Iso.059182 • soldier, worker; Moto; 3°2′ N, 29°30′ E; 1922; L. Burgeon leg.; study code: DJ 0166; initially *C. speciosus* in RMCA; BE RMCA INS.Iso.059179 • soldier, ♀ (alate), ♂ (alate), ♀ (queen); Moto; 3°2′ N, 29°30′ E; 1923; L. Burgeon leg.; study code: DJ 0071; initially *C. speciosus* in RMCA; BE RMCA INS.Iso.059180 • soldier, worker, ♀ (alate), ♂ (alate); Moto; 3°2′ N, 29°30′ E; 1923; L. Burgeon leg.; study code: DJ 0072; initially *C. speciosus* in RMCA; BE RMCA INS.Iso.059181 • soldier, worker, ♀ (alate), ♀ (queen); Epulu; 1°24′ N, 28°36′ E; 2 May 1948; A. Emerson leg.; study code: DJ 0613; initially *C. finitimus*; AMNH • soldier, worker, ♀ (queen); Epulu; 1°24′ N, 28°36′ E; 12 May 1948; A. Emerson leg.; study code: DJ 0618; initially *C. finitimus*; AMNH • soldier, worker; Epulu; 1°24′ N, 28°36′ E; 12 May 1948; A. Emerson leg.; study code: DJ 0619; initially *C. finitimus*; AMNH • soldier, worker, ♀ (queen); Epulu; 1°24′ N, 28°36′ E; 13 May 1948; A. Emerson leg.; study code: DJ 0617; initially *C. finitimus*; AMNH • soldier, worker, ♀ (queen); Epulu; 1°24′ N, 28°36′ E; 15 May 1948; A. Emerson leg.; study code: DJ 0286; initially *C. finitimus*; AMNH • soldier, ♀ (queen); Yangambi; 0°48′ N, 24°29.3′ E; 29 May 1948; A. Emerson leg.; study code: DJ N127; initially *C. fungifaber*; AMNH • soldier, ♂ (king); Stanleyville [= Kisangani]; 0°31′ N, 25°11′ E; 1 Jun. 1948; A. Emerson leg.; study code: DJ N128; initially *C. fungifaber*; AMNH • soldier, ♀ (queen); Stanleyville [= Kisangani]; 0°31′ N, 25°12′ E; 1 Jun. 1948; A. Emerson leg.; study code: DJ 0616; initially *C. finitimus*; AMNH • soldier, ♂ (king); Mondongo; 2°16.5′ N, 19°9.4′ E; 13 Sep. 1966; J. Ruelle leg.; study code: DJ B318; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059173 • soldier, worker; near Mongolo; 2°14′ N, 19°12′ E; 14 Sep. 1966; J. Ruelle leg.; study code: DJ 0874;

initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059170 • soldier, worker; Beronge; 1°30′ S, 19°0′ E; 18 Sep. 1966; P. Cappelle leg.; study code: DJ 0897; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059176 • soldier, worker; Yalosemba; 2°34.5′ N, 21°47.5′ E; 24 Sep. 1966; J. Ruelle leg.; study code: DJ 0876; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059174 • soldier, worker, ♂ (king); Yalosemba; 2°34.5′ N, 21°47.5′ E; 24 Sep. 1966; J. Ruelle leg.; study code: DJ 0877; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059175 • soldier, worker, ♀ (queen); Mondongo; 2°16.5′ N, 19°9.4′ E; 27 Sep. 1966; unknown leg.; study code: DJ 0875; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059171 • soldier, worker; Irangi; 1°54′ S, 28°27′ E; 1 Apr. 1972; A. Bouillon leg.; study code: DJ 0878; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059172 • soldier, worker, ♀ (queen); Kisangani, Masako reserve; 0°38′ N, 25°15′ E; 1990; K. Soki leg.; study code: DJ 0012; BE RMCA INS.Iso.059169 • soldier, worker, ♀ (queen); Yaekela; 0°49.12′ N, 24°16.67′ E; 2 May 2010; B. Le Ru leg.; study code: DJ 0739; GenBank no PQ679218 (mitogenome); BE RMCA INS.Iso.059166 • soldier, worker, ♂ (king); Bomane; 1°15.74′ N, 23°42.4′ E; 19 May 2010; B. Le Ru leg.; study code: DJ 0741; GenBank no PQ679248 (mitogenome); BE RMCA INS.Iso.059168 • soldier, worker; Lokulu; 1°14.12′ N, 23°43.19′ E; 22 May 2010; B. Le Ru leg.; study code: DJ 0742; GenBank no PQ679241 (mitogenome); BE RMCA INS.Iso.059167 • soldier, worker; Yangambi; 0°52.9′ N, 24°19.5′ E; 3 Jul. 2013; Y. Roisin leg.; study code: DJ 0086; GenBank nos MN646708 (*COI*), MN685910 (*COII*), MN685971 (*28S*); BE RMCA INS.Iso.059183 • soldier, worker; Yangambi; 0°47.369′ N, 24°31.08′ E; 5 Jul. 2013; Y. Roisin leg.; study code: DJ 0652; GenBank nos MN646709 (*COI*), MN685911 (*COII*), MN685972 (*28S*); BE RMCA INS.Iso.059184 • soldier; Yangambi; 0°52.957′ N, 24°19.475′ E; 8 Jul. 2013; Y. Roisin leg.; study code: DJ Y143; BE RMCA INS.Iso.059163 • soldier, worker; Yangambi; 0°47.369′ N, 24°31.08′ E; 9 Jul. 2013; Y. Roisin leg.; study code: DJ 0654; BE RMCA INS.Iso.059186 • soldier, worker; Yangambi; 0°47.151′ N, 24°31.437′ E; 10 Jul. 2013; Y. Roisin leg.; study code: DJ 0655; GenBank no PQ679174 (mitogenome); BE RMCA INS.Iso.059187 • soldier; Yangambi; 0°46.851′ N, 24°31.255′ E; 11 Jul. 2013; Y. Roisin leg.; study code: DJ Y147; BE RMCA INS.Iso.059164 • soldier; Yangambi; 0°46.851′ N, 24°31.255′ E; 11 Jul. 2013; Y. Roisin leg.; study code: DJ Y148; BE RMCA INS. Iso.059165 • soldier, worker; Yangambi; 0°46.851′ N, 24°31.255′ E; 11 Jul. 2013; Y. Roisin leg.; study code: DJ 0656; GenBank no PQ679205 (mitogenome); BE RMCA INS.Iso.059188 • soldier, worker, ♀ (alate); Yangambi; 0°46.851′ N, 24°31.255′ E; 11 Jul. 2013; Y. Roisin leg.; study code: DJ 0657; GenBank no PQ679173 (mitogenome); BE RMCA INS.Iso.059189 • soldier; Yangambi; 0°48.152′ N, 24°29.258′ E; 15 Jul. 2013; Y. Roisin leg.; study code: DJ Y149; BE RMCA INS.Iso.059156 • soldier, worker; Yangambi; 0°48.152′ N, 24°29.268′ E; 15 Jul. 2013; Y. Roisin leg.; study code: DJ 0653; GenBank nos MN646710 (*COI*), MN685912 (*COII*), MN685973 (*28S*), PQ679167 (mitogenome); BE RMCA INS.Iso.059185 • soldier; Yangambi; 0°47.598′ N, 24°29.498′ E; 18 Jul. 2013; Y. Roisin leg.; study code: DJ Y144; BE RMCA INS.Iso.059157 • soldier, worker, ♂ (king); Yangambi; 0°47.598′ N, 24°29.498′ E; 18 Jul. 2013; Y. Roisin leg.; study code: DJ 0757; BE RMCA INS.Iso.059190 • soldier; Yangambi; 0°47.598′ N, 24°29.498′ E; 19 Jul. 2013; Y. Roisin leg.; study code: DJ Y145; BE RMCA INS.Iso.059158 • soldier; Yangambi; 0°47.598′ N, 24°29.498′ E; 19 Jul. 2013; Y. Roisin leg.; study code: DJ Y150; BE RMCA INS.Iso.059159 • soldier; Yangambi; 0°47.598′ N, 24°29.498′ E; 19 Jul. 2013; Y. Roisin leg.; study code: DJ Y151; BE RMCA INS.Iso.059160 • soldier; Yangambi; 0°47.598′ N, 24°29.498′ E; 19 Jul. 2013; Y. Roisin leg.; study code: DJ Y152; BE RMCA INS.Iso.059161 • soldier; Yangambi; 0°48.51′ N, 24°31.647′ E; 20 Jul. 2013; Y. Roisin leg.; study code: DJ Y146; BE RMCA INS.Iso.059162 • soldier, worker; Yangambi; 0°48.51′ N, 24°31.647′ E; 20 Jul. 2013; Y. Roisin leg.; study code: DJ 0620; GenBank no KY224569 (mitogenome); BE RMCA INS.Iso.059191 • soldier, worker, ♂ (king); Yangambi; 0°48.51′ N, 24°31.647′ E; 20 Jul. 2013; Y. Roisin leg.; study code: DJ 0758; BE RMCA INS.Iso.059192 • soldier, worker, ♂ (king); Yangambi; 0°48.51′ N, 24°31.647′ E; 20 Jul. 2013; Y. Roisin leg.; study code: DJ 0758; BE RMCA INS.Iso.059192.

UGANDA • soldier, ♀ (queen); Bugondo forest; 1°46′ N, 31°35′ E; 1944; C.J. Eggding and W.V. Harris leg.; study code: DJ U086; initially *C. speciosus*; NHMUK 13671980 • soldier, worker; Kawanda;

0°25.23′ S, 32°32.43′ E; 6 Dec. 1949; W.V. Harris leg.; study code: DJ 0684; initially *C. speciosus*; NHMUK 13671982 • soldier; Kampala–Fort Portal road; 0°22′ N, 32°16.5′ E; 3 Feb. 1955; R.M.C. Williams leg.; study code: DJ U088; initially *C. speciosus*; NHMUK 13671981 • soldier, worker, ♀ (alate); Entebbe–Kampala road; 0°7.5′ N, 32°31.5′ E; 2 Jul. 1970; Kistner leg.; study code: DJ 0681; initially *C. speciosus*; NHMUK 13671985 • soldier; Kisubi forest; 0°7′ N, 32°30′ E; 12 Jul. 1970; Kistner leg.; study code: DJ U087; initially *C. speciosus*; NHMUK 13671987.

**Historical review**

Schmitz (1916: 120–124) described this species under the name *Cubitermes finitimus*. He provided a description and measurements of king, queen, and soldier, mentioning that imagines are like those of *C. zenkeri* while the soldier closely resembles the soldier of *C. fungifaber*.

Sjöstedt (1926: 221–226) included *C. finitimus* in his soldiers' key of *Cubitermes* species and inserted it in a "*zenkeri*-Gruppe" of *Cubitermes* species with relatively shorter soldier's mandibles. He clarified some morphological differences between *C. finitimus*, *C. zenkeri* and *C. fungifaber*.

Snyder (1949: 159) catalogued this species under the name *Cubitermes finitimus* in the sub-family Termitinae and reported its known geographical distribution.

Emerson, in his unpublished "card catalog" considered *C. subarquatus* as a synonym of *C. finitimus* (quoted by Krishna *et al.* 2013: 1938): this is confirmed in this work.

Bouillon & Vincke (1971: 269) described the enteric valve of *C. finitimus* as belonging to the first of three types, the "simple type" without any spatula.

Krishna *et al.* (2013: 1920) housed *Cubitermes finitimus* in the sub-family Cubitermitinae.

Josens & Deligne (2019: 42–44) choose this species as type of the *finitimus* valve pattern group.

Hellemans *et al.* (2021: 231–233) placed this species in the restored genus *Isognathotermes* and within a "*finitimus* clade".

**Redescription**

**Imago**

Colour. **Head capsule**: well sclerotised, dark when fresh, C6–C7, lighter in old, preserved samples (C4–C6); fontanelle concolorous with or somewhat paler than head capsule. Postclypeus C6–C7 slightly paler (one level) than head capsule. Antennae C5–C6 without any difference between proximal and distal articles. **Thorax**: pronotum C6–C7, concolorous with or somewhat paler than head capsule; meso- and metanotum C6–C7, as pronotum. Legs C4–C5. Wings hyaline with brown to grey tinge (Cf3–Cf4), anterior veins darker. **Abdomen**: tergites C6–C7. Sternites appreciably paler in middle (C3–C4) with both sides darker (C4–C6); posterior sternites darker (C4–C6) than anterior.

Setation. **Head capsule** with some prominent setae, mainly near the eyes, and a higher density of shorter, finer setae everywhere. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and many shorter ones in middle; meso- and metanotum with some fine, pale setae, arranged in a medio-longitudinal strip, generally visible at 20 to 80×, with frequently one to four larger setae on metanotum. **Legs** very pilose, frequently furnished (among numerous fine setae) with some strong setae: 6–10 on the carina of fore coxa and 0–2 on the ventral side of fore coxa; tibia pilose; fore, mid, and hind tibia furnished with 10–30 strong setae and

bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 4; Figs 26, 39). **Size**: the imagines of *I. finitimus* are, on average, medium sized in the genus *Isognathotermes*; as shown in Fig. 26. **Head capsule** (Fig. 39): compound eyes nearly round; fontanelle generally a tiny round to elongate marking; ocelli nearly round to oval, removed from eyes by a distance about equal to 0.7–1.5 ocellus small diameter. Antennae: 16 articles on alate individuals, always shortened by amputation by one-three articles in queens and kings. Labrum: cupola shaped. **Left mandible** with apical tooth always longer and more prominent than first marginal; marginal teeth three in number but second one only suggested by a slight undulation of edge between first and third marginal teeth (this undulation disappears in worn mandibles); only the apical tooth is acute in unworn specimens; premolar tooth with proximal end obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth always longer and more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and narrower

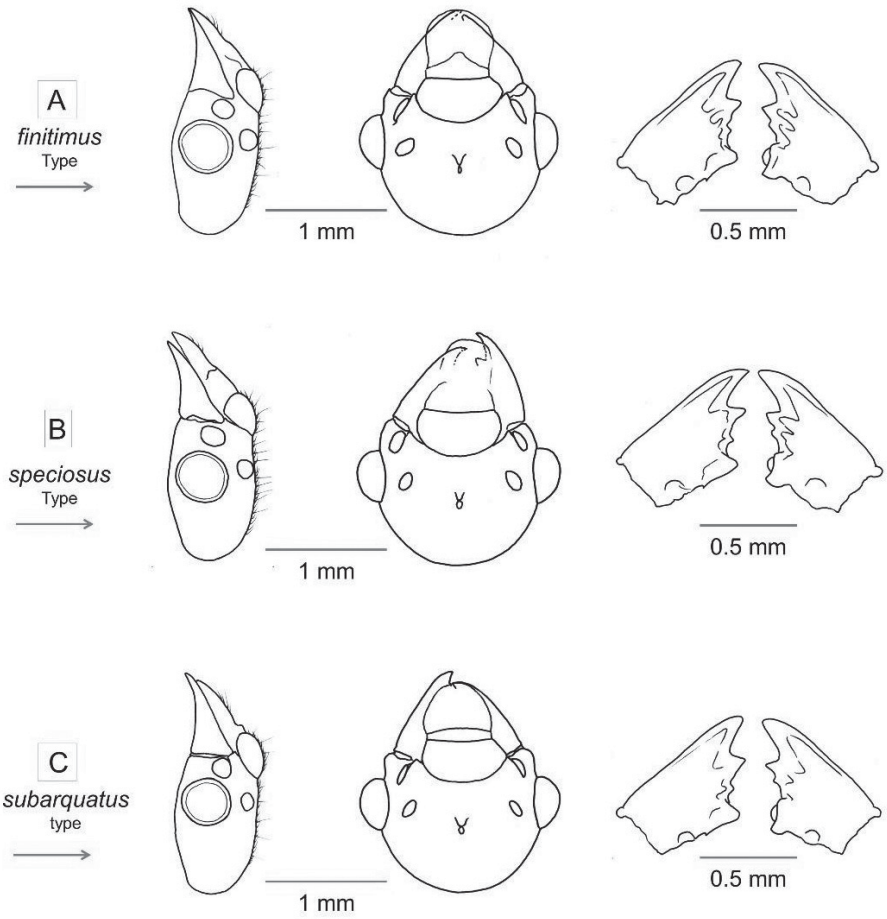


**Fig. 39.** *Isognathotermes finitimus* (Schmitz, 1916) and junior synonym species: imagines. Lateral and dorsal views of an imago's head capsule, and dorsal view of this imago's mandibles. **A**. Queen from the type colony of *Cubitermes finitimus* Schmitz, 1916 (DJ 0291). **B**. Queen from the type colony of *Cubitermes speciosus* Sjöstedt, 1924 (DJ 0061). **C**. Queen from the type colony of *Cubitermes subarquatus* Sjöstedt, 1926 (DJ 0295).

**Table 4.** *Isognathotermes finitimus* (Schmitz, 1916): ranges of significant measures in the three castes, in alphabetical orders of the "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 30) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.37–0.47 | 0.44 |
| | | Head: width across the eyes | IHdW | 1.47–1.71 | 1.61 |
| | | Left mandible: A-m1 distance | IMlAmD | 0.19–0.26 | 0.22 |
| | | Ocellus: large diameter | IOc*D* | 0.15–0.20 | 0.19 |
| | | Postclypeus: width | IPcW | 0.71–0.82 | 0.77 |
| | | Pronotum: maximal width | IPnW | 1.29–1.65 | 1.44 |
| | | Hind tibia: length | IT3L | 1.77–2.22 | 1.99 |
| | | Wing: length (n= 9) | IWgL | 12.2–16.0 | 13.6 |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.07–1.65 | 1.45 |
| Soldiers (n = 58) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.01–0.08 | 0.04 |
| | | Head: length | SHdL | 2.70–3.45 | 3.36 |
| | | Head: width | SHdW | 1.83–2.43 | 2.13 |
| | | Left mandible: lesser sagitta | SMlc | 0.16–0.31 | 0.25 |
| | | Left mandible: ventral length | SMlL | 2.10–2.71 | 2.49 |
| | | Hind tibia: length | ST3L | 1.59–1.88 | 1.79 |
| | Indices | Head elongation index | SHdL/SHdW | 1.33–1.60 | 1.58 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.07–0.12 | 0.10 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.71–1.11 | 0.88 |
| Workers (n = 40) | Raw measures (mm) | Head: width | WHdW | 1.11–1.37 | NA |
| | | Left mandible: A-m1 distance | WMlAmD | 0.16–0.22 | NA |
| | | Left mandible: total length | WMlL | 0.52–0.66 | NA |
| | | Hind tibia: length | WT3L | 1.23–1.52 | NA |
| | | Valve: PC average length | WVP-AvL | 0.54–0.67 | NA |
| | | Valve: PC average width | WVP-AvW | 0.06–0.10 | NA |
| | | Valve: SC average length | WVS-AvL | 0.41–0.51 | NA |
| | | Valve: SC average width | WVS-AvW | 0.17–0.29 | NA |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 5.75–9.91 | NA |

* Abbreviations: see definitions in Material and methods.

than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a more or less sharp carina. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 2–4 and 10–15 branches respectively. **Gut** (only studied in some cases): enteric valve weakly developed and hardly comparable with workers' and soldiers' valves; odd PCs are slightly longer than even PCs (Fig. 6). Caecum present as a small amorphous button.

**Soldier**

Colour. **Head capsule** generally Cd4–Cd6 becoming fader and darker (e.g., Cf5–Cf7) in long preserved samples; there is frequently a gradient from a darker frons to a paler back (e.g., from C6–C4) sometimes giving the impression that the head capsule is bicolorous (Fig. 13). Gulamentum generally concolorous

with head. Antennae and labrum slightly paler (half a level) than head capsule. Mandibles dark (C7–C8) generally with an abrupt clearing on their bases (two palette levels) which is generally the same colour as frons. **Thorax**, nota and legs paler than head capsule (C3–C4). **Abdomen** grey to red-brown owing to digestive bolus, rarely with a yellow tinge on tergites.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Labrum** always with 3–6 large setae on each lobe. **Thorax**: pro- and mesonotum with some setae mainly located on margins. **Legs**: fore coxa furnished with 2–4 (rarely 1 or 5) spines on carina and not any one on ventral side; trochanter generally with some long lined-up setae, sometimes with 4–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively; all tibiae furnished with a row of 7–15 spines. **Abdomen**: tergites with some large setae, mainly or only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 4; Figs 28, 40). **Size**: the soldiers of *I. finitimus* are medium sized in the genus *Isognathotermes*; this can be seen in the soldiers' head lengths (Fig. 28). **Head capsule** (Fig. 40): always clearly sclerotised and appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a slight to very slight narrowing near posterior third or fourth; from antennal sockets sides converge clearly towards bases of mandibles; posterior side variable. **In profile**: upper profile slightly to clearly concave; **frons**: fontanelle overhanged by a very small frontal hump (or sometimes no hump at all). Gulamentum in ventral view always constricted in its posterior half, with sides of anterior part either forming an acute widening or even a kind of ear on each side. Antennae: of 15 articles, rarely 14.5 or 14. **Labrum**: always deeply bifurcate and wider than long, with sides always more or less lyre-shaped; lobes angular, with fine, whitish, or translucent tips; anterior margin concave (Fig. 40). **Mandibles**: sabre-like, generally regularly curved but sometimes almost hooked distally; inner edges smooth with one distinct but generally very small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible generally slightly more curved than left. **Thorax**: pronotum sellate, clearly narrower than head, generally with a slight notch in anterior margin and entire posterior margin. **Fore coxa** flanged ventrally resulting in a more or less sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions showing trilateral symmetry: the odd cushions are on average 18% longer than the even cushions, generally without any hump or with humps weakly developed, however, the pilosity becoming abruptly very dense shows the place where a hump is expected (Fig. 41); secondary cushions wide at the upstream end narrowing noticeably downstream with a homogeneous spine scattering. **Caecum** always rather small, best seen in ventral view, near centre of abdomen, lobed (two to five small lobes).

**Worker**

Colour. **Head capsule** pale (C1–C3) turning grey in long preserved samples. Antennae: proximal articles pale (C2–C3), distal articles always one to two levels darker (C4–C5). **Thorax**, nota and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa always carinated, bearing one fine seta and furnished with 3–7 spines on carina and 0–2 on ventral side; fore trochanter with 5–7 spines or strong setae; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 4; Figs 30, 41). **Size**: the workers of *I. finitimus* are, on average, medium sized in the genus *Isognathotermes* (but with large overlapping on several other species: Fig. 30). **Head capsule** weakly sclerotised (except mandibles). Antennae 14.5 articles, rarely 14. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal well developed but with a blunt tip even when fresh, second marginal faint (visible as an undulated edge and disappearing in worn mandibles), third marginal with a blunt tip; premolar tooth with its proximal end generally hidden under molar prominence; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal well developed with a sharp tip when fresh; second marginal smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 64–74% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in posterior half of

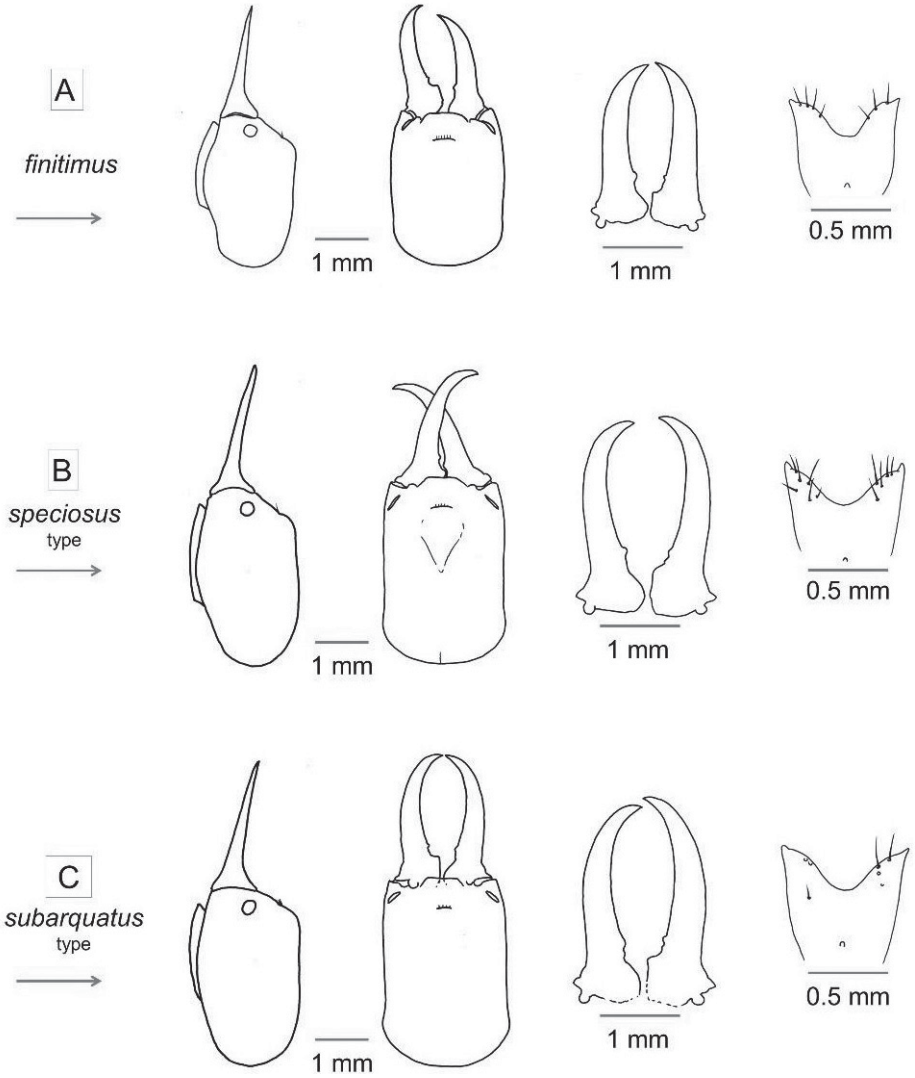


**Fig. 40.** *Isognathotermes finitimus* (Schmitz, 1916) and junior synonym species: soldiers. Lateral and dorsal views of a soldier's head capsule, ventral view of its mandibles, and dorsal view of its labrum. **A**. From a non-type colony of *Isognathotermes finitimus* (DJ 0655). **B**. From type colony of *Cubitermes speciosus* Sjöstedt, 1924 (DJ 0061). **C**. From type colony of *Cubitermes subarquatus* Sjöstedt, 1926 (DJ 0295).

abdomen. Arrangement of enteric valve cushions of the *finitimus* pattern with triradial symmetry: the odd PCs, in their downstream part, are wide and bear at that place a very high density of rather short bristles on a globular bulge (Fig. 41); supporting bristles are generally numerous: 22–29 on each side of the odd PCs; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum always rather small, visible in ventral view, near centre of abdomen, shortly lobed (two to five small lobes, sometimes only sketched).

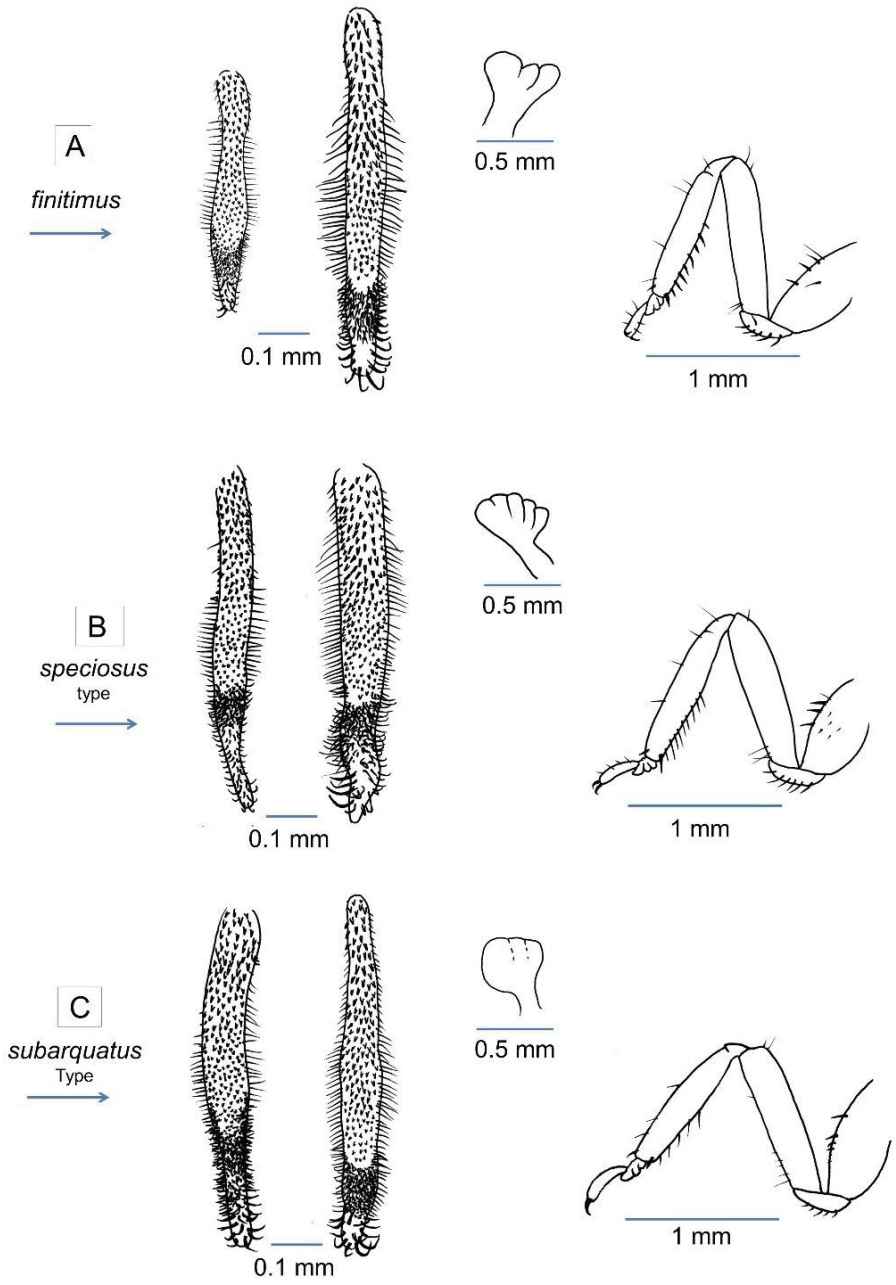


**Fig. 41.** *Isognathotermes finitimus* (Schmitz, 1916) and junior synonym species: soldiers and workers. PC1s of soldier's and worker's enteric valves; worker's caecum and foreleg. **A**. From a non-type colony of *Isognathotermes finitimus* (Schmitz, 1916) (DJ 0655). **B**. From type colony of *Cubitermes speciosus* Sjöstedt, 1924 (DJ 0061). **C**. From type colony of *Cubitermes subarquatus* Sjöstedt, 1926 (DJ 0295).

**Chorology-ecology**

The geographic distribution of *I. finitimus* is linked with the continental forests of central Africa; it includes the central and northeastern Congolian lowland forest and the Victoria Basin forest-savanna mosaic ecoregions (Fig. 38).

**Molecular data**

Seven mitogenomes of *I. finitimus* are published alongside this work (GenBank accessions: see Supp. file 3 and 'Material examined'). They are characterized by less than 1.05% dissimilarity with each other (Supp. file 4), with the sample DJ 0741 being the most dissimilar. Phylogenetic reconstructions based on full mitogenomes placed them in a sister relationship to the species *I. ugandensis* and *I. minitabundus*, to which they exhibit less than 2% dissimilarity.

**Remarks**

In the absence of genetic information, *I. finitimus* is often difficult to ascertain as its morphology places it in the middle of the genus *Isognathotermes*; for the species with a *finitimus* EVA alone, there are partial overlaps with *I. bulbifrons* and *I. planifrons*, and also with *I. phallicaecalis* sp. nov., and *I. phalloides* sp. nov. but these last two are distinguished by their caecum.

Integrative taxonomy comes into its own here: in particular, chorology is a valuable aid: two samples – DJ 0655 and DJ 0656 – collected at Yangambi (Tshopo Province, DRC), were initially identified as *I. gibbifrons* on the basis of their morphology (although in disagreement with the chorology of this species). Mitogenome-based phylogenetic reconstructions subsequently placed these samples in *I. finitimus*.

### ***Isognathotermes fungifaber*** (Sjöstedt, 1896)

Figs 1, 3–4, 6, 26–31, 33, 42–44, distribution map: Fig. 45; Tables 5–6

*Eutermes fungifaber* Sjöstedt, 1896: 297 (alate imago only).
*Mirotermes* (*Cubitermes*) *schmidti* Emerson, 1928: 520–521, fig. 62.
*Mirotermes* (*Cubitermes*) *banksi* Emerson, 1928: 522–523, fig. 63.
*Mirotermes* (*Cubitermes*) *comstocki* Emerson, 1928: 525, fig. 64.

*Eutermes fungifaber* – Sjöstedt 1900: 143–149, pl. IV (all castes).
*Mirotermes* (*Cubitermes*) *fungifaber* — Sjöstedt 1913: 369, pl X, 3. — Emerson 1928: 517–519, fig. 60.
*Cubitermes fungifaber* – Silvestri 1914: 91. — Sjöstedt 1926: 218–225. — Snyder 1949: 159. — Bouillon & Vincke 1971: 269. — Krishna *et al*. 2013: 1921–1922. — Josens & Deligne 2019: 60.
*Cubitermes banksi* – Ruelle 1992: 501. — Krishna *et al.* 2013: 1913.
*Cubitermes comstocki* – Ruelle 1992: 501. — Krishna *et al.* 2013: 1918.
*Cubitermes schmidti* – Ruelle 1992: 501. — Krishna *et al.* 2013: 1935.
*Cubitermes* sp. affinis *subarquatus* "spA" – Roy *et al.* 2006: 4–5.
*Cubitermes* sp. affinis *subarquatus* "spD" – Roy *et al.* 2006: 4–5.
*Isognathotermes fungifaber* – Hellemans *et al.* 2021: 233.

**Diagnosis**

The worker has a *fungifaber* EVA (Fig. 4) but in 2% of the samples examined, it has an EVA intermediate between the *fungifaber* and *finitimus* patterns. The worker itself and its enteric valve are among the smallest in the genus *Isognathotermes* (Fig. 31).

The soldier is among the smallest in the genus *Isognathotermes*; (SHdL = 2.37–3.11 mm, Fig. 28); its EVA generally looks like a *muneris* EVA and is among the smallest in the genus *Isognathotermes* EVAs. In some samples, however, the soldier is as large as the smallest soldiers of *I. severus*. The soldier has,

along with *I. planifrons*, the most evenly curved mandibles from base to tip: ln(SMlpR) - ln(SMldR) = 0.85–1.88.

The imago is, on average and with that of *I. phalloides* sp. nov., the smallest in the genus *Isognathotermes*; (IHdW = 1.40–1.61 mm, Fig. 26).

This species is also defined by its ecology and chorology: it has always been found in evergreen forests from RCI to Gabon at less than 300 km from the Atlantic coast (Fig. 45 but see later, 'Supplementary material of dubious *I. fungifaber*').

**Etymology**

The name *fungifaber* from the Latin *fungus* (mushroom) and *faber* (artisan) doubtless refers to the building of mushroom-shaped epigeous nests.

**Material examined**

One hundred twenty-four samples from 44 locations (plus six samples of "dubious *I. fungifaber*" from five locations). Of the 64 old museum samples examined, 49 were initially labelled as *C. fungifaber*, one as *C. fungifaber* var. *elongata*, four as *C. banksi*, one as *C. comstocki*, three as *C. gaigei*, three as *C. kemneri*, two as *C. modestior*, and one as *C. schmidti*. Of the six samples of "dubious *I. fungifaber*", four were initially labelled as *C. fungifaber* and two not identified.

This species also includes *C.* aff. *subarquatus* "spA" and "spD" (in Roy *et al.* 2006).

**Syntypes of *Eutermes fungifaber* Sjöstedt, 1896**

CAMEROON • soldier, worker, ♀ (alate), ♀ (queen); Mbongé; 4°32.18′ N, 9°6.67′ E; Oct. 1891; Y. Sjöstedt leg.; study code: DJ 0271; initially *Eutermes fungifaber*; NHMM • soldier, worker, ♀ (queen); Mbongé; 4°32.18′ N, 9°6.67′ E; 27 Oct. 1891; Y. Sjöstedt leg.; study code: DJ 0272; initially *Eutermes fungifaber*; AMNH • worker, ♀ (alate); Mbongé (?); 4°32.18′ N, 9°6.67′ E; 1891; Y. Sjöstedt leg.; study code: DJ 0965; initially *Eutermes fungifaber ex typis*; RBINS.

Krishna *et al.* (2013: 1921) mention that other syntype samples are deposited in NHRM, not examined.

**Paratypes of *Mirotermes* (*Cubitermes*) *banksi* Emerson, 1928**

CAMEROON • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0287; initially *Mirotermes* (*C.*) *banksi* → *C. fungifaber*; AMNH • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0097; initially *C. banksi* in RMCA; BE RMCA INS.Iso.059210.

Krishna *et al.* (2013: 1913) mention that the holotype and paratypes are deposited in UMMZ, not examined.

**Paratypes of *Mirotermes* (*Cubitermes*) *comstocki* Emerson, 1928**

CAMEROON • soldier, worker, ♀ (queen); Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0273; initially *Mirotermes* (*C.*) *comstocki* → *C. fungifaber*; AMNH • soldier, worker, ♀ (alate); Bipindi?; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0278; initially *C. comstocki* → *C. fungifaber*; AMNH • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0121; initially *C. comstocki* in RMCA; BE RMCA INS.Iso.059212.

Krishna *et al.* (2013: 1918) mention that the holotype (soldier) and paratypes are deposited in UMMZ, not examined, and that other paratypes are deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, not examined.

**Paratypes of *Mirotermes* (*Cubitermes*) *schmidti* Emerson, 1928**

CAMEROON • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0275; initially *C. schmidti* → *C. fungifaber* in AMNH • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0124; initially *Mirotermes* (*C.*) *schmidti* in RMCA; BE RMCA INS. Iso.059213

**Other material examined**

CAMEROON • soldier; Abonando [= Ossidinge]; 5°54′ N, 9°8′ E; no date; G. Mansfeld leg.; study code: DJ N123; initially *C. fungifaber*; AMNH • soldier, worker, ♀ (alate); Mungo; 5°12′ N, 9°31′ E; 1903; Rohde leg.; study code: DJ 0269; initially *C. fungifaber* var. *elongata*; AMNH • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0963; initially *Eutermes fungifaber*; RBINS • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0964; initially *Eutermes fungifaber*; RBINS • soldier; Réserve du Nyong; 3°50′ N, 10°50′ E; 6 Dec. 1949; J. Birkett-Smith and J. Dahl leg.; study code: DJ U036; initially *C. fungifaber*; NHMUK 13671854 • soldier; Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ U033; initially *C. fungifaber*; NHMUK 13671851 • soldier; Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ U039; initially *C. fungifaber*; NHMUK 13671847 • soldier; Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ U040; initially *C. fungifaber*; NHMUK 13671850 • soldier; Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ U041; initially *C. fungifaber*; NHMUK 13671848 • soldier; Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ U042; initially *C. fungifaber*; NHMUK 13671846 • soldier; Mbalmayo; 3°30′ N, 11°31′ E; 1 Dec. 1962; G. Becker leg.; study code: DJ U065; initially *C. fungifaber*; NHMUK 13671852 • soldier, worker; Mamfe–Ikom road; 5°47′ N, 8°58′ E; 18 Sep. 1966; W. Wilkinson leg.; study code: DJ 0718; initially *C. gaigei*; NHMUK 13671886 • worker, ♂ (king); Edea; 3°29′ N, 9°50′ E; Jul.–Sep. 1973; N.M. Collins leg.; study code: DJ 0649; initially *C. fungifaber*; NHMUK 13671846 • soldier, worker, ♀ (alate); Ebodjié; 2°38′ N, 9°53′ E; Nov. 1991; A. Dejean leg.; study code: DJ 0096; initially *C. banksi* in RMCA; BE RMCA INS.Iso.059211 • soldier; Akok; 3°53′ N, 11°57′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U049; initially *C. fungifaber*; NHMUK 13671877 • soldier; Akok; 3°53′ N, 11°57′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U050; initially *C. fungifaber*; NHMUK 13671876 • soldier; Akok; 3°53′ N, 11°57′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U052; initially *C. fungifaber*; NHMUK 13671879 • soldier; Akok; 3°53′ N, 11°57′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U053; initially *C. fungifaber*; NHMUK 13671880 • soldier, ♀ (alate); Ebogo; 3°23′ N, 11°28′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U045; initially *C. fungifaber*; NHMUK 13671874 • soldier; Ebogo; 3°23.5′ N, 11°28′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U068; initially *C. kemneri*; NHMUK 13672024 • soldier; Ebogo; 3°23.5′ N, 11°28′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U069; initially *C. kemneri*; NHMUK 13672025 • soldier; Ebogo; 3°31′ N, 11°30′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U092; initially *C. banksi*; NHMUK 13671831 • soldier, ♂ (king), ♀ (queen); Eboufek; 3°31′ N, 11°30′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U051; initially *C. fungifaber*; NHMUK 13671875 • soldier, worker, ♂ (king); Eboufek; 3°30′ N, 11°53′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ 0651; initially *C. kemneri*; NHMUK 13672023 • soldier, worker, ♂ (alate); Eboufek; 3°30′ N, 11°53′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ 0707; initially *C. banksi*; NHMUK 13671828 • soldier, ♂ (king); Ekombitié; 3°28′ N, 11°31′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U048; initially *C. fungifaber*; NHMUK 13671872 • soldier; Mbalmayo; 3°27′ N, 11°29′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U047; initially *C. fungifaber*; NHMUK 13671871 • soldier; Mbalmayo; 3°27′ N, 11°29′ E; Feb. 1996; P. Eggleton *et al.* leg.; study code: DJ U044; initially *C. fungifaber*; NHMUK 13671870 • soldier; Mbalmayo; 3°27′ N, 11°29′ E; Mar. 1996; P. Eggleton *et al.* leg.; study code: DJ U046; initially *C. fungifaber*; NHMUK 13671859 • soldier; Mbalmayo; 3°27′ N, 11°29′ E; Aug. 1996; P. Eggleton *et al.* leg.; study code: DJ U043; initially *C. fungifaber*; NHMUK 13671873 • soldier; Nsimi; 3°10′ N, 11°58′ E; Nov. 1996; M. Harry leg.; study code: DJ P136; GenBank no PQ679252 (mitogenome); MNHN EP9869 •

soldier; Nsimi; 3°10′ N, 11°58′ E; Nov. 1996; M. Harry leg.; study code: DJ P137; MNHN EP9870 • soldier; Nsimi; 3°10′ N, 11°58′ E; Nov. 1996; M. Harry leg.; study code: DJ P138; MNHN EP9871 • soldier; Nsimi; 3°10′ N, 11°58′ E; Nov. 1996; M. Harry leg.; study code: DJ P139; MNHN EP9872 • soldier; Nsimi; 3°10′ N, 11°58′ E; Nov. 1996; M. Harry leg.; study code: DJ P140; MNHN EP9873 • soldier, worker, ♂ (alate); Makak; 3°38′ N, 11°4′ E; 27 Nov. 2013; J. Birkett-Smith and J. Dahl leg.; study code: DJ 0650; initially *C. fungifaber*; NHMUK 13671853 • soldier, worker, ♂ (alate); Bipindi; 3°5′ N, 10°24.5′ E; 23 Nov. 2016; P. Akama leg.; study code: DJ 0452; GenBank nos MN646713 (*COI*), MN685915 (*COII*), MN685976 (*28S*), PQ679181 (mitogenome); BE RMCA INS.Iso.059200 • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 23 Nov. 2016; P. Akama leg.; study code: DJ 0468; GenBank no PQ679188 (mitogenome); BE RMCA INS.Iso.059196 • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 23 Nov. 2016; P. Akama leg.; study code: DJ 0469; GenBank no PQ679195 (mitogenome); BE RMCA INS. Iso.059195 • soldier, worker, ♀ (alate); Mbongé; 4°32.2′ N, 9°6.7′ E; 30 Nov. 2016; P. Akama leg.; study code: DJ 0450; GenBank nos MN646712 (*COI*), MN685914 (*COII*), MN685975 (*28S*); BE RMCA INS. Iso.059194 • soldier, worker; Mbongé; 4°32.2′ N, 9°6.7′ E; 30 Nov. 2016; P. Akama leg.; study code: DJ 0451; GenBank no PQ679193 (mitogenome); BE RMCA INS.Iso.059202 • soldier, worker, ♂ (alate); Mbongé; 4°32.2′ N, 9°6.7′ E; 30 Nov. 2016; P. Akama leg.; study code: DJ 0466; GenBank no PQ679246 (mitogenome); BE RMCA INS.Iso.059198 • soldier, worker, ♂ (alate); Mbongé; 4°32.2′ N, 9°6.7′ E; 30 Nov. 2016; P. Akama leg.; study code: DJ 0467; GenBank no PQ679226 (mitogenome); BE RMCA INS. Iso.059203 • soldier, worker, ♀ (queen); Ebogo; 3°22.894′ N, 11°27.862′ E; 23 May 2017; Y. Roisin leg.; study code: DJ 0506; GenBank nos MN646714 (*COI*), MN685916 (*COII*), MN685977 (*28S*); BE RMCA INS.Iso.059206 • soldier, worker; Ebogo; 3°22.872′ N, 11°27.796′ E; 6 Jun. 2017; Y. Roisin leg.; study code: DJ 0521; GenBank no PQ679222 (mitogenome); BE RMCA INS.Iso.059205 • soldier, worker; Mbalmayo; 3°28.841′ N, 11°34.646′ E; 6 Jun. 2017; Y. Roisin leg.; study code: DJ 0520; GenBank no PQ679185 (mitogenome); BE RMCA INS.Iso.059207

CÔTE D'IVOIRE • soldier; Banco N.P.; 5°23′ N, 4°3′ W; 1 Jan. 1934; P.-P. Grassé leg.; study code: DJ P199; MNHN EP9849 • soldier; Banco N.P.; 5°23′ N, 4°3′ W; 8 Jan. 1934; P.-P. Grassé leg.; study code: DJ P153; MNHN EP9844 • soldier, worker; Banco N.P.; 5°24′ N, 4°3′ W; 9 Jan. 1934; P.-P. Grassé leg.; study code: DJ 0203; initially *C. fungifaber* in MNHN; MNHN EP9840 • soldier; Banco N.P.; 5°23′ N, 4°3′ W; Jan. 1939; P.-P. Grassé leg.; study code: DJ P157; MNHN EP9845 • soldier, ♀ (queen); Banco N.P.; 5°23′ N, 4°3′ W; 6 Feb. 1947; C. Noirot leg.; study code: DJ P194; MNHN EP9848 • soldier, ♂ (king); Adiopodoumé; 5°19.75′ N, 4°8′ W; 22 May 1947; C. Noirot leg.; study code: DJ P193; MNHN EP9847 • soldier; Banco N.P.; 5°19′ N, 4°10′ W; 26 Jul. 1947; C. Noirot leg.; study code: DJ P325; MNHN EP9863 • soldier; Mambo; 5°46′ N, 4°3′ W; 19 Oct. 1947; C. Noirot leg.; study code: DJ P324; MNHN EP9862 • soldier; Mambo; 5°46′ N, 4°3′ W; 19 Oct. 1947; C. Noirot leg.; study code: DJ P333; MNHN EP9948 • soldier; Mambo; 5°46′ N, 4°3′ W; 20 Oct. 1947; C. Noirot leg.; study code: DJ P334; MNHN EP9949 • soldier; Yapo; 5°44′ N, 4°5′ W; 10 Oct. 1947; C. Noirot leg.; study code: DJ P326; MNHN EP9864 • soldier, worker, ♀ (alate); Petit Yapo réserve forestière; 5°46′ N, 4°8′ W; 22 Aug. 1953; M. Lüscher leg.; study code: DJ 0277; initially *C. fungifaber*; AMNH • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 6 Dec. 1959; C. Noirot leg.; study code: DJ P211; MNHN EP9860 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 25 Dec. 1959; C. Noirot leg.; study code: DJ P208; MNHN EP9857 • soldier, worker, ♂ (alate); near Abidjan; 5°23′ N, 4°3′ W; ca 1960; C. Noirot leg.; study code: DJ 0268; initially *C. fungifaber*; AMNH • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 17 Jan. 1960; C. Noirot (?) leg.; study code: DJ P203; MNHN EP9852 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 17 Jan. 1960; C. Noirot (?) leg.; study code: DJ P205; MNHN EP9854 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 17 Jan. 1960; C. Noirot (?) leg.; study code: DJ P207; MNHN EP9856 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 17 Jan. 1960; C. Noirot leg.; study code: DJ P209; MNHN EP9858 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 17 Jan. 1960; C. Noirot leg.; study code: DJ P210; MNHN EP9859 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 30 Jan. 1960; C. Noirot (?) leg.; study code: DJ P201; MNHN EP9850 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 30 Jan. 1960; C. Noirot (?) leg.; study code: DJ P204; MNHN EP9853 • soldier; Banco N.P.;

5°24′ N, 4°3′ W; 20 Mar. 1960; C. Noirot leg.; study code: DJ P329; MNHN EP9866 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 7 May 1960; C. Noirot (?) leg.; study code: DJ P202; MNHN EP9851 • soldier, ♂ (alate); Banco N.P.; 5°24′ N, 4°3′ W; 7 May 1960; C. Noirot (?) leg.; study code: DJ P206; MNHN EP9855 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 12 Jun. 1960; C. Noirot leg.; study code: DJ P330; MNHN EP9867 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 17 Jun. 1960; C. Noirot leg.; study code: DJ P336; MNHN EP9951 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 9 Oct. 1960; C. Noirot leg.; study code: DJ P327; MNHN EP9865 • soldier; Banco N.P.; 5°24′ N, 4°3′ W; 9 Oct. 1960; C. Noirot leg.; study code: DJ P331; MNHN EP9868 • soldier, ♂ (king); Abidjan; 5°20′ N, 3°59′ W; 29 Dec. 1960; C. Noirot leg.; study code: DJ P347; MNHN • soldier, ♂ (alate); Adiaké; 5°22′ N, 3°19.7′ W; 15 Apr. 1963; C. Noirot leg.; study code: DJ P348; MNHN • soldier; Banco N.P.; 5°23′ N, 4°3′ W; 21 Aug. 1968; G. Josens leg.; study code: DJ U001; initially *C. modestior*; NHMUK 13671927 • soldier, worker; Banco N.P.; 5°24′ N, 4°3′ W; 21 Aug. 1968; G. Josens leg.; study code: DJ 0202; initially *C. modestior* in RMCA; BE RMCA INS.Iso.059204 • soldier, worker; Ahoutoué; 5°28′ N, 3°45′ W; 9 Aug. 1969; Vincent leg.; study code: DJ 0229; BE RMCA INS.Iso.059209 • soldier, worker; Banco N.P.; 5°23.005′ N, 4°3.341′ W; 17 Feb. 2015; G. Josens leg.; study code: DJ 0412; GenBank nos MN646711 (*COI*), MN685913 (*COII*), MN685974 (*28S*), PQ679172 (mitogenome); BE RMCA INS.Iso.059208.

EQUATORIAL GUINEA • soldier; Punta Frailes; 3°47′ N, 8°43′ E; ca 1894; R.M. Downes leg.; study code: DJ U110; initially *C. gaigei*; NHMUK 13671887 • soldier, worker, ♀ (alate); Punta Frailes; 3°47′ N, 8°43′ E; Oct. 1901; L. Fea leg.; study code: DJ 0311; initially *C. fungifaber*; MCGD.

GABON • soldier; Mekambo; 1°1′ N, 13°56′ E; Jan. 1957; P.-P. Grassé and C. Noirot leg.; study code: DJ P167; MNHN EP9846 • soldier, worker; Piste du Bouéni; 0°13′ N, 11°48′ E; 1 Jan. 1957; P.-P. Grassé and C. Noirot leg.; study code: DJ 0855; MNHN EP9843 • soldier, worker; Piste du Bouéni, km 53; 0°44′ N, 13°12′ E; 1 Jan. 1957; P.-P. Grassé and C. Noirot leg.; study code: DJ 0853; MNHN EP9841 • soldier, worker, ♂ (king), ♀ (queen); forêt dense de Djidji; 0°13′ N, 11°48′ E; 25 Jan. 1957; P.-P. Grassé and C. Noirot leg.; study code: DJ 0854; MNHN EP9842 • soldier, worker; La Lopé N.P.; 0°15′ S, 11°35′ E; 9 Mar. 1998; M. Harry leg.; study code: DJ P242; MNHN EP9875 • soldier, worker; La Lopé N.P.; 0°12.7′ S, 11°33.5′ E; 9 Mar. 1998; M. Harry leg.; study code: DJ 0623; GenBank nos DQ127302 (*COII*), DQ246527 (*ITS2*), PQ679189 (mitogenome); initially *C.* aff. *subarquatus* "spA" (cf. Roy *et al.* 2006); MNHN EP9878 • soldier, worker; Doda (north of La Lopé N.P.); 0°4.5′ S, 11°25.5′ E; 10 Mar. 1998; M. Harry leg.; study code: DJ 0625; GenBank nos DQ246541 (*COII*), DQ246526 (*ITS2*) initially *C.* aff. *subarquatus* "spD" (cf. Roy *et al.* 2006); MNHN EP9879 • soldier, ♀ (queen); La Lopé N.P.; 0°15′ S, 11°35′ E; 13 Mar. 1998; M. Harry leg.; study code: DJ P243; MNHN EP9876 • soldier, worker; La Lopé N.P.; 0°12.7′ S, 11°33.5′ E; 13 Mar. 1998; M. Harry leg.; study code: DJ 0626; GenBank nos DQ127299 (*COII*), DQ246529 (*ITS2*), PQ679214 (mitogenome); initially *C.* aff. *subarquatus* "spA" (cf. Roy *et al.* 2006); MNHN EP9880 • soldier; La Lopé N.P.; 0°9′ S, 11°36′ E; 6 Mar. 1998; M. Harry leg.; study code: DJ P232; MNHN EP9874 • soldier, worker; Bitam; 2°5′ N, 11°30′ E; 15 Apr. 2017; G. Trembleau leg.; study code: DJ 0456; BE RMCA INS.Iso.059197 • soldier, worker; Bitam; 2°5′ N, 11°30′ E; 15 Apr. 2017; G. Trembleau leg.; study code: DJ 0457; BE RMCA INS.Iso.059201 • soldier; Bitam; 2°5′ N, 11°30′ E; 15 Apr. 2017; G. Trembleau leg.; study code: DJ 0458; BE RMCA INS.Iso.059199 • soldier, worker; Nkobissimo [= Nkolmengboua ?]; 2°14.3′ N, 11°29.25′ E; 15 Apr. 2017; G. Trembleau leg.; study code: DJ 0453; GenBank no PQ679216 (mitogenome); BE RMCA INS. Iso.059193 • soldier, worker; Ipassa; 0°30.66′ N, 12°48′ E; 27 Jan. 2025; J. Šobotnik leg.; study code: DJ 0974; BE RMCA INS.Iso.059949.

GHANA • soldier, ♀ (queen); Bobiri Forest Reserve; 6°40′ N, 1°21′ W; 21 Feb. 1959; W.A. Sands leg.; study code: DJ U114; initially *C. gaigei*; NHMUK 13671881.

NIGERIA • soldier; Ijebu–Ode road; 6°50′ N, 3°54′ E; 2 May 1950; G.C. Webb leg.; study code: DJ N126; initially *C. fungifaber*; AMNH • soldier; North of Lagos; 6°49′ N, 3°13′ E; 11 Feb. 1955; W.V. Harris leg.; study code: DJ U063; initially *C. fungifaber*; NHMUK 13671865 • soldier; Mofu River forest reserve; 6°10′ N, 7°10′ E; 15 Feb. 1955; W.V. Harris leg.; study code: DJ U062; initially *C. fungifaber*; NHMUK 13671864 • soldier; Port Harcourt; 4°46′ N, 7°1′ E; 5 Dec. 1955; D. Kay leg.; study code: DJ U057; initially *C. fungifaber*; NHMUK 13671868 • soldier; Sapele; 5°53′ N, 5°41′ E; 31 Jan. 1956; D. Kay leg.; study code: DJ U056; initially *C. fungifaber*; NHMUK 13671866 • soldier; Obanikoro; 6°33′ N, 3°22′ E; 8 Jan. 1957; W. Wilkinson leg.; study code: DJ U034; initially *C. fungifaber*; NHMUK 13671861 • soldier; Ugo; 6°5′ N, 6°0′ E; 11 Jan. 1957; W. Wilkinson leg.; study code: DJ U061; initially *C. fungifaber*; NHMUK 13671860 • soldier, worker; Ilaro (near)?; 7°26′ N, 3°5′ E; 6 Apr. 1957; W. Wilkinson leg.; study code: DJ 0549; initially *C. fungifaber*; NHMUK • soldier, ♀ (queen); Calabar-Mamfe road; 5°17′ N, 8°34′ E; 22 Apr. 1957; W. Wilkinson leg.; study code: DJ U035; initially *C. fungifaber*; NHMUK 13671863 • soldier; Port Harcourt–Owerri road; 5°11′ N, 6°52′ E; 19 Jun. 1957; W. Wilkinson leg.; study code: DJ U064; initially *C. fungifaber*; NHMUK 13671867 • soldier, worker; Port Harcourt–Owerri road; 5°9.5′ N, 6°51′ E; 19 Jun. 1957; W. Wilkinson leg.; study code: DJ 0548; initially *C. fungifaber*; NHMUK • soldier; Mamu forest reserve; 6°11′ N, 7°10′ E; 28 Feb. 1958; W.A. Sands leg.; study code: DJ U058; initially *C. fungifaber*; NHMUK 13671862 • soldier; Enugu–Otukpo road; 6°45′ N, 7°28′ E; 5 Mar. 1958; W.A. Sands leg.; study code: DJ U055; initially *C. fungifaber*; NHMUK 13671858 • soldier; Ayangba; 7°30′ N, 7°10′ E; 6 Mar. 1958; W.A. Sands leg.; study code: DJ U059; initially *C. fungifaber*; NHMUK 13671857 • soldier; Ijebu–Ode road; 6°49′ N, 3°55′ E; 12 Dec. 1959; W.A. Sands leg.; study code: DJ U060; initially *C. fungifaber*; NHMUK 13671859.

**Supplementary material of dubious *I. fungifaber***

Four samples from the CAR, near Bangui, and two from eastern DRC (Fig. 45) show a soldier's morphology entirely consistent with that of *I. fungifaber*. As these samples come from semi-deciduous forest and forest galleries (which is not characteristic of *I. fungifaber*) and as it was not possible to sequence them, these six samples, are presented here as "dubious, possibly cryptic *I. fungifaber*". The distance between Bangui and the nearest harvesting point in Gabon is around 500 km, and between Bangui and eastern DRC, the distance is around 1300 km.

Of the six old museum samples examined, four samples were initially labelled as *C. fungifaber* and two not identified.

CENTRAL AFRICAN REPUBLIC • soldier; route Mbaïki–Bagandou; 3°52′ N, 17°52′ E; 21 Jun. 1948; P.-P. Grassé and C. Noirot leg.; study code: DJ P188; MNHN EP9825 • soldier; Boukoko; 3°54′ N, 17°55′ E; 2 Jul. 1948; P.-P. Grassé and C. Noirot leg.; study code: DJ P189; MNHN EP9826 • soldier; Bangui; 4°27′ N, 18°32′ E; 1975; Becker leg.; study code: DJ U037; initially *C. fungifaber*; NHMUK 13671856 • soldier; Bangui; 4°27′ N, 18°32′ E; 1975; Becker leg.; study code: DJ U038; initially *C. fungifaber*; NHMUK 13671855.

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker, ♀ (queen); "Alto Uele, foresta"; 2°30′ N, 29°30′ E; [no date]; S. Patrizi leg.; study code: DJ 0312; initially *C. fungifaber* in MCGD • soldier, ♀ (alate); Epulu; 1°24′ N, 28°34′ E; 15 May 1948; A. Emerson leg.; study code: DJ N129; initially *C. fungifaber* in AMNH.

**Historical review**

The alate imago from Bonge [= Mbongé], Cameroon, was briefly described by Sjöstedt (1896: 297) under the name *Eutermes fungifaber*, mentioning it as very close to *Eutermes mordax* (Smeathman, 1781).

Four years later, Sjöstedt (1900: 143–149) provided more detailed descriptions (text and figures) of all castes and nest. Sjöstedt (1926: 218–225) included *Cubitermes fungifaber* in imagines' and soldiers' keys of *Cubitermes* species and inserted it in a "*fungifaber*-Gruppe" of species with a not forward humped soldier's frons.

Emerson (1928: 517–519) referred to this species as *Mirotermes* (*Cubitermes*) *fungifaber*; he provided further descriptions and measurements of all castes, based on samples collected by G. Zenker in Cameroon.

Snyder (1949: 159) catalogued this species under the name *Cubitermes fungifaber* in the sub-family Termitinae.

Bouillon & Vincke (1971: 269) described the enteric valve of *C. fungifaber* as belonging to the first of three types, the "simple type" without any spatula.

*Cubitermes fungifaber* was considered as a senior synonym of (a) *C. banksi*, (b) *C. comstocki* and (c) *C. schmidti* (Emerson unpublished "Card catalog"; Ruelle 1992: 501; Krishna *et al.* 2013: 1913, 1918, 1935). These three species are somewhat smaller than *C. fungifaber*, but synonymies are compatible with their enteric valve patterns (Josens & Deligne 2019: 39–42).

To obtain genetic sequences of *I. fungifaber*, one of us (PA) went and collected samples at Mbongé, type location of *I. fungifaber*, and at Bipindi, type location of *I. banksi*, *I. comstocki* and *I. schmidti*; some of the soldiers in those samples were as small as the soldiers of *C. comstocki* and Hellemans *et al.* (2021: 233) confirmed their synonymies and placed the species in the restored genus *Isognathotermes*.

*Cubitermes fungifaber* was considered a senior synonym of *C. fungifaber* var. *elongata* (Krishna *et al.* 2013: 1923) and a possible senior synonym of *C. planifrons* (Emerson in his unpublished "card catalog", quoted by Krishna *et al.* 2013: 1931) but these synonymies are rejected because the two taxa proposed as junior synonyms do not have enteric valves of the *fungifaber* pattern, but well of the *finitimus* one (Josens & Deligne 2019: 42–44).

*Cubitermes* aff. *subarquatus* "spA" and *Cubitermes* aff. *subarquatus* "spD" were mentioned by Roy *et al.* (2006) in La Lopé National Parc, Gabon; on a genetical base they were considered as cryptic species. Hellemans *et al.* (2021: 231) placed these species in the restored genus *Isognathotermes* as synonyms of *I. fungifaber*.

As already mentioned, the geographic distribution of *I. fungifaber* is clearly dependant on humid, forest environments. In at least one documented case, its geographic distribution has been changing during the second half of the 20th century, possibly in relation with global and local climate change. *Isognathotermes fungifaber* used to be common in the Banco National Park near Abidjan, RCI: see the publications by Noirot *et al.* (1986), Han & Lepage (1991), and personal observation (GJ, in 1970); however, nowadays, this national park is almost totally included within the city of Abidjan, which presumably influences the local climate. Moreover, the annual rainfall in Côte d'Ivoire has been declining by about 20% during the last decades, mainly during the late sixties and early seventies (Servat *et al.* 1999), possibly linked with huge deforestation. This might explain that two of us (GJ and YR) could hardly find a single nest of this species in 2015 in the Banco National Park.

**Redescription**

**Imago**

Colour. **Head capsule**: well sclerotised, fresh samples very dark, C7–C8 (C6–C7 in long preserved imagines); fontanelle concolorous or almost so with head capsule. Postclypeus C6–C7 slightly paler (one level) than head capsule. Antennae C5–C6 without any difference between proximal and distal

articles. **Thorax**: pronotum C6–C8 (C5–C7 in long preserved imagines), as postclypeus, generally one level paler than head capsule; meso- and metanotum C5–C7, sometimes somewhat paler than pronotum. Legs C3–C5; tibia usually slightly (one level) darker than femur. Wings hyaline with brown to grey tinge (Cf3–Cf4), anterior veins darker. **Abdomen**: tergites C5–C7. Sternites appreciably paler in middle (C3–C4) with both sides darker (C4–C6); posterior sternites darker (C4–C6) than anterior.

Setation. **Head capsule**, with some prominent setae set amongst a high density of short, fine setae forming a dense mat. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and shorter ones in middle; meso- and metanotum with some fine, pale setae, arranged in a medio-longitudinal strip, generally visible at 40×, sometimes only at 80×. **Legs** very pilose, furnished (among numerous fine setae) with some stronger setae: 5–12 on the carina of fore coxa and 1–8 on the ventral side of fore coxa and trochanter; tibia pilose fore, mid, and hind tibia furnished with 30–40 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 5; Fig. 42). **Size**: the imagines of *I. fungifaber* are, on average, among the smallest of the genus *Isognathotermes* (Fig. 26). **Head capsule**: compound eyes shortly oval; ocelli

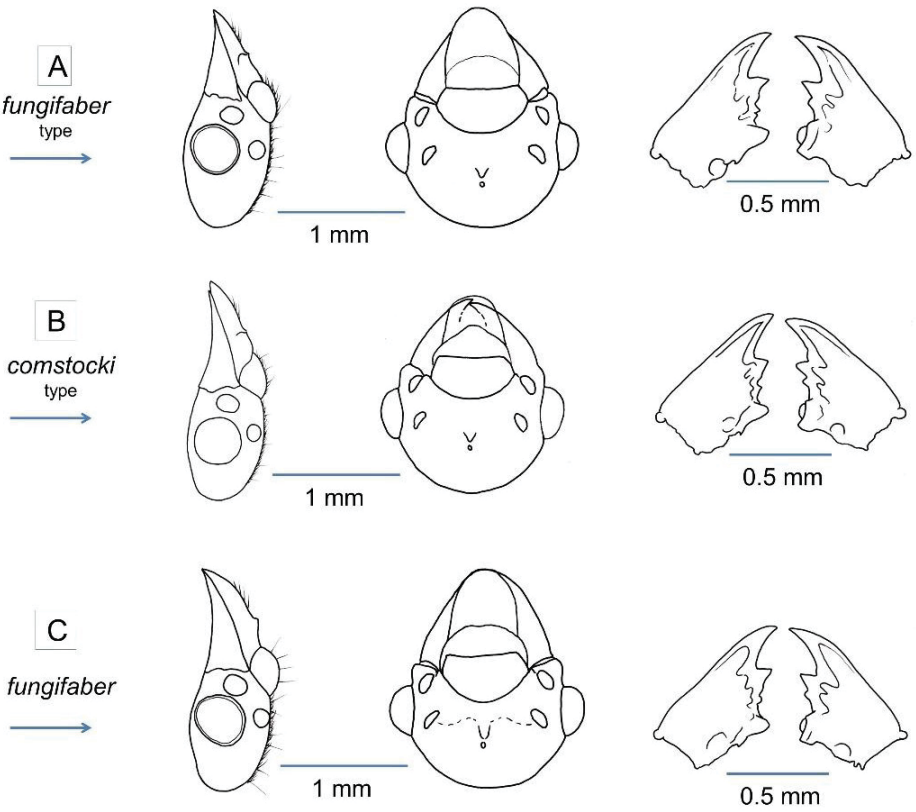


**Fig. 42.** *Isognathotermes fungifaber* (Sjöstedt, 1896) and junior synonym species: imagines. Lateral and dorsal views of an imago's head capsule, and dorsal view of this imago's mandibles. **A**. Alate female from the type colony of *Eutermes fungifaber* Sjöstedt, 1896 (DJ 0271). **B**. Queen from the type colony of *Mirotermes* (*Cubitermes*) *comstocki* Emerson, 1928 (DJ 0273). **C**. Alate male from a non-type colony of *I. fungifaber* (Sjöstedt, 1896) (DJ 0268).

**Table 5.** *Isognathotermes fungifaber* (Sjöstedt, 1896): ranges of significant measures in the three castes, in alphabetical orders of the "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 35) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.36–0.44 | 0.42 |
| | | Head: width across the eyes | IHdW | 1.40–1.61 | 1.51 |
| | | Left mandible: A-m1 distance | IMlAmD | 0.22–0.28 | 0.24 |
| | | Ocellus: large diameter | IOc*D* | 0.13–0.21 | 0.17 |
| | | Postclypeus: width | IPcW | 0.65–0.80 | 0.71 |
| | | Pronotum: maximal width | IPnW | 1.17–1.48 | 1.35 |
| | | Hind tibia: length | IT3L | 1.47–1.77 | 1.62 |
| | | Wing: length (n= 18) | IWgL | 10.4–14.1 | 12.5 |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.30–2.06 | 1.56 |
| Soldiers (n = 129) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.00–0.06 | 0.02 |
| | | Head: length | SHdL | 2.37–3.11 | 2.83 |
| | | Head: width | SHdW | 1.58–2.17 | 1.91 |
| | | Left mandible: lesser sagitta | SMlc | 0.18–0.33 | 0.25 |
| | | Left mandible: ventral length | SMlL | 1.74–2.46 | 2.17 |
| | | Hind tibia: length | ST3L | 1.26–1.67 | 1.49 |
| | Indices | Head elongation index | SHdL/SHdW | 1.30–1.62 | 1.48 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.09–0.15 | 0.12 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.85–1.22 | 0.97 |
| Workers (n = 54) | Raw measures (mm) | Head: width | WHdW | 0.94–1.25 | 1.15 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.15–0.21 | 0.18 |
| | | Left mandible: total length | WMlL | 0.47–0.60 | 0.56 |
| | | Hind tibia: length | WT3L | 1.05–1.38 | 1.21 |
| | | Valve: PC average length | WVP-AvL | 0.43–0.72 | 0.61 |
| | | Valve: PC average width | WVP-AvW | 0.04–0.08 | 0.06 |
| | | Valve: SC average length | WVS-AvL | 0.40–0.58 | 0.50 |
| | | Valve: SC average width | WVS-AvW | 0.19–0.35 | 0.26 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 7.21–13.2 | 11.4 |

* Abbreviations: see definitions in Material and methods.

shortly oval to oval, removed from eyes by a distance equal to 0.7–1.4 ocellus small diameter; fontanelle generally a tiny round or elongate marking. Antennae: generally 16 articles on alate individuals, rarely 17 (one individual out of 16), always shortened by amputation by three to four articles in queens and kings. Labrum: cupola shaped, wider than long. **Left mandible** with apical tooth on average longer than in most other species of the genus (Fig. 27) and always more prominent than first marginal; marginal teeth three in number but second one only suggested by an undulation of edge between first and third marginal teeth; only the apical tooth is acute in unworn specimens; premolar tooth with proximal end obscured or partly obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth always more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth

**Table 6.** *Isognathotermes fungifaber* clade: comparison of soldiers' head lengths.

| Species/Population | n | Range (mm) |
|---|---|---|
| *I. banksi* paratype | 2 | 2.63–2.71 |
| *I. comstocki* paratype | 2 | 2.40–2.43 |
| *I. schmidti* paratype | 2 | 2.65–2.76 |
| *I. fungifaber* paratype | 2 | 2.81–2.87 |
| Recent samples from Bipindi | 3 | 2.57–2.68 |
| Recent samples from Mbongé | 4 | 2.76–3.03 |
| All *I. fungifaber* samples | 129 | 2.37–3.11 |

bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a more or less sharp carina. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 3–5 and 7–11 branches respectively. **Gut** (only studied in some cases): enteric valve weakly developed and hardly comparable with workers' and soldiers' valves; odd PCs are slightly longer than even PCs (Fig. 6). Caecum present as a small amorphous button.

**Soldier**

Colour. **Head capsule** generally tending towards deep palette (Cd4–Cd6) becoming fader and darker (e.g., Cf5–Cf7) in long preserved samples; there is always a gradient from a darker frons to a paler back (e.g., from C6–C4), smooth and extended in 55% of the samples examined but more abrupt in the remaining 45% giving in some cases the impression that the head capsule is bicolorous (as in Fig. 13). Antennae and labrum sometimes concolorous or one level paler than head capsule. Mandibles dark (C6–C8) generally with an abrupt clearing on their bases (two palette levels) which is generally the same colour as frons; in long preserved samples, this clearing tends to disappear. **Thorax** and legs paler than head capsule (C2–C4) somewhat darker in long preserved samples. **Abdomen** grey to red-brown owing to digestive bolus, sometimes with a yellow to reddish-brown tinge on tergites.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Labrum** always with some large setae on lobes. **Thorax**: pro- and mesonotum with a small number of setae mainly located on margins. **Legs**: fore coxa bears at least one fine seta but not any spines (in 68% of the samples examined) or furnished with 1–3 spines on carina and 0–2 on ventral side; trochanter generally with some long lined-up setae, sometimes with six or seven spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively (the latter sometimes weakly developed) and a row of 6–15 spines along their shaft. **Abdomen**: tergites with some large setae, mainly or only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 5; Fig. 43). **Size**: the soldiers of *I. fungifaber* are among the smallest of the genus *Isognathotermes* (Fig. 28). **Head capsule**: always clearly sclerotised; appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with (in 86% of the samples examined) a narrowing near posterior third or fourth; from antennal sockets sides converge more or less clearly towards bases of mandibles; posterior side regularly rounded or sometimes (in 29% of the samples examined) with a short straight or even concave part in the middle. **In profile**: upper profile almost always slightly concave; angle between extended mandibles and frons varies from right to a little obtuse;

frons with a sketched or without any anterior hump. Gulamentum in ventral view always constricted in its posterior half, with sides of anterior part either roundly convex or forming an acute widening or even a kind of ear on each side. Antennae: of 14.5–15 articles. **Labrum**: always deeply bifurcate and wider than long, with sides varying from lyre-shaped (in 84% of the samples examined) to slightly convex; lobes angular, frequently with fine, whitish, or translucent tips; anterior margin concave. **Mandibles**: sabre-like strongly curved (on average, *I. fungifaber*, and *I. planifrons*, have the highest left mandible apical curvature index in the genus *Isognathotermes*); inner edges generally smooth with one distinct but small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible generally slightly more curved than left. **Thorax**: pronotum sellate, as wide as 55–70% of head width, with generally entire anterior and posterior margins. **Fore coxa** flanged ventrally resulting in a more or less sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in second half of abdomen. **Caecum** always rather small, best seen in ventral view, near centre of abdomen, lobed, sometimes (in 18% of the samples examined) with a lobe expanded somewhat forward. Arrangement of enteric valve cushions showing trilateral symmetry, the odd cushions being about 20% longer than the even cushions, generally without any crest or with crests very weakly developed.

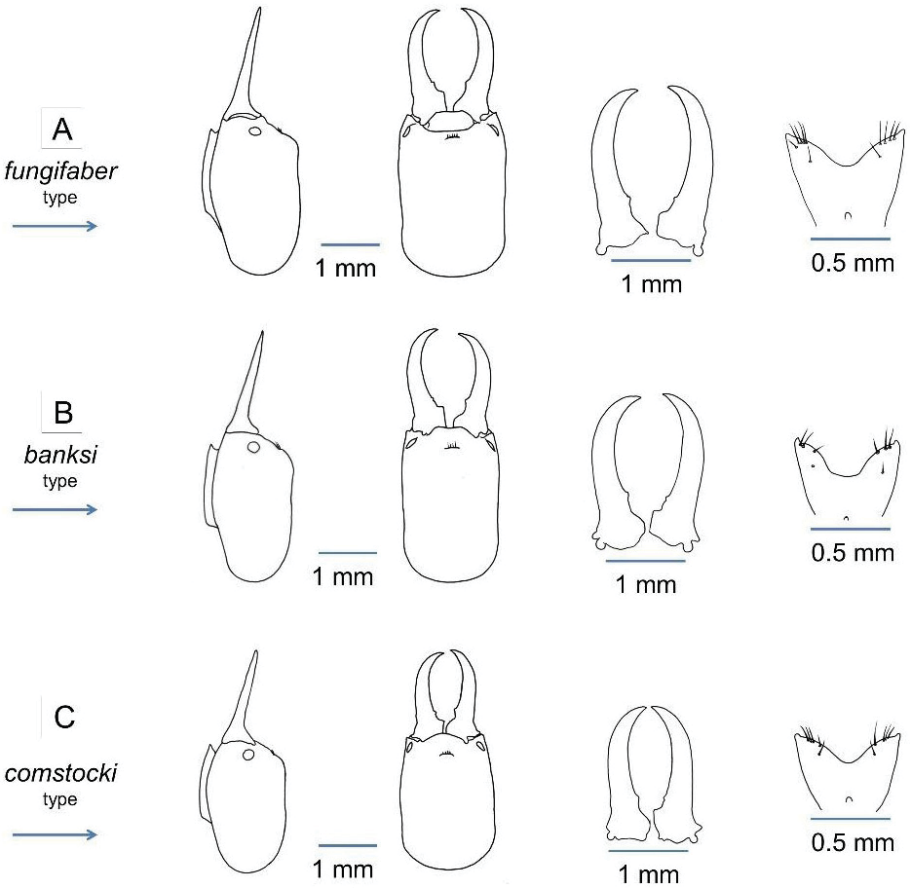


**Fig. 43** (continued on next page). *Isognathotermes fungifaber* (Sjöstedt, 1896) and junior synonym species: soldiers. Lateral and dorsal views of a soldier's head capsule, ventral view of its mandibles, and dorsal view of its labrum. **A**. From type colony of *Eutermes fungifaber* Sjöstedt, 1896 (DJ 0271). **B**. From type colony of *Mirotermes* (*Cubitermes*) *banksi* Emerson, 1928 (DJ 0287). **C**. From type colony of *Mirotermes* (*Cubitermes*) *comstocki* Emerson, 1928 (DJ 0273).

**Worker**

Colour. **Head capsule** pale (C1–C3) turning grey in long preserved samples. Antennae: proximal articles pale (C2–C3), distal articles always one to two levels darker (C4–C5). **Thorax**, nota, and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect, scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50 × or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa always carinated, bearing one fine seta and furnished with 3–5 spines on carina and 1–4 on ventral side; fore trochanter with 5–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively (the latter sometimes weakly developed) and a row of spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 5, Fig. 44). **Size**: the workers of *I. fungifaber* are, on average, among the smallest of the genus *Isognathotermes* (but with large overlapping on several other species: Fig. 31). **Head capsule**: weakly sclerotised (except mandibles). Antennae of 14.5 (rarely 14) articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal tooth well developed but with a blunt tip even when fresh, second marginal tooth faint (visible as an undulated edge and disappearing in worn mandibles), third marginal tooth with

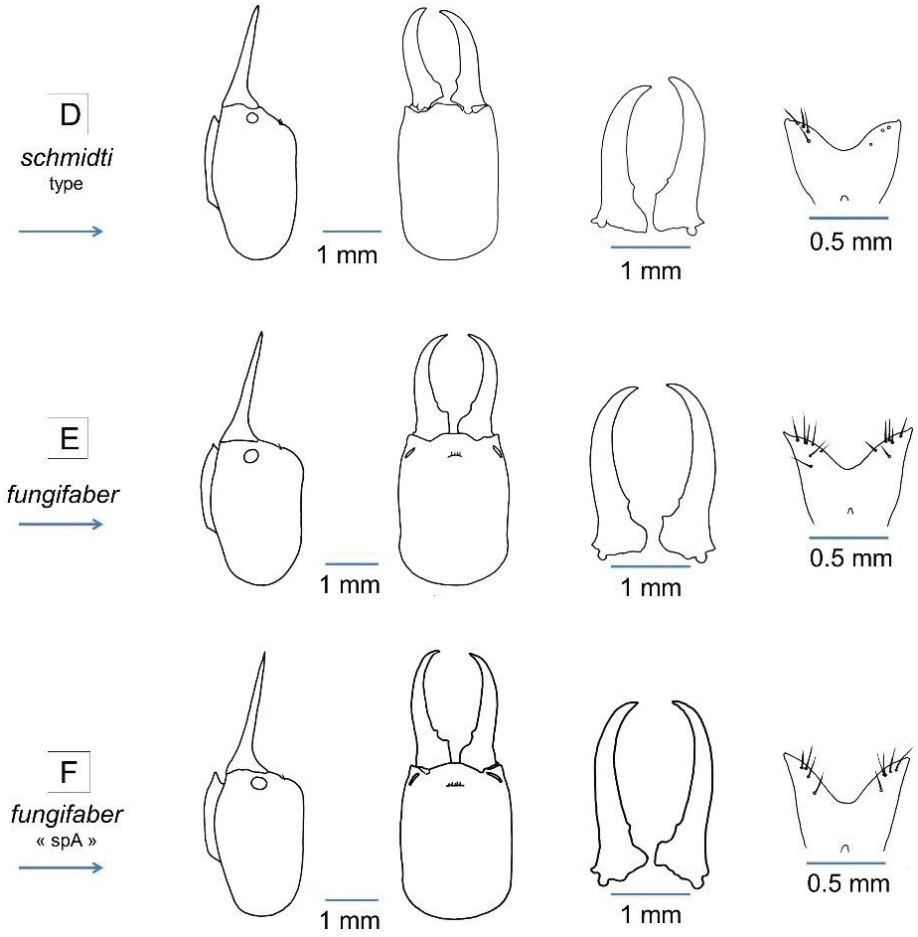


**Fig. 43** (continued). **D**. From type colony of *Mirotermes* (*Cubitermes*) *schmidti* Emerson, 1928 (DJ 0124). **E**. From a non-type colony of *I. fungifaber* (Sjöstedt, 1896) (DJ 0268). **F**. From a colony suspected to be a cryptic species of "*Cubitermes* aff. *subarquatus* spA" (DJ 0626).

a blunt tip; premolar tooth with its proximal end generally hidden under molar prominence; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 57–70% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in second half of abdomen. Arrangement of enteric valve cushions of the *fungifaber* pattern with triradial symmetry: the odd PCs, in their downstream part, are rather narrow and bear crests that are as high as or higher than they are wide, with long and strong bristles; supporting bristles are generally numerous:

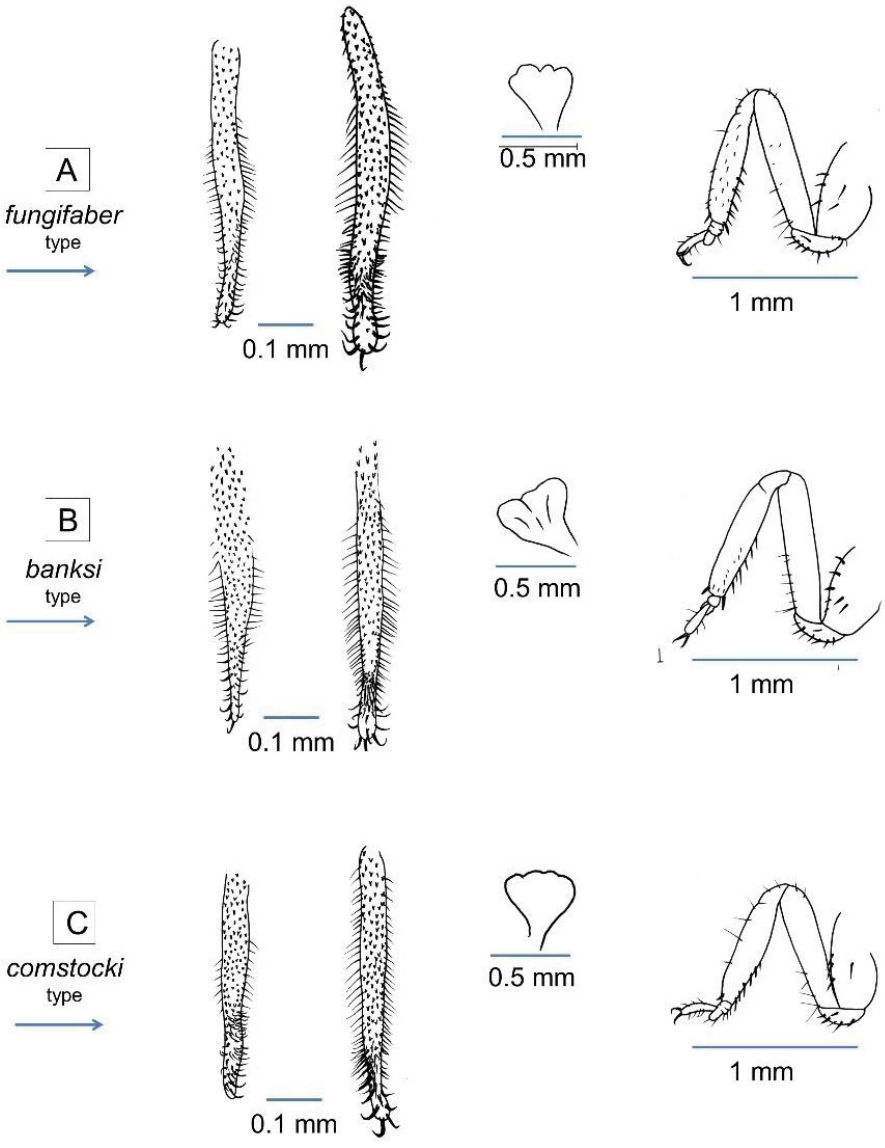


**Fig. 44** (continued on next page). *Isognathotermes fungifaber* (Sjöstedt, 1896) and junior synonym species: soldiers and workers. PC1s of soldier's and worker's enteric valves, worker's caecum and foreleg. **A**. From type colony of *Eutermes fungifaber* Sjöstedt, 1896 (DJ 0271). **B**. From type colony of *Mirotermes* (*Cubitermes*) *banksi* Emerson, 1928 (DJ 0287). **C**. From type colony of *Mirotermes* (*Cubitermes*) *comstocki* Emerson, 1928 (DJ 0273).

14–38 on each side of the odd PCs; only three samples (out of 54) show an intermediate EVA between the *fungifaber* and *finitimus* patterns; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum always rather small, visible in ventral view, near centre of abdomen, generally with two or three (up to five) short lobes, sometimes (in 14% of the samples examined) with a lobe expanded forward.

**Chorology-ecology**

The geographic distribution of *I. fungifaber* is clearly linked with humid, evergreen forests generally at less than 300 km from the Atlantic coast (Fig. 45): it includes from west to east the eastern Guinean forests, the Cross-Sanaga-Bioko coastal forests, the Atlantic Equatorial coastal forests, and

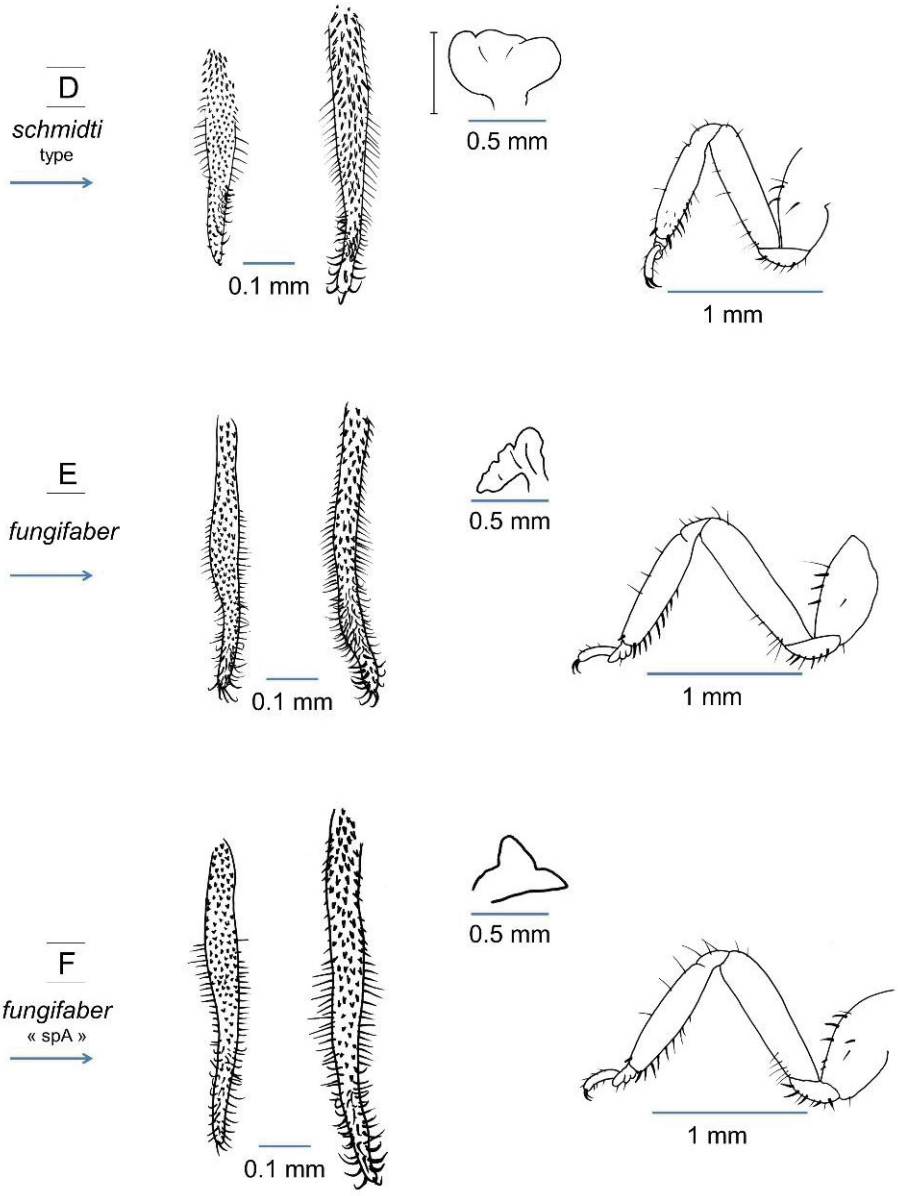


**Fig. 44** (continued). **D**. From type colony of *Mirotermes* (*Cubitermes*) *schmidti* Emerson, 1928 (DJ 0124). **E**. From a non-type colony of *Isognathotermes fungifaber* (Sjöstedt, 1896) (DJ 0268). **F**. From a colony suspected to be a cryptic species of "*Cubitermes* aff. *subarquatus* spA" (DJ 0626).

the Northwestern Congolian lowland forests ecoregions. This distribution partly resembles that of *I. planifrons* (that has a different EVA).

However, some samples of "dubious *I. fungifaber*" come from the northeastern Congolian lowland forests ecoregion without it being possible to guarantee the true species of these samples.

**Molecular data**

Thirteen mitogenomes of *I. fungifaber* are published alongside this work (GenBank accessions: see Supp. file 3 and 'Material examined'). These were collected from RCI, Cameroon, and Gabon. Most samples exhibit less than 1% dissimilarity with each other (Supp. file 4); except for sample DJ 0451 being the most dissimilar (1.50%) collected in one of the type localities of the species, and for sample DJ 0412, collected at the westernmost part of its distribution (1.32%). Our phylogenetic reconstructions based on the *COII* gene (Figure SF2) includes samples identified as "*Cubitermes* aff. *subarquatus* spA" (DJ 0623 and DJ 0626) and "spD" (DQ246541, DJ 0625) of Roy *et al.* (2006). The two mitogenomes of "spA" samples were successfully re-sequenced from the samples having produced the *COII* sequences published under accession DQ127302 and DQ127299 but not that of the "spD" sample. Therefore, the cryptic species status of the "spD" proposed by Roy *et al*. (2006) cannot be discussed here.

**Remarks**

*Isognathotermes fungifaber* is quite variable in size and much more in soldiers and workers than in imagines: we can deduct from Table 5 that variability in head width for *I. fungifaber* is 14% in imagines, but 31% in soldiers and 28% in workers

The soldiers of several samples have an intermediate morphology between *I. fungifaber* and *I. severus* (having the same kind of EVA): the easiest way to distinguish them is their origin since they seem to be

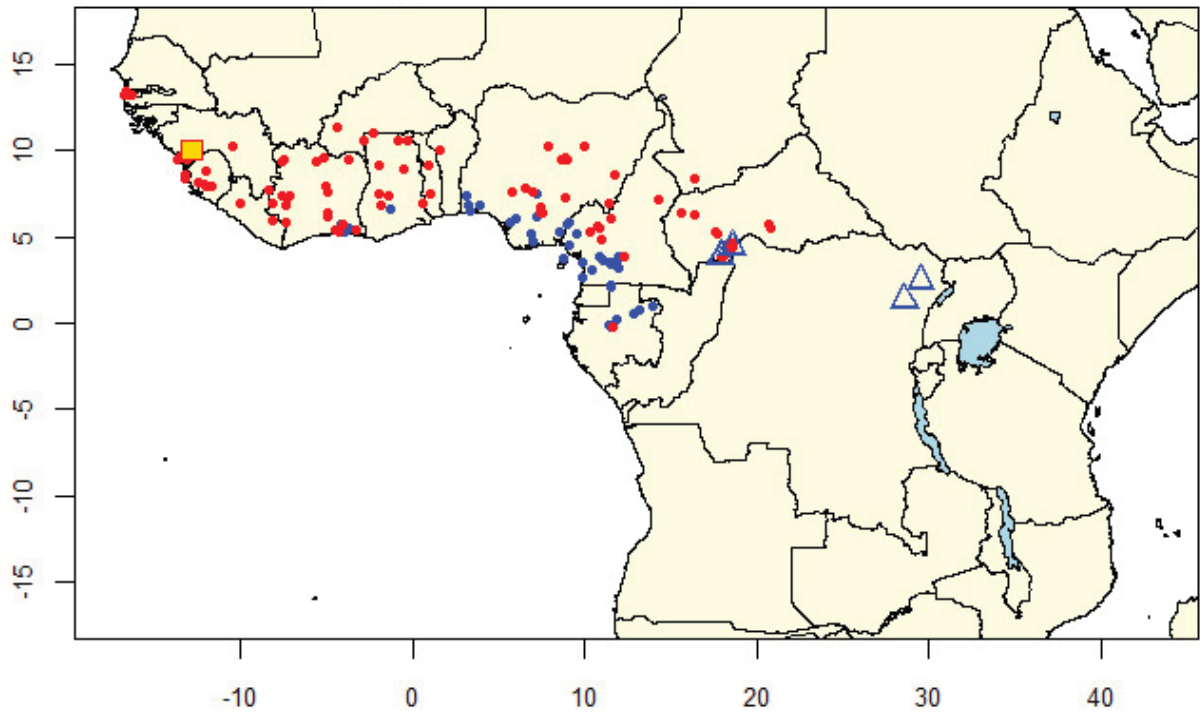


**Fig. 45.** Distribution map of *Isognathotermes fungifaber* (Sjöstedt, 1896) (blue dots); dubious *I. fungifaber* (blue empty triangles); *I. severus* (Silvestri, 1914) (red dots); *I. severus modestior* (Silvestri, 1914) (yellow square).

mutually exclusive. This is linked with their preferred habitat: on the one hand, *I. fungifaber* seems to be restricted to evergreen forests with, however, one known exception: DJ 0625, that was proposed as a cryptic species ("spD") by Roy *et al.* 2006: it was collected in the Doda gallery forest, surrounded with savannahs, north of La Lopé National Park, Gabon. On the other hand, *I. severus* is common in savanna landscapes of West and Central Africa (from Gambia to CAR) but also in orchards, secondary forests and, in some regions, it is also found in evergreen forest but only in places where *I. fungifaber* is absent as for example in RCI near the border with Liberia.

***Isognathotermes magniplanifrons*** Josens & Deligne sp. nov.
urn:lsid:zoobank.org:act:6AAAE9B8-6907-4716-BD3D-CB10E171B2D8
Figs 26–31, 46, distribution map: Fig. 47; Table 7

**Diagnosis**

The worker has a *finitimus* EVA and is among the large workers of the genus *Isognathotermes* (WHdW = 1.30–1.42 mm, Fig. 30) but rather difficult to distinguish from that of other species.

The soldier has generally a recognizable *finitimus* EVA; it is, on average, and with the soldier of *I. bulbifrons*, the largest of the *Isognathotermes* species with a *finitimus* EVA (SHdL = 2.98–3.77 mm, Fig. 28), with more curved mandibles (SMlc = 0.24–0.36 mm, Fig. 29), as in *I. planifrons*; its head is slightly bulbous (SHdC = 0.0–0.07 mm), less than that of *I. bulbifrons* and similar to *I. planifrons*.

The imago is, on average, and with the imago of *I. bulbifrons*, the largest in the genus *Isognathotermes* with a *finitimus* EVA (IHdW = 1.62–1.78 mm, Fig. 26); but its mandibular apico-marginal distance is generally smaller (IMlAmD = 0.20–0.24 mm, Fig. 27) than in *I. bulbifrons* (IMlAmD = 0.20–0.30 mm in *I. bulbifrons*).

*Isognathotermes magniplanifrons* sp. nov., is therefore morphologically close to *I. bulbifrons* but their chorology is different: to date, *I. magniplanifrons* is only known from the north-east of the DRC (Haut-Uele and Kivu provinces).

**Etymology**

The name *magniplanifrons* is from the Latin *magnus* (large) and the species name *planifrons*, referring to the resemblance with *I. planifrons* but with larger individuals in all castes.

**Material examined**

Twenty-four samples from two locations. Of the 24 old museum samples, one was initially labelled as *C. minitabundus*, one as *C. speciosus*, and 22 as *Cubitermes* sp.

**Holotype**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier; Irangi; 1°54′ S, 28°27′ E; 7 Sep. 1970; A. Wabo leg.; study code: DJ 0920; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059253.

**Paratypes**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker, ♂ (alate), ♀ (queen); same data as for holotype; BE RMCA INS.Iso.059935.

**Other material examined**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker; Moto; 3°2′ N, 29°30′ E; 1923; L. Burgeon leg.; study code: DJ 0070; initially *C. speciosus* in RMCA; BE RMCA INS.Iso.059258 •

soldier, worker; Irangi; 1°54′ S, 28°27′ E; 10 Apr. 1952; A. Wabo leg.; study code: DJ 0896; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059256 • soldier, worker, ♂ (alate); Irangi; 1°54′ S, 28°27′ E; 4 Sep. 1970; A. Wabo leg.; study code: DJ 0894; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059252 • soldier, worker, ♂ (king); Irangi; 1°54′ S, 28°27′ E; 4 Sep. 1970; A. Wabo leg.; study code: DJ 0919; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059251 • soldier, worker, ♂ (king), ♀ (queen); Irangi; 1°54′ S, 28°27′ E; 6 Sep. 1970; A. Wabo leg.; study code: DJ 0929; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059254 • soldier; Irangi; 1°54′ S, 28°27′ E; 21 Sep. 1970; A. Wabo leg.; study code: DJ B262; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059238 • soldier; Irangi; 1°54′ S, 28°27′ E; 21 Sep. 1970; A. Wabo leg.; study code: DJ B263; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059239 • soldier; Irangi; 1°54′ S, 28°27′ E; 21 Sep. 1970; A. Wabo leg.; study code: DJ B264; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059240 • soldier; Irangi; 1°54′ S, 28°27′ E; 21 Sep. 1970; A. Wabo leg.; study code: DJ B265; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059241 • soldier; Irangi; 1°54′ S, 28°27′ E; 20 Sep. 1970; A. Wabo leg.; study code: DJ B267; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059236 • soldier; Irangi; 1°54′ S, 28°27′ E; 20 Sep. 1970; A. Wabo leg.; study code: DJ B268; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059237 • soldier; Irangi; 1°54′ S, 28°27′ E; 20 Sep. 1970; A. Wabo leg.; study code: DJ B269; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059243 • soldier; Irangi; 1°54′ S, 28°27′ E; 25 Jan. 1972; A. Wabo leg.; study code: DJ B272; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059246 • soldier; Irangi; 1°54′ S, 28°27′ E; 28 Feb. 1972; A. Wabo leg.; study code: DJ B303; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059249 • soldier; Irangi; 1°54′ S, 28°27′ E; 13 Mar. 1972; A. Wabo leg.; study code: DJ B304; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059250 • soldier; Irangi; 1°54′ S, 28°27′ E; 31 Mar. 1972; A. Wabo leg.; study code: DJ B261; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059235 • soldier; Irangi; 1°54′ S, 28°27′ E; 13 Mar. 1972; A. Wabo leg.; study code: DJ B274; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059248 • soldier; Irangi; 1°54′ S, 28°27′ E; 1 Apr. 1972; A. Wabo leg.; study code: DJ B273; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059247 • soldier; Irangi; 1°54′ S, 28°27′ E; 9 May 1972; A. Wabo leg.; study code: DJ B270; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059244 • soldier, ♀ (alate); Irangi; 1°54′ S, 28°27′ E; 1972 ?; A. Wabo leg.; study code: DJ B316; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059255 • soldier, ♀ (alate); Irangi; 1°54′ S, 28°27′ E; 1972 ?; A. Wabo leg.; study code: DJ B317; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059257 • soldier; Irangi; 1°54′ S, 28°27′ E; 11 Sep. 1972; A. Wabo leg.; study code: DJ B266; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059242 • soldier; Irangi; 1°54′ S, 28°27′ E; 15 Sep. 1972; A. Wabo leg.; study code: DJ B271; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059245.

### Historical review

This species is described here. It was collected in 1923 in the Haut-Uele Province, DRC (and misidentified), and in 1970 in Kivu, DRC. This species is known from 24 samples, 23 of which come from the same locality.

### Description

#### Imago

Colour. **Head capsule**: well sclerotised, dark, C6–C7; fontanelle concolorous or almost so with head capsule. Postclypeus C5–C7 concolorous or slightly paler (one level) than head capsule. Antennae C4–C6 without any difference between proximal and distal articles. **Thorax**: pronotum C5–C6, as head capsule or slightly paler (one level); meso- and metanotum C4–C6, as pronotum or slightly paler. Legs C4–C5. Wings hyaline with brown to grey tinge (Cf3), anterior veins darker. **Abdomen**: tergites C4–C6. Sternites appreciably paler in middle (C3–C4) with both sides darker (C4–C6); posterior sternites darker (C4–C6) than anterior.

Setation. **Head capsule** with some prominent setae, mainly near the eyes, and a higher density of shorter, finer setae everywhere. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at magnification 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and many shorter ones in middle; meso- and metanotum without any visible setae or with some fine, pale setae, arranged in a medio-longitudinal strip, visible at 40×; generally three to four larger setae on metanotum. **Legs** very pilose, furnished (among numerous fine setae) with some fine spines: 6–10 on the carina of fore coxa and 0–2 on the ventral side; tibia pilose; fore, mid, and hind tibia furnished with 20–30 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 7, Fig. 46). **Size**: the imagines of *I. magniplanifrons* sp. nov. are, on average, rather large (but not the largest of the genus *Isognathotermes*) (IHdW = 1.62–1.78 mm). **Head capsule**: compound eyes nearly round; fontanelle generally a tiny elongate marking; ocelli nearly round to oval removed from eyes by a distance about equal to 0.7–1.1 ocellus small diameter. Antennae: 16 articles on alate individuals, shortened by amputation by five to six articles in queens and kings. Labrum: cupola shaped. **Left mandible** with mandibular apico-marginal distance clearly smaller (IMlAmD = 0.20–0.24 mm) than in *I. bulbifrons* (Fig. 27); apical tooth longer and more prominent than first marginal; marginal teeth three in number but second one only suggested by a slight undulation of edge between first and third marginal teeth; only the apical tooth is acute in unworn specimens; premolar tooth with proximal end obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth longer and more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and slightly narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a sharp carina. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 2–3 and 12–13 branches, respectively.

**Soldier**

Colour. **Head capsule** generally C6–C7, paler (C5) in a long-preserved sample; with a gradient from a darker frons to a paler back (e.g., C6 → C4). Gulamentum concolorous with head. Antennae and labrum somewhat paler (1–2 levels) than head capsule. Mandibles dark (C8) with or without a slight clearing on their bases (one palette level) which is generally the same colour as frons. **Thorax**, nota and legs paler than head capsule (C4–C5). **Abdomen** grey to red-brown owing to digestive bolus, sometimes with a yellow tinge on tergites.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of hair-like setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Labrum** always with 5–7 large setae on each lobe. **Thorax**: pro- and mesonotum with some setae located mainly on margins. **Legs**: fore coxa furnished with 1–2 spines on carina and not any one on ventral side; trochanter generally with some long lined-up setae, sometimes with two spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively; all tibiae furnished with a row of 6–15 spines. **Abdomen**: tergites with some large setae, mainly or only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 7; Fig. 46). **Size**: the soldiers of *I. magniplanifrons* sp. nov. are, on average, the largest of the genus *Isognathotermes* (Fig. 28). **Head capsule**: always clearly sclerotised

and appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a narrowing near posterior third or fourth; from antennal sockets sides converge more or less clearly towards bases of mandibles. **In profile**: upper profile slightly concave (as in *I. planifrons*, much less than in *I. bulbifrons*); frons with no hump overhanging the fontanelle. Gulamentum in ventral view always more or less constricted in its posterior half, with sides of anterior part either forming an acute widening or even a kind of ear on each side; generally, with a flat posterior part from side view. Antennae: of 15 articles. **Labrum**: always deeply bifurcate and wider than long, with lyre-shaped sides; lobes angular, with fine, whitish, or translucent tips; anterior margin concave. **Mandibles**: sabre-like; inner edges smooth with one small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible generally slightly more curved than left. **Thorax**: pronotum sellate, as wide as 57–63% of head width, with generally entire anterior and posterior margins. **Fore coxa** flanged ventrally resulting in a carina. **Gut**: enteric valve seating

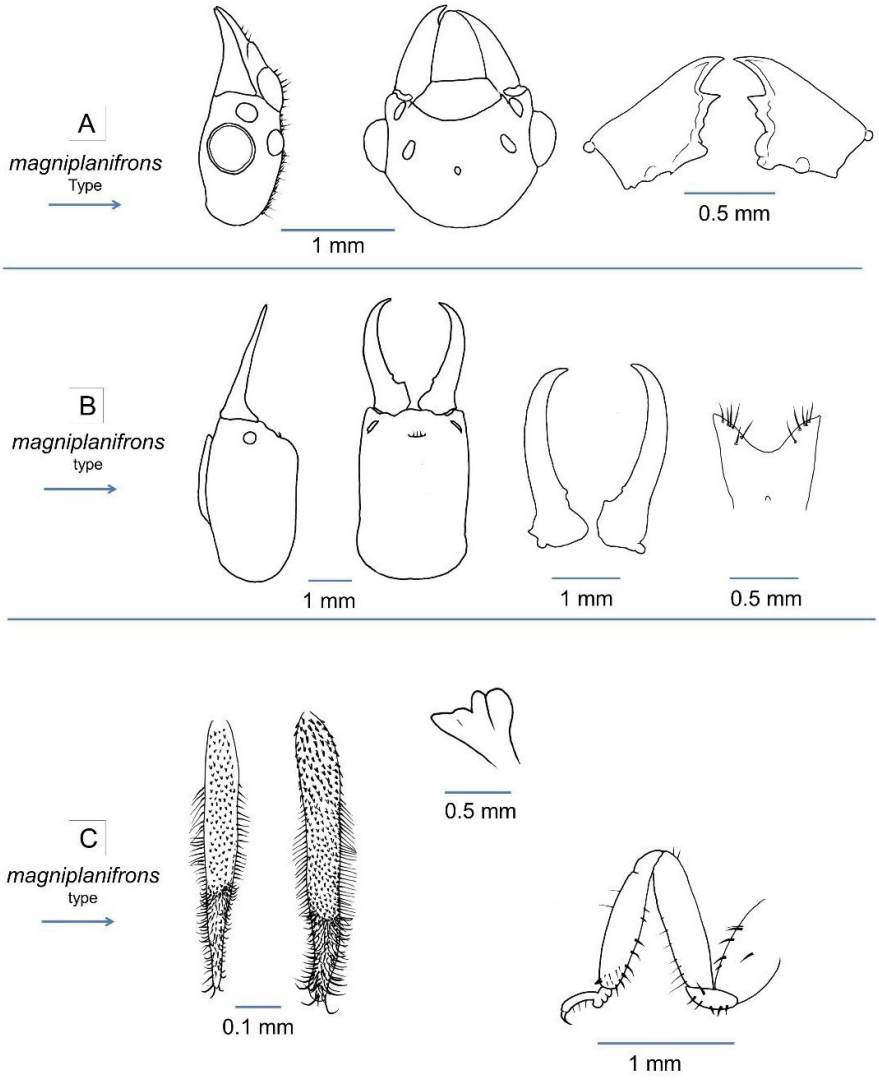


**Fig. 46.** *Isognathotermes magniplanifrons* Josens & Deligne sp. nov.: imago, soldier, and worker. **A**. Lateral and dorsal views of the head capsule, and dorsal view of mandibles of an alate male from the type colony of *I. magniplanifrons* (DJ 0920). **B**. Lateral and dorsal views of the head capsule; ventral view of mandibles; and dorsal view of labrum of a soldier from the type colony of *I. magniplanifrons* (DJ 0920). **C**. PC1s of soldier's and worker's enteric valves; caecum and foreleg of this worker from the type colony of *I. magniplanifrons*.

**Table 7.** *Isognathotermes magniplanifrons* Josens & Deligne sp. nov.: ranges of significant measures in the three castes, in alphabetical orders of the "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 8) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.43–0.48 | 0.47 |
| | | Head: width across the eyes | IHdW | 1.62–1.78 | 1.71 |
| | | Left mandible: A-m1 distance | IMlAmD | 0.20–0.24 | 0.21 |
| | | Ocellus: large diameter | IOc*D* | 0.17–0.21 | 0.19 |
| | | Postclypeus: width | IPcW | 0.77–0.85 | 0.81 |
| | | Pronotum: maximal width | IPnW | 1.40–1.63 | 1.56 |
| | | Hind tibia: length | IT3L | 1.99–2.29 | 2.17 |
| | | Wing: length (n= 4) | IWgL | 14.2–14.3 | NA |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.16–1.46 | 1.29 |
| Soldiers (n = 24) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.00–0.07 | 0.02 |
| | | Head: length | SHdL | 2.98–3.77 | 3.62 |
| | | Head: width | SHdW | 2.07–2.49 | 2.40 |
| | | Left mandible: lesser sagitta | SMlc | 0.24–0.36 | 0.32 |
| | | Left mandible: ventral length | SMlL | 2.45–2.99 | 2.81 |
| | | Hind tibia: length | ST3L | 1.77–2.01 | 1.91 |
| | Indices | Head elongation index | SHdL/SHdW | 1.37–1.59 | 1.51 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.09–0.13 | 0.11 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.76–1.10 | 0.96 |
| Workers (n = 6) | Raw measures (mm) | Head: width | WHdW | 1.30–1.42 | 1.32 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.19–0.21 | 0.19 |
| | | Left mandible: total length | WMlL | 0.63–0.68 | 0.64 |
| | | Hind tibia: length | WT3L | 1.39–1.57 | 1.43 |
| | | Valve: PC average length | WVP-AvL | 0.61–0.70 | 0.61 |
| | | Valve: PC average width | WVP-AvW | 0.08–0.10 | 0.08 |
| | | Valve: SC average length | WVS-AvL | 0.48–0.52 | 0.48 |
| | | Valve: SC average width | WVS-AvW | 0.22–0.28 | 0.22 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 6.54–9.38 | 7.80 |

* Abbreviations: see definitions in Material and methods.

on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions showing trilateral symmetry: the odd cushions are on average 14% longer than the even cushions, generally without any hump or with humps weakly developed; however, the pilosity becoming abruptly very dense shows the place where a hump is expected (Fig. 46); secondary cushions wide at the upstream end narrowing noticeably downstream with a homogeneous spine scattering. **Caecum** always rather small, best seen in ventral view, near centre of abdomen, lobed (2–4 small lobes).

**Worker**

Colour. **Head capsule** pale (C1–C3) turning grey in long preserved samples. Antennae: proximal articles pale (C2–C3), distal articles always one to two levels darker (C4–C5). **Thorax**, nota and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50 × or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa always carinated, bearing one fine seta and furnished with 3–5 spines on carina and 1–2 on ventral side; fore trochanter with 6–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 7, Fig. 46). **Size**: the workers of *I. magniplanifrons* sp. nov. are, on average, among the largest of the genus *Isognathotermes* (but with large overlapping on several other species: Fig. 30). **Fore coxa** flanged ventrally resulting in a sharp carina. **Head capsule**: weakly sclerotised (except mandibles). Antennae: 14.5 articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal well developed but with a blunt tip even when fresh, second marginal faint (visible as an undulated edge), third marginal with a blunt tip; premolar tooth with its proximal end hidden under molar prominence; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal well developed with a sharp tip when fresh; second marginal smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 70% of head width. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions of the *finitimus* pattern with triradial symmetry: the odd PCs, in their downstream part, are wide and bear at that place a high density of rather short bristles on a globular bulge; supporting bristles are generally numerous: 20–38 on each side of the odd PCs; secondary cushions are wide at the upstream

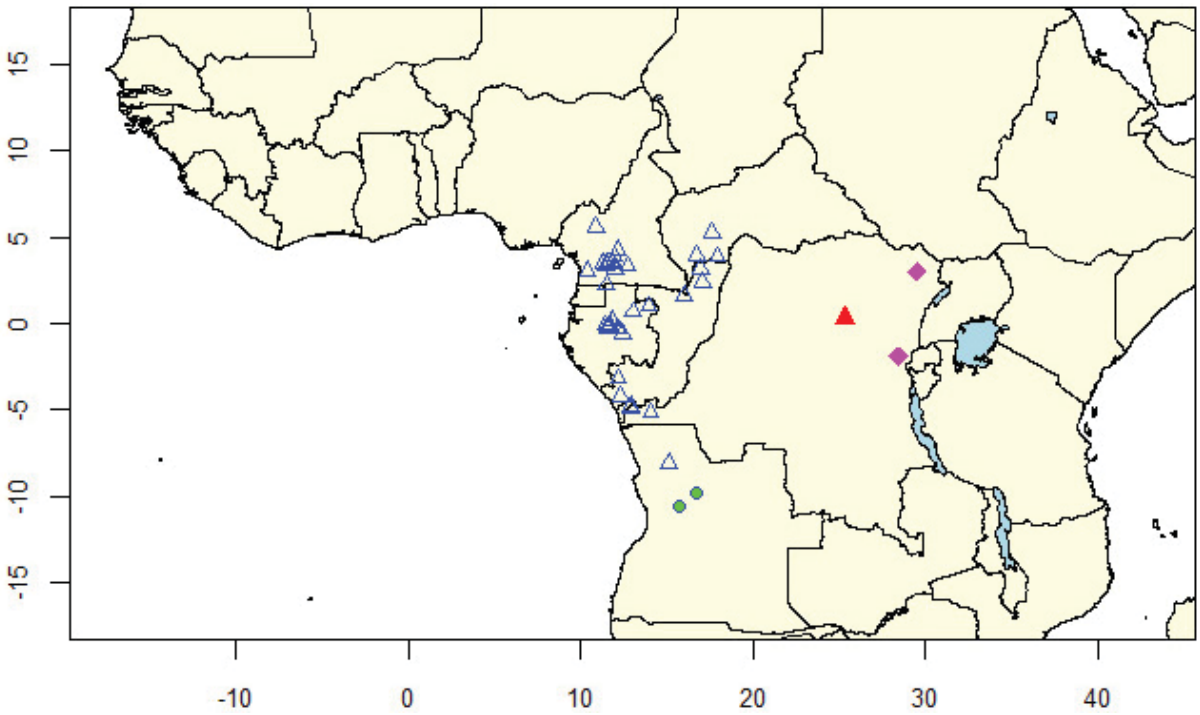


**Fig. 47.** Distribution map of *Isognathotermes acristatus* Josens & Deligne sp. nov. (green dots); *I. magniplanifrons* Josens & Deligne sp. nov. (pink diamonds); *I. planifrons* (Sjöstedt, 1924) (blue empty triangles); *I. similifinitimus* Josens & Deligne sp. nov. (red triangle).

end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum always rather small, visible in ventral view, near centre of abdomen, shortly lobed (3–4 small lobes).

**Chorology-ecology**

The geographic distribution of *I. magniplanifrons* sp. nov. is linked with the northeastern Congolian lowland forests ecoregion (Fig. 47).

**Molecular data**

No genetic sequence is currently available.

***Isognathotermes minitabundus*** (Sjöstedt, 1913)
Figs 2, 8–12, 26–31, 33, 48, distribution map: Fig. 49; Table 8

*Eutermes* (*Cubitermes*) *minitabundus* Sjöstedt, 1913: 368–369 (soldier only).

*Eutermes* (*Trinervitermes*) *carbo* – Sjöstedt 1924a: 42 (the alate imago described under this name actually belonged to *Cubitermes minitabundus*).
*Isognathotermes minitabundus* – Sjöstedt 1926: 216–217, fig. 48. — Hellemans *et al.* 2021: 233.
*Cubitermes minitabundus* – Snyder 1949: 161. — Harris 1958: 13–14, figs 20–23. — Williams 1966: 90–92, figs 6, 22, 38, 54, 72. — Bouillon & Vincke 1971: 269. — Krishna *et al.* 2013: 1927. — Josens & Deligne 2019: 60–61.

**Diagnosis**

This species is very close to *I. ugandensis* (and *I. severus*).

The worker has a *fungifaber* EVA (Fig. 4) but in 3% of the samples examined, it has an EVA intermediate between the *fungifaber* and *finitimus* patterns. It is among the medium-sized workers of the genus *Isognathotermes* (Fig. 30). As in *I. ugandensis*, the premolar tooth on left mandible is more apparent than in most other species.

The soldier is among the large-sized soldiers in the genus *Isognathotermes* (Fig. 28), on average somewhat larger than that of *I. ugandensis*; it has a left mandible very slightly curved to almost straight at the base and generally less curved than the right mandible (SMlc/SMrc = 0.51–1.03, with a weaker asymmetry than in *I. ugandensis*: SMlc/SMrc = 0.92–1.14), resulting in a low soldiers' left mandible apical curvature index (Fig. 29); its head is generally clearly bulbous (but this is shared with *I. ugandensis* and *I. severus*, and also with *I. bulbifrons* which has a *finitimus* EVA).

The imago is among the medium- to large-sized imagines in the genus *Isognathotermes* (Figs 26, 65); the eyes and ocelli are relatively small, as a consequence, the eye to ocellus minimal distance index is high: IEyOcD/IOc*d* = 1.16–1.61 (vs 0.54–1.58 in *I. ugandensis*). The premolar tooth on left mandible is better seen than in most other species (but this is shared with *I. severus* and *I. ugandensis*).

This species is also defined by its ecology and chorology: it is the southernmost species of the genus *Isognathotermes*, it has been found in forest-savannah mosaics and woodlands (miombo) to the south and east of the Congolian forests (Fig. 49).

**Etymology**

The epithet *minitabundus* from the Latin *minitabundus* (threatening) probably refers to a supposed threat.

**Material examined**

Thirty-six samples from 15 locations. Of the 24 old museum samples, 18 were initially labelled as *C. minitabundus*, four as *C. ugandensis*, one as *Eutermes fungifaber* and one as *Cubitermes* sp.

**Syntype of *Eutermes* (*Cubitermes*) *minitabundus* (Sjöstedt, 1913)**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier; Lumata; 12°0.05′ S, 27°31′ E; 6 Jun. 1912; J. Bequaert leg.; study code: DJ 0129; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059280.

**Other material examined**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker; Hemptine Saint Benoît [= Bunkonde]; 6°18′ S, 22°31′ E; 1912; P. Callewaert leg.; study code: DJ 0140; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059284 • soldier, worker, ♀ (queen); Luluabourg [= Kananga]; 5°53′ S, 22°26′ E; 21 Jan. 1912; P. Callewaert leg.; study code: DJ 0094; initially *Eutermes fungifaber* in RMCA; BE RMCA INS.Iso.059274 • soldier, worker; Hemptine Saint Benoît [= Bunkonde]; 6°18′ S, 22°32′ E; 26 Jan. 1912; P. Callewaert leg.; study code: DJ 0015; initially *C. minitabundus* in RMCA; BE RMCA INS. Iso.059286 • soldier, worker, ♀ (queen); Luluabourg [= Kananga]; 5°53′ S, 22°26′ E; 26 Oct. 1921; P. Callewaert leg.; study code: DJ 0139; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059283 • soldier, worker, ♀ (queen); Luluabourg [= Kananga]; 5°53′ S, 22°26′ E; 26 Oct. 1921; P. Callewaert leg.; study code: DJ 0157; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059276 • soldier, worker, ♀ (alate), ♂ (alate), ♀ (queen); Luluabourg [= Kananga]; 5°53′ S, 22°26′ E; 27 Oct. 1921; P. Callewaert leg.; study code: DJ 0144; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059285 • soldier, worker, ♀ (alate), ♂ (alate), ♀ (queen); Luluabourg [= Kananga]; 5°53′ S, 22°26′ E; 27 Oct. 1921; P. Callewaert leg.; study code: DJ 0155; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059278 • soldier, worker, ♀ (alate), ♂ (alate), ♀ (queen); Luluabourg [= Kananga]; 5°53′ S, 22°26′ E; 27 Oct. 1921; P. Callewaert leg.; study code: DJ 0156; initially *C. minitabundus* in RMCA; BE RMCA INS. Iso.059275 • soldier, worker, ♀ (alate); Luluabourg [= Kananga]; 5°53′ S, 22°26′ E; 27 Oct. 1921; P. Callewaert leg.; study code: DJ 0158; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059277 • soldier, worker, ♀ (alate); Luluabourg [= Kananga]; 5°53′ S, 22°26′ E; 27 Oct. 1921; P. Callewaert leg.; study code: DJ 0728; initially *C. minitabundus*; AMNH • soldier, worker; Upemba N.P., Lusinga; 8°56.4′ S, 27°8′ E; 17 Jul. 1947; G.F. De Witte *et al.* leg.; study code: DJ 0137; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059282 • soldier, worker, ♂ (king), ♀ (queen); Upemba N.P., Lusinga; 8°56.4′ S, 27°8′ E; 17 Jul. 1947; G.F. De Witte *et al.* leg.; study code: DJ 0138; initially *C. minitabundus* in RMCA; BE RMCA INS.Iso.059281 • soldier, worker, ♂ (king); Keyberg (Lubumbashi); 11°47′ S, 27°25′ E; 21 Apr. 1948; A. Emerson leg.; study code: DJ 0729; initially *C. minitabundus* in AMNH • soldier, worker, ♂ (king); Likasi; 10°59.3′ S, 26°4.27′ E; 1 Dec. 1971; P. Vincke leg.; study code: DJ 0898; initially *C. ugandensis* in RMCA; BE RMCA INS.Iso.059271 • soldier, worker, ♂ (alate); Kundelungu P.N.; 10°27′ S, 27°42′ E; 15 Oct. 1972; P. Vincke leg.; study code: DJ 0899; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059272 • soldier, worker; Kipopo; 11°33′ S, 27°21′ E; 2 Nov. 1972; P. Vincke leg.; study code: DJ 0908; initially *C. ugandensis* in RMCA; BE RMCA INS. Iso.059273 • soldier, worker; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.3′ E; 11 Feb. 2011; G. Josens leg.; study code: DJ 0010; BE RMCA INS.Iso.059279 • soldier, worker; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.3′ E; Jun. 2016; P. Kasangij leg.; study code: DJ 0348; GenBank nos MN646704 (*COI*), MN685906 (*COII*), MN685967 (*28S*), PQ679238 (mitogenome); BE RMCA INS. Iso.059270 • soldier; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.3′ E; 3 Jun. 2016; P. Kasangij leg.; study code: DJ B008; BE RMCA INS.Iso.059259 • soldier; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.3′ E; 3 Jun. 2016; P. Kasangij leg.; study code: DJ B009; GenBank no PQ679225 (mitogenome); BE RMCA INS.Iso.059260 • soldier; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.3′ E; 3 Jun. 2016; P. Kasangij leg.; study code: DJ B010; BE RMCA INS.Iso.059261 • soldier; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.3′ E; 3 Jun. 2016; P. Kasangij leg.; study code: DJ B011; BE RMCA INS.Iso.059262 • soldier; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.18′ E;

14 Jun. 2016; P. Kasangij leg.; study code: DJ B012; BE RMCA INS.Iso.059263 • soldier; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.18′ E; 14 Jun. 2016; P. Kasangij leg.; study code: DJ B014; BE RMCA INS.Iso.059264 • soldier; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.2′ E; 14 Jun. 2016; P. Kasangij leg.; study code: DJ B017; BE RMCA INS.Iso.059265 • soldier; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.2′ E; 14 Jun. 2016; P. Kasangij leg.; study code: DJ B018; BE RMCA INS. Iso.059266 • soldier; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.2′ E; 22 Jun. 2016; P. Kasangij leg.; study code: DJ B019; BE RMCA INS.Iso.059267 • soldier; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.2′ E; 22 Jun. 2016; P. Kasangij leg.; study code: DJ B020; BE RMCA INS.Iso.059268 • soldier; Kisangwe, Mikembo sanctuary; 11°29.1′ S, 27°39.2′ E; 2 Jul. 2016; P. Kasangij leg.; study code: DJ B021; BE RMCA INS.Iso.059269.

ZAMBIA • soldier, worker; Kitwe, Mwekera Forest reserve; 12°52′ S, 28°21′ E; 25 Jan. 1956; W.G.H. Coaton leg.; study code: DJ 0696; initially *C. minitabundus*; NHMUK 13671922 • soldier, worker; Samfya; 11°22′ S, 29°33′ E; 27 Jan. 1957; W.G.H. Coaton leg.; study code: DJ 0665; initially *C. ugandensis*; NHMUK 13672010 • soldier, worker; Chembe; 11°57.5′ S, 28°44′ E; 28 Jan. 1957; W.G.H. Coaton leg.; study code: DJ 0685; initially *C. minitabundus*; NHMUK 13671920 • soldier; Ndola–Kitwe road; 12°59′ S, 28°24.5′ E; 30 Jan. 1957; W.G.H. Coaton leg.; study code: DJ 0694; initially *C. minitabundus*; NHMUK 13671921 • soldier, worker; Kasama–Mpika road; 11°0′ S, 31°0′ E; 19 Dec. 1969; M.G. Bingham leg.; study code: DJ 0695; initially *C. minitabundus*; NHMUK 13671925 • soldier, worker; Chililabombwe; 12°23′ S, 27°50′ E; 22 Dec. 1970; M.G. Bingham leg.; study code: DJ 0693; initially *C. minitabundus*; NHMUK 13671926.

**Historical review**

Sjöstedt (1913: 368–369) described the soldier of his species under the name *Eutermes* (*Cubitermes*) *minitabundus.*

Schmitz (1916: 119) referred to this species under the name *Cubitermes minitabundus*.

Sjöstedt (1924a: 42) described the imago of *Eutermes* (*Trinervitermes*) *carbo* that was in fact the imago of *Cubitermes minitabundus* (see Sands 1965: 98 and Krishna *et al.* 2013: 1858).

Sjöstedt (1926: 216–217) transferred the species in a new, monotypic genus (*Isognathotermes*). He provided figures of the soldier and a description of imago and worker.

Snyder (1949: 161) catalogued this species under the name *Cubitermes minitabundus* and housed it in the sub-family Termitinae.

Harris (1958: 13–14) provided measurements and figures of imago and soldier on basis of specimens collected in the Upemba National Park (Haut-Katanga Province, DRC).

Williams (1966: 90–92) provided a detailed redescription of imago and soldier along with measurements and figures.

Bouillon & Vincke (1971: 269) described the enteric valve of *C. minitabundus* as belonging to the first of three types, the “simple type” without any spatula.

Krishna *et al.* (2013: 1927) referred to this species under the name *Cubitermes minitabundus* and housed it in the sub-family Cubitermitinae.

Josens & Deligne (2019: 39–42) placed this species within the *fungifaber* valve pattern group.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

**Redescription**

**Imago**

Colour. **Head capsule**: well sclerotised, fresh samples very dark, C6–C8 (C5–C7 in long preserved samples); fontanelle concolorous or almost so with head capsule. Postclypeus C5–C7 concolorous or slightly paler (one level) than head capsule. Antennae C4–C6 without any difference between proximal and distal articles. **Thorax**: pronotum C5–C7, as postclypeus, concolorous or one level paler than head capsule; meso- and metanotum C4–C7, sometimes somewhat paler than pronotum. Legs C3–C5; tibia usually concolorous with femur. Wings hyaline with brown to grey tinge (Cf2–Cf3), anterior veins darker. **Abdomen**: tergites C4–C6. Sternites appreciably paler in middle (C2–C3) with both sides darker (C3–C4); posterior sternites darker (C3–C4) than anterior.

Setation. **Head capsule**, with some prominent setae set amongst a high density of short, fine setae forming a dense mat. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and shorter ones in middle; meso- and metanotum with some fine, pale setae, arranged in a medio-longitudinal strip, generally visible at 20–80×, but rarely even not visible at 80×; when present, these fine setae do not extend over the posterior margin; sometimes a small number of large setae are present on metanotum. **Legs** very pilose, furnished (among numerous fine setae) with some stronger setae: 8–12 on the carina of fore coxa and 0–6 on the ventral side of fore coxa and trochanter; tibia pilose fore, mid, and hind tibia furnished with 20–40 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 8; Fig. 48). **Size**: the imagines of *I. minitabundus* are among the medium- to large-sized species of the genus *Isognathotermes* (as *I. ugandensis*) (Fig. 26). **Head capsule**: compound eyes nearly round to oval; ocelli shortly to moderately oval, removed from eyes with a higher eye to ocellus minimal distance index: IEyOcD/IOc*d* = 1.16–1.61 (0.54–1.58 in *I. ugandensis*); fontanelle generally a tiny round or elongate marking. Antennae: 16 articles on alate individuals, always shortened by amputation by two to five articles in queens and kings. Labrum: cupola shaped, wider than long. **Left mandible** with apical tooth medium to large sized (IMlAmD = 0.21–0.27 mm vs 0.19–0.27 in *I. ugandensis*, Fig. 27) and always more prominent than first marginal; marginal teeth three in number but second one only suggested by an undulation of edge between first and third marginal teeth; only the apical tooth is acute in unworn specimens; premolar tooth with proximal end hardly obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth always more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a carina. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 2–4 and 10–12 branches, respectively. **Gut** not studied.

**Soldier**

Colour. **Head capsule** generally tending towards deep palette (Cd4–Cd6) becoming fader (Cf4–Cf5) in long preserved samples; there is generally a smooth gradient from a darker frons to a paler back. Antennae and labrum generally one to two palette levels paler than head capsule. Mandibles dark (C6–C8) generally with an abrupt clearing on their bases (two levels) which is generally the same colour

as frons; in long preserved samples, this clearing tends to disappear. **Thorax** and legs paler than head capsule (C3–C5) somewhat darker in long preserved samples. **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of very fine, bent setae (visible only at high magnification, 50×

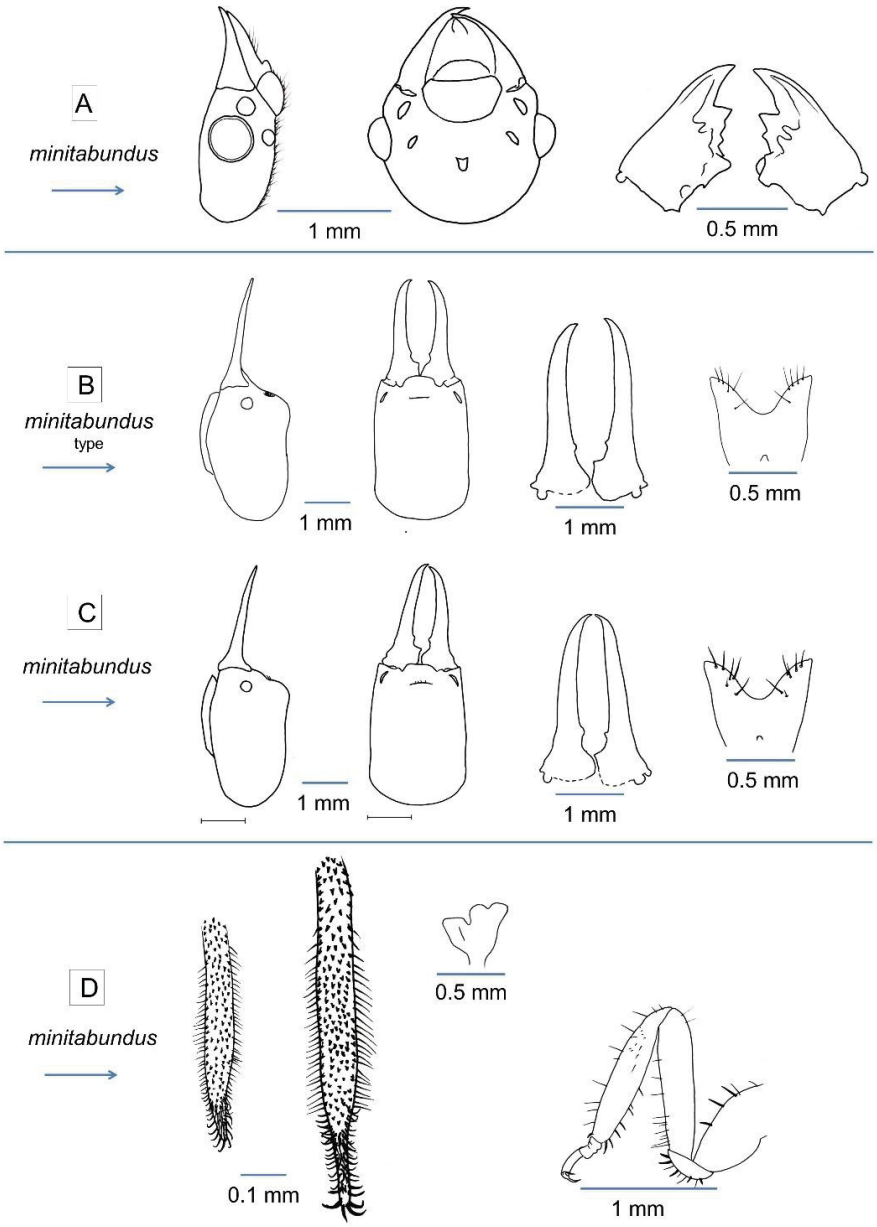


**Fig. 48.** *Isognathotermes minitabundus* (Sjöstedt, 1913): imago, soldier, and worker. **A**. Lateral and dorsal views of the head capsule of the king from a non-type colony of *I. minitabundus* (DJ 0155), and dorsal view of this imago's mandibles. **B**. Lateral and dorsal views of a soldier from the type colony of *I. minitabundus* (DJ 0129). **C**. The same of a soldier from a non-type *I. minitabundus* sample (DJ 0155). **D**. PC1s of soldier's and worker's enteric valves from a non-type colony of *I. minitabundus* (DJ 0155); caecum and foreleg of this worker.

**Table 8.** *Isognathotermes minitabundus* (Sjöstedt, 1913): ranges of significant measures in the three castes, in alphabetical orders of the "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 19) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.38–0.45 | NA |
| | | Head: width across the eyes | IHdW | 1.62–1.81 | NA |
| | | Left mandible: A-m1 distance | IMlAmD | 0.21–0.27 | NA |
| | | Ocellus: large diameter | IOc*D* | 0.12–0.18 | NA |
| | | Postclypeus: width | IPcW | 0.74–0.90 | NA |
| | | Pronotum: maximal width | IPnW | 1.39–1.67 | NA |
| | | Hind tibia: length | IT3L | 1.79–2.35 | NA |
| | | Wing: length (n= 11) | IWgL | 13.7–17.1 | NA |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.27–1.73 | NA |
| Soldiers (n = 37) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.01–0.11 | 0.07 |
| | | Head: length | SHdL | 2.91–3.50 | 3.16 |
| | | Head: width | SHdW | 2.00–2.37 | 2.13 |
| | | Left mandible: lesser sagitta | SMlc | 0.08–0.24 | 0.12 |
| | | Left mandible: ventral length | SMlL | 2.40–2.75 | 2.58 |
| | | Hind tibia: length | ST3L | 1.54–1.94 | 1.72 |
| | Indices | Head elongation index | SHdL/SHdW | 1.35–1.55 | 1.48 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.03–0.09 | 0.05 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.51–1.03 | 0.77 |
| Workers (n = 24) | Raw measures (mm) | Head: width | WHdW | 1.21–1.42 | NA |
| | | Left mandible: A-m1 distance | WMlAmD | 0.19–0.24 | NA |
| | | Left mandible: total length | WMlL | 0.57–0.68 | NA |
| | | Hind tibia: length | WT3L | 1.21–1.44 | NA |
| | | Valve: PC average length | WVP-AvL | 0.61–0.75 | NA |
| | | Valve: PC average width | WVP-AvW | 0.06–0.10 | NA |
| | | Valve: SC average length | WVS-AvL | 0.50–0.65 | NA |
| | | Valve: SC average width | WVS-AvW | 0.26–0.38 | NA |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 6.38–11.0 | NA |

* Abbreviations: see definitions in Material and methods.

or more). **Labrum** with 5–8 large setae on each lobe. **Thorax**: pro- and mesonotum with a small number of setae mainly located on margins. **Legs**: fore coxa bears at least one fine seta and 1–3 spines (exceptionally 5) on carina and not any spine on ventral side; trochanter generally with some strong lined-up setae, or with 3–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively (the latter sometimes weakly developed) and a row of 7–18 spines along their shaft. **Abdomen**: tergites with some large setae, mainly or only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 8; Fig. 48). **Size**: the soldiers of *I. minitabundus* are part of the medium to larger soldiers in the genus *Isognathotermes* (Fig. 28). **Head capsule**: always clearly sclerotised; appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a clear or

slight narrowing near posterior third or fourth; from antennal sockets sides converge towards bases of mandibles; posterior side regularly convex or sometimes with short straight or even concave parts. **In profile**: upper profile always slightly to strongly concave; angle between extended mandibles and frons obtuse; frons with an outlined or clear anterior hump. Gulamentum in ventral view always constricted in its posterior half, with sides of anterior part either roundly convex or more frequently forming an acute widening or even a kind of ear on each side. Antennae: of 14–15 articles. **Labrum**: always deeply bifurcate and wider than long, with sides varying from lyre-shaped (in 87% of the samples examined) to almost straight; lobes angular, frequently with fine, whitish, or translucent tips; anterior margin concave. **Mandibles**: sabre-like and rather clearly asymmetrical, the left mandible is slightly curved to almost straight and hooked distally and obviously less curved than the right mandible; inner edges generally smooth with one distinct but very small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible always clearly more curved than left. **Thorax**: pronotum sellate, as wide as 52–61% of head width, with straight or indented anterior margin and posterior straight margins. **Fore coxa** flanged ventrally resulting in a more or less sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in second half of abdomen. **Caecum** always rather small, best seen in ventral view, near centre of abdomen, three-lobed. Arrangement of enteric valve cushions showing trilateral symmetry, the odd cushions being about 18% longer than the even cushions, generally without any crest or with crests very weakly developed.

**Worker**

Colour. **Head capsule** pale (C1–C3) turning grey in long preserved samples. Antennae: proximal articles pale (C2–C3), distal articles always one to two levels darker (C4–C5). **Thorax**, nota, and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect, scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa always carinated, bearing one fine seta and furnished with 4–6 spines on carina and 0–2 on ventral side; fore trochanter with 6–8 spines, all except one lined up; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of 8–18 spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 8, Fig. 48). **Size**: the workers of *I. minitabundus* are part of the medium-sized workers in the genus *Isognathotermes* (with large overlapping on several other species: Fig. 30). **Head capsule**: weakly sclerotised (except mandibles). Antennae of 14.5 (sometimes 14) articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal tooth well developed but with a blunt tip even when fresh, second marginal appearing as an undulated edge, reduced but still present in worn mandibles (more visible than in other species), third marginal tooth with a blunt tip; premolar tooth generally well visible (more than in other species); molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh and frequently with a wavy inner edge near the base; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 65–70% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in second half of abdomen. Arrangement of enteric valve cushions of the *fungifaber* pattern with triradial symmetry: the odd PCs, in their downstream part, are rather narrow and bear crests that are as high as or higher than they are wide, with long and strong bristles; 15–26 supporting bristles on each side of the odd PCs;

secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum always rather small, visible in ventral view, near centre of abdomen, generally with three to five short lobes.

**Chorology-ecology**

The geographic distribution of *I. minitabundus* is linked with the southern Congolian forest-savanna mosaic and the Central Zambezian Miombo woodland ecoregions; this is, with *I. ugandensis malawii* subsp. nov., the southernmost species of the genus *Isognathotermes* (Fig. 49).

**Molecular data**

The species *I. minitabundus* was previously referred to as "I. afug" (DJ 0348) by Hellemans *et al.* (2021), which was identified as a close species to *I. ugandensis*. Herein, we recognise this sample to belong to its own species, due to distinct morphologies and geographical distributions.

Two mitogenomes of this species (both collected from Kisangwe, DRC, Haut-Katanga Province) are published alongside this work (GenBank accessions: see Supp. file 3 and 'Material examined').

The difficulty of morphological delimitation between *I. minitabundus* and *I. ugandensis* is also reflected from analyses of their mitogenomes, with *I. minitabundus* placed as sister to *I. ugandensis* in a phylogenetic reconstruction (Fig. 33), and with whom they exhibit on average less than 2% dissimilarity (Supp. file 4). However, they also exhibit less than 2% dissimilarity with *I. finitimus* (Supp. file 4).

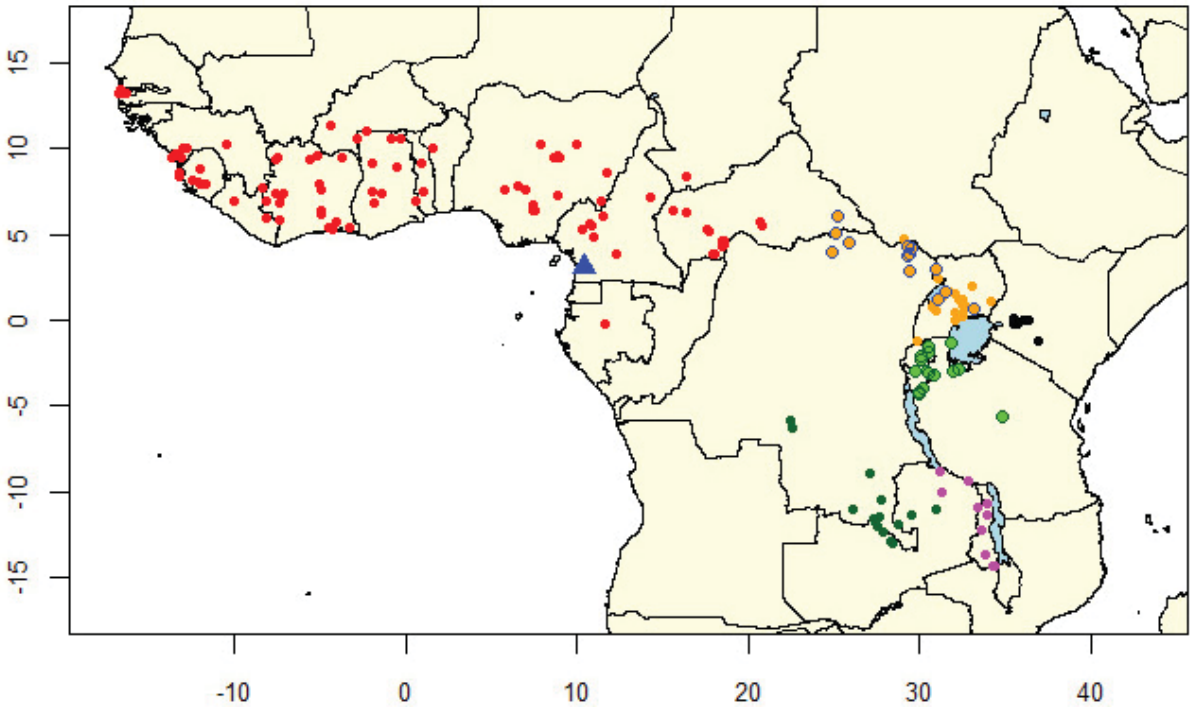


**Fig. 49.** Distribution map of *Isognathotermes minitabundus* (Sjöstedt, 1913) (dark green dots); *I. severus* (Silvestri, 1914) (red dots); *I. ugandensis burundii* ssp. nov. (light-green dots); *I. ugandensis kenyae* ssp. nov. (black dots); *I. ugandensis malawii* ssp. nov. (pink dots); *I. ugandensis ugandensis* ssp. nov. (orange dots); *I. ugandensis ugandensis* ssp. nov. previously known as *I. antennalis* (Sjöstedt, 1924) (orange dots with blue circles); *I. zenkeri* (Desneux, 1904) (blue triangle).

***Isognathotermes modicus*** Josens & Deligne sp. nov.
urn:lsid:zoobank.org:act:CC5AB255-A7F9-4CA6-A497-9771F6FA6507
Figs 26–31, 50, distribution map: Fig. 53; Table 9

**Diagnosis**

This is a very small species (the smallest with a *finitimus* EVA), so small that the first sample was initially thought to come from an incipient colony, but a physogastric queen ruled out this possibility.

The worker has a *finitimus* EVA and is among the smallest in the genus *Isognathotermes*: (WT3L = 1.12–1.20 mm), and its enteric valve is also the smallest (Fig. 31).

The soldier is among the smallest in the genus *Isognathotermes* (SHdL = 2.42–2.66 mm), as small as the smallest *I. fungifaber* but with a *finitimus* EVA. It has evenly curved mandibles with a very low acceleration index of the mandible curvature between proximal and distal parts (ln(SMlpR) - ln(SMldR) = 0.96–1.44) as it is the case for some *I. planifrons* but with different sizes.

The imago, however, is among the medium-sized imagines in the genus *Isognathotermes* (Fig. 26) and rather like those of *I. finitimus*, *I. rectimalatus* sp. nov., and *I. planifrons*.

To date, this species is only known from the "forêt des Abeilles", Gabon.

**Etymology**

The epithet *modicus* means 'modest' in Latin. It refers to the small size of this species.

**Material examined**

Five samples from one location.

**Holotype**

GABON • soldier; Forêt des Abeilles; 0°19′ S, 12°7′ E; 1995; C. Bordereau and A. Robert leg.; study code: DJ 0862; MNHN EP9886.

**Paratypes**

GABON • worker, ♂ (king), ♀ (queen); same data as for holotype; MNHN EP9886.

**Other material examined**

GABON • soldier, ♀ (queen); Forêt des Abeilles; 0°19′ S, 12°7′ E; 1995; C. Bordereau (?) leg.; study code: DJ P214; MNHN EP9887 • soldier; Forêt des Abeilles; 0°19′ S, 12°7′ E; 1995; C. Bordereau (?) leg.; study code: DJ P216; MNHN EP9888 • soldier, worker; Forêt des Abeilles; 0°35′ S, 12°25′ E; 1995; C. Bordereau and A. Robert leg.; study code: DJ 0858; MNHN EP9884 • soldier, worker, ♂ (king), ♀ (queen); Forêt des Abeilles; 0°35′ S, 12°25′ E; 1995; C. Bordereau and A. Robert leg.; study code: DJ 0859; MNHN EP9885.

**Historical review**

This species is described here. It was discovered by C. Bordereau and A. Robert in the so-called "forêt des Abeilles", Gabon.

**Description**

**Imago**

Colour. **Head capsule**: well sclerotised and dark C6–C7; fontanelle concolorous with head. Postclypeus one level paler than head capsule. Antennae C5–C6. **Thorax**: pronotum concolorous or almost so with

head capsule; meso- and metanotum C6 slightly paler than head. Legs C4. **Abdomen**: tergites C6. Sternites appreciably paler in the middle (C3–C5) with both sides darker (C5–C6) than anterior.

Setation. **Head capsule**, with some prominent setae set amongst a high density of short, fine setae forming a dense mat. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and shorter ones in middle; meso- and metanotum with some fine, pale setae, arranged in a medio-longitudinal strip, generally visible at 20–40×; sometimes with one or two large setae on posterior lobe. **Legs** very pilose, furnished (among numerous fine setae) with 7–11 stronger setae on the carina of fore coxa and 1–3 on the ventral side of fore coxa and trochanter; tibia pilose, fore, mid, and hind tibia furnished with 30–40 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 9, Fig. 50). **Size**: the imagines of *I. modicus* sp. nov. are, on average, medium sized in the genus *Isognathotermes* (Fig. 26). **Head capsule**: compound eyes nearly round; ocelli shortly oval, removed from eyes by a distance equal to 0.9–1.3 ocellus small diameter; fontanelle

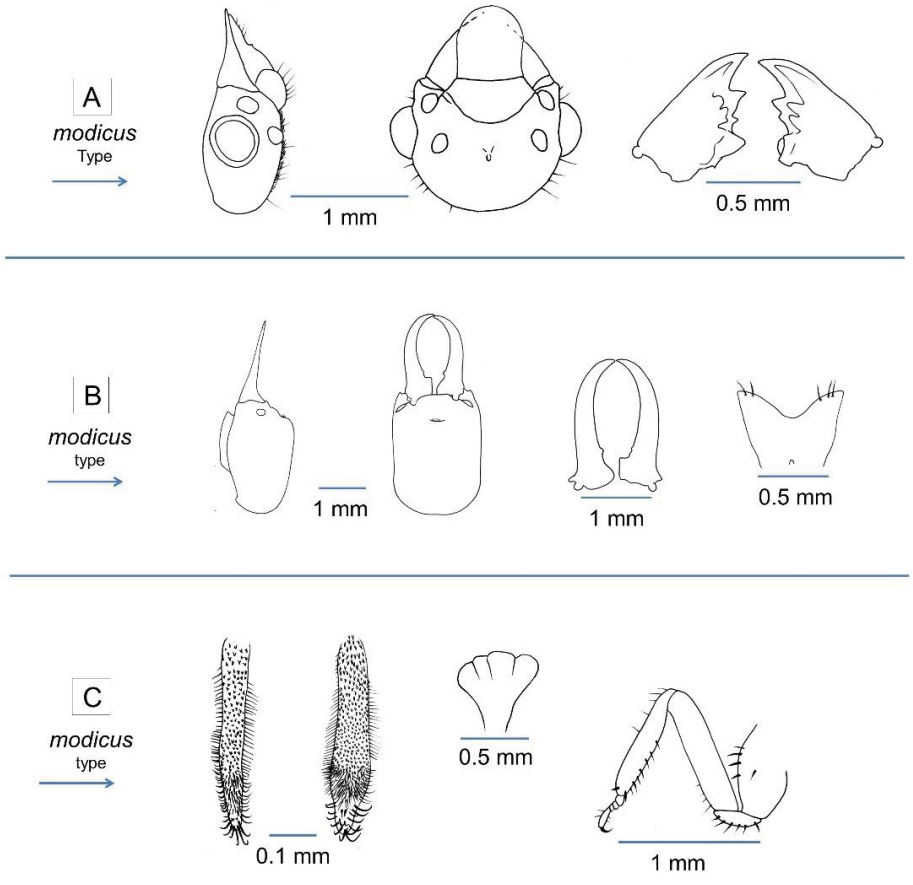


**Fig. 50.** *Isognathotermes modicus* Josens & Deligne sp. nov.: imago, soldier, and worker. **A**. Lateral and dorsal views of the king's head capsule from the type colony of *I. modicus* (DJ 0862), and dorsal view of this imago's mandibles. **B**. Lateral and dorsal views of a soldier's head capsule from the type colony, ventral view of its mandibles, and dorsal view of its labrum. **C**. PC1s of soldier's and worker's enteric valves from the type colony, and caecum and foreleg of this worker.

**Table 9.** *Isognathotermes modicus* Josens & Deligne sp. nov.: ranges of significant measures in the three castes, in alphabetical orders of the "Code" column; five samples from one location.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 5) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.41–0.46 | 0.45 |
| | | Head: width across the eyes | IHdW | 1.56–1.65 | 1.64 |
| | | Left mandible: A-m1 distance | IMlAmD | 0.21–0.24 | 0.22 |
| | | Ocellus: large diameter | IOc*D* | 0.15–0.18 | 0.17 |
| | | Postclypeus: width | IPcW | 0.77–0.82 | 0.79 |
| | | Pronotum: maximal width | IPnW | 1.38–1.48 | 1.41 |
| | | Hind tibia: length | IT3L | 1.82–1.97 | 1.90 |
| | | Wing: length (n = 0) | IWgL | NA | NA |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.28–1.78 | 1.41 |
| Soldiers (n = 5) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.00–0.05 | 0.01 |
| | | Head: length | SHdL | 2.42–2.66 | 2.58 |
| | | Head: width | SHdW | 1.80–1.89 | 1.88 |
| | | Left mandible: lesser sagitta | SMlc | 0.22–0.26 | 0.25 |
| | | Left mandible: ventral length | SMlL | 1.93–2.16 | 2.01 |
| | | Hind tibia: length | ST3L | 1.41–1.52 | 1.51 |
| | Indices | Head elongation index | SHdL/SHdW | 1.32–1.44 | 1.37 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.11–0.13 | 0.12 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.88–1.12 | 1.03 |
| Workers (n = 3) | Raw measures (mm) | Head: width | WHdW | 1.07–1.13 | 1.13 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.17–0.18 | 0.18 |
| | | Left mandible: total length | WMlL | 0.52–0.57 | 0.56 |
| | | Hind tibia: length | WT3L | 1.12–1.20 | 1.20 |
| | | Valve: PC average length | WVP-AvL | 0.45–0.48 | 0.45 |
| | | Valve: PC average width | WVP-AvW | 0.06–0.08 | 0.08 |
| | | Valve: SC average length | WVS-AvL | 0.36–0.39 | 0.36 |
| | | Valve: SC average width | WVS-AvW | 0.16–0.22 | 0.17 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 4.85–7.20 | 5.16 |

* Abbreviations: see definitions in Material and methods.

generally a tiny round or elongate marking. Antennae: shortened to 12 articles by amputation of probably four articles in queens and kings. Labrum: cupola shaped, wider than long. **Left mandible** with apical tooth medium sized in the genus (Fig. 27) and always more prominent than first marginal; marginal teeth three in number but second one only suggested by an undulation of edge between first and third marginal teeth; only the apical tooth is acute in unworn specimens; premolar tooth almost totally obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth always more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long

and narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut** not studied.

**Soldier**

Colour. **Head capsule** uniformly C5. Antennae and labrum one to two palette levels paler than head capsule. Mandibles dark (C6) with an abrupt clearing on their bases (one levels) which is generally the same colour as frons. **Thorax** and legs paler than head capsule (C4). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Labrum** with 4–6 large setae on each lobe. **Thorax**: pro- and mesonotum with a small number of setae mainly located on margins. **Legs**: fore coxa with at least one fine seta and 2–3 spines on carina and not any spine on ventral side; trochanter generally with some strong lined-up setae, including 3–4 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively (the latter sometimes weakly developed) and a row of 6–12 spines along their shaft. **Abdomen**: tergites with some large setae, mainly or only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 9, Fig. 50). **Size**: the soldiers of *I. modicus* sp. nov. are part of the smallest soldiers in the genus *Isognathotermes* (Fig. 28). **Head capsule**: always clearly sclerotised; appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a very slight narrowing near posterior third or fourth; from antennal sockets sides converge towards bases of mandibles; posterior side regularly convex. Slightly concave or straight **upper profile**; angle between extended mandibles and frons obtuse; frons flat or with a small anterior hump. Gulamentum in ventral view always constricted in its posterior half, with sides of anterior part roundly convex. Antennae: of 14.5–15 articles. **Labrum**: always deeply bifurcate and wider than long, with lyre-shaped sides; lobes angular, with fine, whitish, or translucent tips; anterior margin concave. **Mandibles**: sabre-like; inner edges smooth with one distinct but small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible slightly more curved than left. **Thorax**: pronotum sellate, as wide as 56–60% of head width, with straight anterior and posterior margins. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in second half of abdomen. **Caecum** rather small, best seen in ventral view, near centre of abdomen, three-lobed. Arrangement of enteric valve cushions showing trilateral symmetry, the odd cushions recognizable as a *finitimus* EVA.

**Worker**

Colour. **Head capsule** pale (C2–C3). Antennae: proximal articles pale (C2), distal articles two levels darker (C4). **Thorax**, nota, and legs pale (C2–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect, scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa carinated, bearing one fine seta and furnished with 3–5 spines on carina and not any one on ventral side; fore trochanter with 4–6 lined up spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of 6–12 spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 9, Fig. 50). **Size**: the workers of *I. modicus* sp. nov. are the smallest workers with a *finitimus* EVA, of the same size as the smallest workers of *I. fungifaber* (which have a *fungifaber* EVA). **Head capsule**: weakly sclerotised (except mandibles). Antennae: 14.5 articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal well developed but with a blunt tip even when fresh, second marginal faint (visible as an undulated edge and disappearing in worn mandibles), third marginal with a blunt tip; premolar tooth with its proximal end generally hidden under molar prominence; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal well developed with a sharp tip when fresh; second marginal smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as about 64% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions of the *finitimus* pattern with triradial symmetry: the odd PCs, in their downstream part, are wide and bear at that place a high density of rather short bristles on a globular bulge (Fig. 50); supporting bristles are rather numerous: 20–28 on each side of the odd PCs; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum always rather small, visible in ventral view, near centre of abdomen, shortly lobed (three or four small lobes).

**Chorology-ecology**

To date, this species is only known only from the "Forêt des Abeilles", Gabon, at the limit of the northwestern Congolian lowland forests and the Atlantic equatorial coastal forest ecoregions (Fig. 53).

**Molecular data**

No genetic sequence is currently available.

***Isognathotermes phallicaecalis*** Josens & Deligne sp. nov.
urn:lsid:zoobank.org:act:0647CCCF-BF5A-4FEA-9C01-84FF782A06D9
Figs 26–31, 33, 51–52, distribution map: Fig. 53; Table 10

**Diagnosis**

Soldiers and workers of *Isognathotermes phallicaecalis* sp. nov. and *I. phalloides* sp. nov. share the same kind of phalloid cecum, extended forward in a finger-like process that can be swollen distally or capped or crowned (Figs 52, 56), which distinguishes them from all other species of *Isognathotermes*; they have morphologically similar soldiers, with a slight difference in the curvature of the mandibles (Fig. 22); however, they come from different ecosystems: continental evergreen forest in the case of *I. phallicaecalis*, forest galleries in the case of *I. phalloides*.

The worker of *I. phallicaecalis* sp. nov. has a *finitimus* EVA and is among the small workers in the genus *Isognathotermes*. Its head is, on average, somewhat wider than that of *I. phalloides* sp. nov. (Fig. 30).

The soldier's EVA can generally be recognized as belonging to the *finitimus* pattern; on average it has longer mandibles than *I. phalloides* sp. nov.: SMlL = 2.17 –2.53 mm (vs 1.99–2.36 mm in *I. phalloides*).

The imago is unknown.

This species is also defined by its ecology and chorology: to date it has been found only in forested environments of the northern Congo Republic and Cameroon (Fig. 53).

**Etymology**

The epithet *phallicaecalis* from the Greek φαλλός (*phallos*, phallus) and the Latin *caecalis* (of the caecum) refers to the caecum phalloid morphology in workers and soldiers.

**Material examined**

Twelve samples from three locations.

**Holotype**

CONGO REPUBLIC • soldier; Loundoungou; 2°22.827′ N, 17°4.226′ E; 4 Dec. 2017; Y. Roisin leg.; study code: DJ 0529; GenBank nos MN646722 (*COI*) MN685925 (*COII*) MN685986 (*28S*) PQ679196 (mitogenome); BE RMCA INS.Iso.059288.

**Paratypes**

CONGO REPUBLIC • soldier, worker; same data as for holotype; BE RMCA INS.Iso.059936.

**Other material examined**

CAMEROON • soldier; Dja Rock; 3°20.73′ N, 12°42.84′ E; 30 Mar. 2015; J. Šobotnik leg.; study code: DJ B320; BE RMCA INS.Iso.059287.

CONGO REPUBLIC • soldier, worker; Mokabi; 3°8.796′ N, 16°57.869′ E; 8 Dec. 2017; Y. Roisin leg.; study code: DJ 0527; GenBank no PQ679190 (mitogenome); BE RMCA INS.Iso.059290 • soldier, worker; Mokabi; 3°8.795′ N, 16°57.826′ E; 8 Dec. 2017; Y. Roisin leg.; study code: DJ 0528; BE RMCA INS.Iso.059289 • soldier, worker; Loundoungou; 2°22.929′ N, 17°4.301′ E; Dec. 2018; S. Lenz leg.; study code: DJ 0759; GenBank no PV564652 (mitogenome); BE RMCA INS.Iso.059296 • soldier, worker; Loundoungou; 2°22.93′ N, 17°4.301′ E; Dec. 2018; S. Lenz leg.; study code: DJ 0760; GenBank no PV564657 (mitogenome); BE RMCA INS.Iso.059291 • soldier, worker; Loundoungou; 2°22.93′ N, 17°4.301′ E; Dec. 2018; S. Lenz leg.; study code: DJ 0761; GenBank no PQ679202 (mitogenome); BE RMCA INS.Iso.059297 • soldier, worker; Loundoungou; 2°22.93′ N, 17°4.301′ E; Dec. 2018; S. Lenz leg.; study code: DJ 0762; BE RMCA INS.Iso.059292 • soldier, worker; Loundoungou; 2°22.93′ N, 17°4.301′ E; Dec. 2018; S. Lenz leg.; study code: DJ 0763; BE RMCA INS.Iso.059295 • soldier, worker; Loundoungou; 2°22.93′ N, 17°4.301′ E; Dec. 2018; S. Lenz leg.; study code: DJ 0764; BE RMCA INS.Iso.059293 • soldier, worker; Loundoungou; 2°22.93′ N, 17°4.301′ E; Dec. 2018; S. Lenz leg.; study code: DJ 0765; BE RMCA INS.Iso.059298 • soldier, worker; Loundoungou; 2°22.93′ N, 17°4.301′ E; Dec. 2018; S. Lenz leg.; study code: DJ 0766; GenBank no PV564655 (mitogenome); BE RMCA INS.Iso.059294.

**Historical review**

This species is described here; the imago is still unknown. It was recently discovered by three of us (JŠ, YR & SL) in Cameroon and Northern Congo.

**Description**

**Imago**

The imago is unknown.

**Soldier**

Colour. **Head capsule** tending towards faded palette (Cf4–Cf5); there is a gradient from a darker frons to a paler back. Antennae and labrum concolorous with or somewhat paler than frons. Mandibles dark (C7–C8) with an abrupt clearing on their bases (C5–C6) which is concolorous with frons. **Thorax** and legs generally paler (C3–C4) than head capsule. **Abdomen** grey to red-brown owing to digestive bolus, sometimes with a yellowish tinge on tergites.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50 × or more). **Labrum** always with 3–6 large setae on each lobe. **Thorax**: pro- and mesonotum with a small number of setae mainly located on margins. **Legs**: fore coxa bear 1–3 spines on carina and none (rarely one) on ventral side; trochanter with 2–8 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of 8–15 spines along their shaft. **Abdomen**: tergites with some large setae, mainly on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 10; Figs 51–52). **Size**: the soldiers of *I. phallicaecalis* sp. nov. are medium sized among of the genus *Isognathotermes* (Fig. 28). **Head capsule**: always clearly sclerotised, appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a clear narrowing near posterior fourth (Fig. 51), from antennal sockets sides converge more or less clearly towards bases of mandibles; posterior side regularly rounded or with a short straight middle part; **upper profile** concave. Angle between extended mandibles and frons a little obtuse; frons without any or with a week anterior hump. Gulamentum in ventral view always constricted in its posterior half, with sides of anterior part forming an acute widening or a kind of ear on each side. Antennae: of 14.5–15 articles. **Labrum**: always deeply bifurcate and wider than long, with lyre-shaped sides; lobes angular, with fine, translucent tips; anterior margin concave. **Mandibles**: sabre-like with a middle-sized curvature in the genus *Isognathotermes*; inner edges generally smooth with one distinct but very small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and

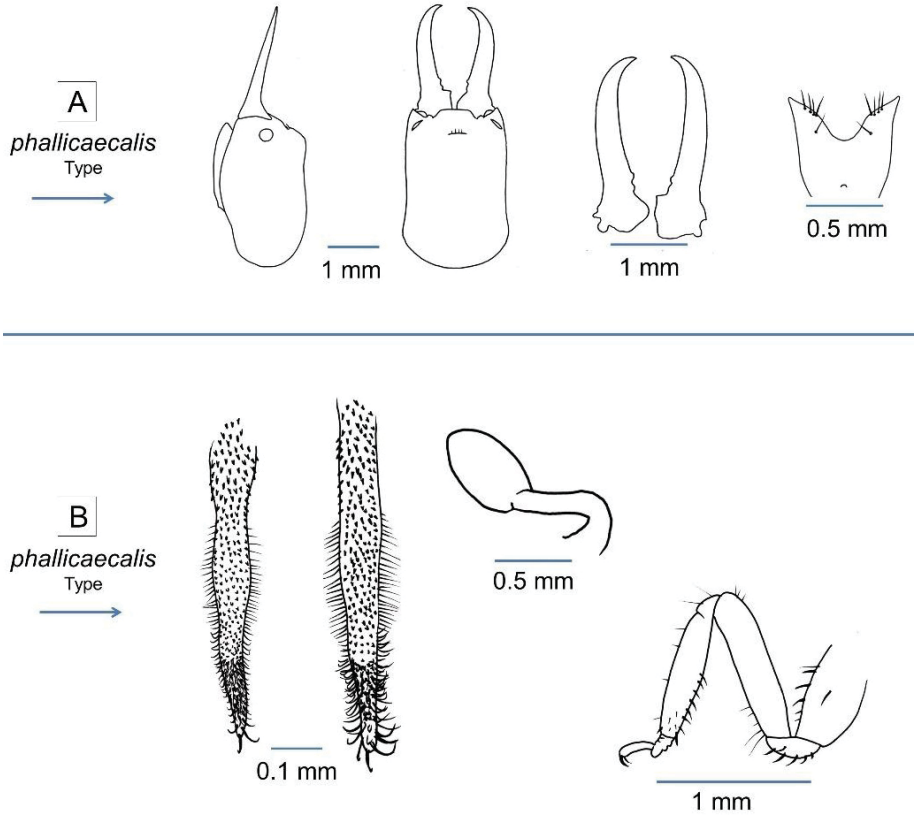


**Fig. 51.** *Isognathotermes phallicaecalis* Josens & Deligne sp. nov.: soldier, and worker. **A**. Lateral and dorsal views of the head capsule, ventral view of mandibles, and dorsal view of labrum of a soldier from the *I. phallicaecalis* type colony (DJ 0529). **B**. PC1s of soldier's and worker's enteric valves; caecum, and foreleg of this worker.

**Table 10.** *Isognathotermes phallicaecalis* Josens & Deligne sp. nov.: ranges of significant measures in soldiers and workers (imagines are unknown), in alphabetical orders of "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Soldiers (n = 12) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.02–0.07 | 0.06 |
| | | Head: length | SHdL | 2.71–3.12 | 3.11 |
| | | Head: width | SHdW | 1.84–2.13 | 2.07 |
| | | Left mandible: lesser sagitta | SMlc | 0.18–0.26 | 0.21 |
| | | Left mandible: ventral length | SMlL | 2.17–2.53 | 2.40 |
| | | Hind tibia: length | ST3L | 1.52–1.69 | 1.64 |
| | Indices | Head elongation index | SHdL/SHdW | 1.35–1.57 | 1.50 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.08–0.11 | 0.09 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.76–1.01 | 0.92 |
| Workers (n = 11) | Raw measures (mm) | Head: width | WHdW | 1.15–1.26 | 1.21 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.16–0.20 | 0.18 |
| | | Left mandible: total length | WMlL | 0.54–0.59 | 0.57 |
| | | Hind tibia: length | WT3L | 1.22–1.37 | 1.31 |
| | | Valve: PC average length | WVP-AvL | 0.53–0.61 | 0.60 |
| | | Valve: PC average width | WVP-AvW | 0.06–0.08 | 0.08 |
| | | Valve: SC average length | WVS-AvL | 0.42–0.47 | 0.43 |
| | | Valve: SC average width | WVS-AvW | 0.19–0.24 | 0.23 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 6.76–10.2 | 8.27 |

* Abbreviations: see definitions in Material and methods.

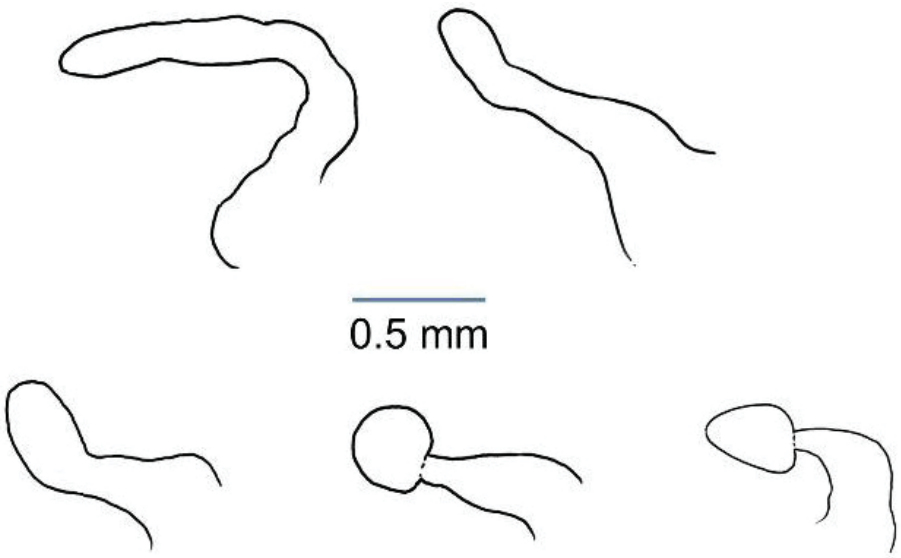


**Fig. 52.** *Isognathotermes phallicaecalis* Josens & Deligne sp. nov. and *I. phalloides* Josens & Deligne sp. nov. Diversity of phalloid caecum morphology in soldiers and workers from five different colonies.

glossy. Right mandible slightly more curved than left. **Thorax**: pronotum sellate, as wide as 59–64% of head width, with generally entire anterior and posterior margins. **Fore coxa** flanged ventrally resulting in a more or less sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in second half of abdomen. **Caecum** always rather well developed, best seen in ventral view, near centre of abdomen, as a typical finger-like process, extended forward and generally swollen distally or seeming to be capped (Figs 52, 56). Arrangement of enteric valve cushions showing trilateral symmetry, the odd cushions being 20–25% longer than the even cushions, with a pilosity becoming very dense distally showing the place where a hump would be expected (in comparison with the worker's EVA).

**Worker**

Colour. **Head capsule** pale (C2–C3). Antennae: proximal articles pale (C2), distal articles two levels darker (C4). **Thorax**, nota, and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect, scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50 × or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa carinated, bearing one fine seta and furnished with 3–6 spines on carina and 1–2 on ventral side; fore trochanter with 5–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of 6–15 spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 10; Figs 51–52). **Size**: the workers of *I. phallicaecalis* sp. nov. are, on average, medium sized among the genus *Isognathotermes* (Fig. 30). **Head capsule**: weakly sclerotised (except mandibles). Antennae of 14.5 (rarely 14) articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal tooth well developed but with a blunt tip even when fresh, second marginal tooth faint (visible as an undulated edge and disappearing in worn mandibles), third marginal tooth with a blunt tip; premolar tooth with its proximal end not hidden under molar prominence; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 66–71% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in second half of abdomen. Arrangement of enteric valve cushions of the *finitimus* pattern (Fig. 5) with triradial symmetry: the odd PCs, in their downstream part, bear a higher density of rather short bristles on a globular bulge, the latter sometimes weakly developed; supporting bristles are numerous: 18–33 on each side of the odd PCs (Fig. 51); secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum always well developed, best seen in ventral view, near centre of abdomen, as a finger-like process, extended forward and often swollen distally or seeming to be capped (Figs 52, 56).

**Chorology-ecology**

To date, this species is only known from two sites in the northern Congo Republic and one in Cameroon (in the northwestern Congolian lowland forest ecoregion: Fig. 53).

**Molecular data**

This species was previously published under the label "pha2" (DJ 0529), established as sister to *I. planifrons* (Hellemans *et al.* 2021). Six mitogenomes of *I. phallicaecalis* sp. nov. are published alongside this work (GenBank accessions: see Supp. file 3 and 'Material examined'). The mitogenomes

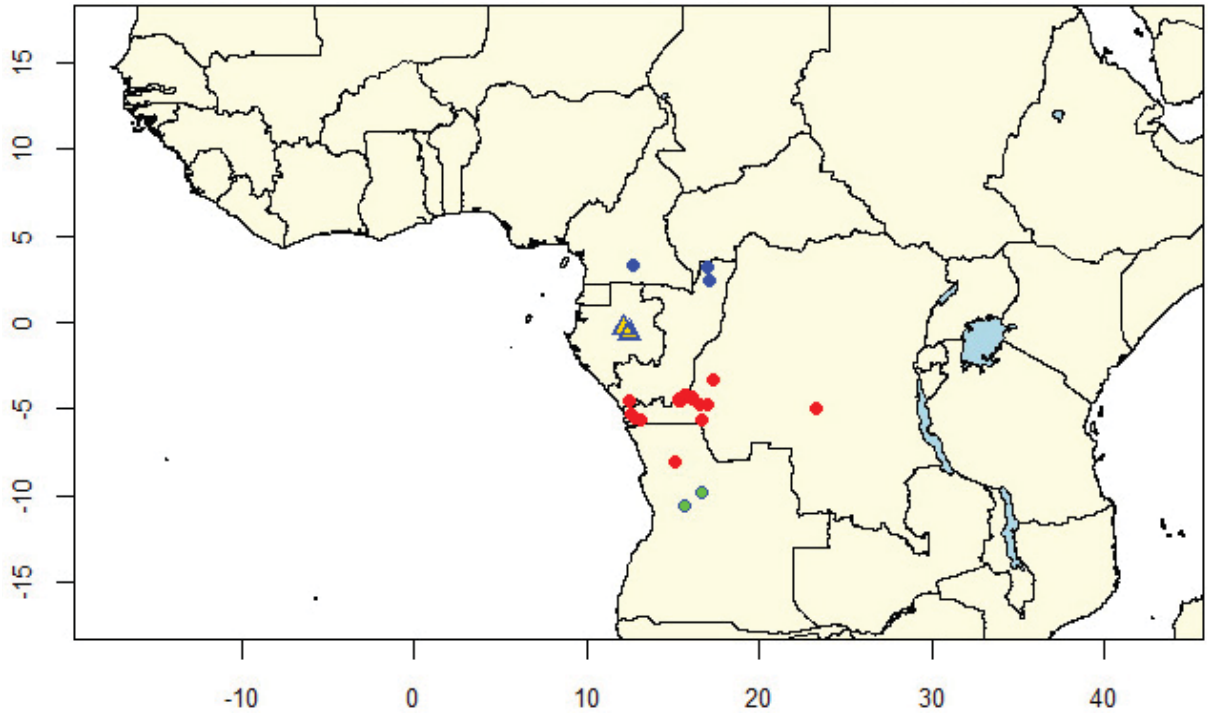


**Fig. 53.** Distribution map of *Isognathotermes modicus* Josens & Deligne sp. nov. (blue triangles); *I. phallicaecalis* Josens & Deligne sp. nov. (blue dots); *I. phalloides* Josens & Deligne sp. nov. (red dots); *I. rectimalatus* Josens & Deligne sp. nov. (green dots).

exhibit less than 1.21% dissimilarity with each other (Supp. file 4); and a dissimilarity of up to 2.26% with *I. phalloides* sp. nov. – the other samples exhibiting phalloid caeca – which justifies the creation of two different (new) species. Of note, *I. phallicaecalis* sp. nov. is paraphyletic with respect to *I. similifinitimus* sp. nov. (Fig. 33), to which mitogenomes are less than 1.50% dissimilar. Even though these two species were found non-monophyletic, the clear morphological and anatomical differences (e.g., caecum) support their recognition as distinct species. Our use of (maternally inherited) mitogenomes only may have limited our ability to resolve their evolutionary relationships. Thus, we posit that their respective paraphylies may either stem from incomplete lineage sorting, or mitogenome introgression following hybridization. Future analyses leveraging nuclear loci will be crucial to shed further light on their relationships.

***Isognathotermes phalloides*** Josens & Deligne sp. nov.
urn:lsid:zoobank.org:act:0B43D017-1D4C-46CD-B30C-52B9226BDD36
Figs 26–31, 33, 54–56, distribution map: Fig. 53; Table 11

**Diagnosis**

This species is close to *I. phallicaecalis* sp. nov.; like the latter, its soldier and worker are characterised by a phalloid caecum, extended forward in a finger-like process that can be swollen distally or capped or crowned (Figs 52, 56). The imago's caecum, without being phalloid, is also more developed than in imagines of other species and takes the appearance of a forward-pointing comma.

*Isognathotermes phallicaecalis* sp. nov. and *I. phalloides* sp. nov. have morphologically similar soldiers, with a slight difference in the curvature of the mandibles (Fig. 22); however, they come from different

ecosystems: continental evergreen forest in the case of *I. phallicaecalis*, forest galleries in the case of *I. phalloides*.

The worker has a *finitimus* EVA and is among the smallest workers in the genus *Isognathotermes*; its head is, on average, narrower than that of *I. phallicaecalis* sp. nov. (Fig. 30).

The soldier can be distinguished from *I. phallicaecalis* sp. nov. by its shorter mandibles, SMlL = 1.99–2.36 mm (vs SMlL = 2.17–2.53 mm in *I. phallicaecalis*); its EVA can generally be recognized as belonging to the *finitimus* pattern.

The imago is, on average and with *I. fungifaber*, the smallest in the genus *Isognathotermes*: IHdW = 1.38–1.54 mm (Fig. 26).

This species is also defined by its ecology and chorology: all samples come from forest galleries south-east of the Congolian forests (Fig. 53).

**Etymology**

The epithet *phalloides* from the Greek φαλλός (*phallos*, phallus) and εἶδος (*eidos*, like) refers to the caecum morphology in workers and soldiers.

**Material examined**

Fifty-two samples from 17 locations. Of the 46 old museum samples examined, six were initially labelled as *C. fungifaber*, three as *C. fungifaber* var. *elongata*, five as *C. gibbifrons*, and 32 as *Cubitermes* sp.

**Holotype**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier; Kondué; 4°58′ S, 23°19′ E; ca 1905; E. Luja leg.; study code: DJ 0087; initially *C. gibbifrons* in RMCA; BE RMCA INS.Iso.059341.

**Paratypes**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker, ♀ (alate), ♂ (alate); same data as for holotype; BE RMCA INS.Iso.059937.

**Other material examined**

ANGOLA • soldier, worker; Quimucanda; 8°5.14′ S, 15°7.43′ E; 27 Nov. 2024; J. Šobotnik leg.; study code: DJ 0971; BE RMCA INS.Iso.059427 • soldier, worker; Quimucanda; 8°5.14′ S, 15°7.43′ E; 27 Nov. 2024; J. Šobotnik leg.; study code: DJ 0972; BE RMCA INS.Iso.059428.

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker, ♀ (alate), ♂ (alate); Kondué; 4°58′ S, 23°19′ E; ca 1905; E. Luja leg.; study code: DJ 0088; initially *C. gibbifrons* in RMCA; BE RMCA INS.Iso.059342 • worker; Kondué; 4°58′ S, 23°19′ E; ca 1905; E. Luja leg.; study code: DJ 0089; initially *C. gibbifrons* in RMCA; BE RMCA INS.Iso.059343 • soldier, worker, ♀ (alate), ♂ (alate); Kondué; 4°58′ S, 23°19′ E; ca 1905; E. Luja leg.; study code: DJ 0090; initially *C. gibbifrons* in RMCA; BE RMCA INS.Iso.059344 • soldier, worker, ♀ (queen); Kondué; 4°58′ S, 23°19′ E; 1905; E. Luja leg.; study code: DJ 0095; initially *Eutermes fungifaber* in RMCA; BE RMCA INS.Iso.059338 • worker, ♂ (alate); Kondué; 4°58′ S, 23°19′ E; ca 1905; E. Luja leg.; study code: DJ 0098; initially *C. fungifaber* var. *elongata* in RMCA; BE RMCA INS.Iso.059339 • worker, ♀ (alate), ♂ (alate);; 4°58′ S, 23°19′ E; ca 1905; E. Luja leg.; study code: DJ 0099; initially *C. fungifaber* var. *elongata* in RMCA; BE RMCA INS.Iso.059340 • worker, ♂ (alate); Kondué (?); 4°58′ S, 23°19′ E; ca 1905; E. Luja leg.; study code: DJ 0606; initially *C. gibbifrons*; IEAP • soldier, worker, ♀ (alate); Bandundu; 3°19′ S, 17°20′ E; 28 Aug. 1939; J. Ruelle leg.; study code: DJ 0879; initially *C. fungifaber* var. *elongata* in RMCA; BE RMCA

INS.Iso.059326 • soldier, worker, ♂ (king); Kinshasa Campus Lovanium) [= Unikin]; 4°25′ S, 15°18′ E; 25 Feb. 1960; A. Bouillon leg.; study code: DJ 0913; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059336 • soldier; Kinshasa Campus Lovanium) [= Unikin]; 4°25.16′ S, 15°18.55′ E; 5 Mar. 1960; unknown leg.; study code: DJ B293; initially *Cubitermes* sp. in RMCA; BE RMCA INS. Iso.059300 • soldier, ♀ (queen); Kenje; 4°45′ S, 16°57′ E; 14 Apr. 1964; G. Mathot leg.; study code: DJ B299; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059332 • soldier; Route vers Sanda; 4°33.75′ S, 12°24.5′ E; 19 Apr. 1964; G. Mathot leg.; study code: DJ B314; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059311 • soldier; Route vers Sanda; 4°33.75′ S, 12°24.5′ E; 19 Apr. 1964; G. Mathot leg.; study code: DJ B315; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059312 • soldier, worker; Takundi; 4°45′ S, 16°33′ E; 19 Apr. 1964; G. Mathot leg.; study code: DJ 0880; initially *C. fungifaber* in RMCA; BE RMCA INS.Iso.059328 • soldier, worker; Takundi; 4°45′ S, 16°33′ E; 19 Apr. 1964; G. Mathot leg.; study code: DJ 0883; initially *C. fungifaber* in RMCA; BE RMCA INS. Iso.059321 • soldier, worker; Takundi; 4°45′ S, 16°33′ E; 19 Apr. 1964; G. Mathot leg.; study code: DJ 0884; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059322 • soldier, worker; Takundi; 4°45′ S, 16°33′ E; 19 Apr. 1964; G. Mathot leg.; study code: DJ 0885; initially *C. fungifaber* in RMCA; BE RMCA INS.Iso.059324 • soldier; Kimwenza; 4°28.5′ S, 15°18.25′ E; 17 Mar. 1965; S. Kikomba leg.; study code: DJ B294; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059299 • soldier; Kinshasa Campus Lovanium) [= Unikin]; 4°25.16′ S, 15°18.55′ E; 13 Mat. 1965; C. Nkakala leg.; study code: DJ B292; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059307 • soldier, worker, ♂ (king); Maluku; 4°21′ S, 15°48′ E; 25 May 1967; C. Nkakala leg.; study code: DJ 0912; initially *C. fungifaber* in RMCA; BE RMCA INS.Iso.059335 • soldier, worker, ♀ (queen); Ndjili; 4°28′ S, 15°21′ E; 1 Feb. 1968; A. Bouillon leg.; study code: DJ 0914; initially *C. fungifaber* in RMCA; BE RMCA INS.Iso.059337 • soldier; Route vers Sanda; 4°33.5′ S, 15°24.5′ E; 19 Apr. 1969; G. Mathot leg.; study code: DJ B302; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059306 • soldier; Kinshasa Campus Lovanium) [= Unikin]; 4°25.16′ S, 15°18.55′ E; 7 Aug. 1969; C. Nkakala leg.; study code: DJ B290; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059305 • soldier; Kinshasa Campus Lovanium) [= Unikin]; 4°25.16′ S, 15°18.55′ E; 7 Aug. 1969; C. Nkakala leg.; study code: DJ B291; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059310 • soldier, ♂ (alate); Ndjili; 4°24′ S, 15°25′ E; 5 Oct. 1970; A. Bouillon leg.; study code: DJ B296; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059327 • soldier, worker, ♀ (alate); Ndjili; 4°27.22′ S, 15°20.6′ E; 5 Nov. 1970; A. Bouillon leg.; study code: DJ 0909; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059325 • soldier; Ndjili; 4°24′ S, 15°25′ E; 12 Jan. 1971; A. Wabo leg.; study code: DJ B297; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059144 • soldier; Luki; 5°39′ S, 13°4′ E; 1 Apr. 1971; A. Bouillon leg.; study code: DJ B275; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059303 • soldier; Luki; 5°39′ S, 13°4′ E; 1 Apr. 1971; A. Bouillon leg.; study code: DJ B276; initially Cubitermes 2 in RMCA; BE RMCA INS.Iso.059308 • soldier; Luki; 5°39′ S, 13°4′ E; 1 Apr. 1971; A. Bouillon leg.; study code: DJ B277; initially Cubitermes 2 in RMCA; BE RMCA INS.Iso.059309 • soldier; Luki; 5°39′ S, 13°4′ E; 1 Apr. 1971; A. Bouillon leg.; study code: DJ B282; initially Cubitermes 2 in RMCA; BE RMCA INS. Iso.059313 • soldier; Luki; 5°39′ S, 13°4′ E; 1 Apr. 1971; A. Bouillon leg.; study code: DJ B283; initially Cubitermes 2 in RMCA; BE RMCA INS.Iso.059315 • soldier; Luki; 5°39′ S, 13°4′ E; 1 Apr. 1971; A. Bouillon leg.; study code: DJ B285; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059318 • soldier; Luki; 5°39′ S, 13°4′ E; 1 Apr. 1971; A. Bouillon leg.; study code: DJ B286; initially Cubitermes 2 in RMCA; BE RMCA INS.Iso.059319 • soldier; Luki; 5°39′ S, 13°4′ E; 1 Apr. 1971; A. Bouillon leg.; study code: DJ B287; initially Cubitermes 2 in RMCA; BE RMCA INS.Iso.059314 • soldier; Kiemi; 5°32′ S, 12°49′ E; 2 Apr. 1971; A. Bouillon leg.; study code: DJ B308; initially Cubitermes 2 in RMCA; BE RMCA INS.Iso.059316 • soldier; Kiemi; 5°32′ S, 12°49′ E; 2 Apr. 1971; A. Bouillon leg.; study code: DJ B309; initially Cubitermes 2 in RMCA; BE RMCA INS.Iso.059317 • soldier, worker; Kiemi; 5°16′ S, 12°34′ E; 2 Apr. 1971; A. Bouillon leg.; study code: DJ 0891; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059329 • soldier; Kenje; 4°12′ S, 15°43′ E; 14 Juil. 1971; P. Vincke leg.; study code: DJ B300; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059301 • soldier, ♂ (king);

Menkao; 4°12′ S, 15°39′ E; 14 Jul. 1971; P. Vincke leg.; study code: DJ B298; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059323 • soldier; Menkao; 4°12′ S, 15°43′ E; 14 Juil. 1971; P. Vincke leg.; study code: DJ B301; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059302 • soldier, worker, ♂ (king); Menkao; 4°10′ S, 15°42′ E; 14 Jul. 1971; P. Vincke leg.; study code: DJ 0910; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059333 • soldier, worker, ♀ (queen); Menkao; 4°10′ S, 15°42′ E; 14 Jul. 1971; P. Vincke leg.; study code: DJ 0911; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059334 • soldier; Kimwenza; 4°29′ S, 15°18′ E; 20 Apr. 1973; P. Vincke leg.; study code: DJ B295; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059304 • soldier, worker; Itaanda (Popokabaka); 5°41′ S, 16°40′ E; 22 Apr. 1973; P. Vincke leg.; study code: DJ 0881; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059330 • soldier, worker, ♂ (king), ♀ (queen); Itaanda (Popokabaka); 5°41′ S, 16°40′ E; 4 May 1973; P. Vincke leg.; study code: DJ 0882; BE RMCA INS.Iso.059331 • soldier, worker; Duale; 4°20′ S, 16°5′ E; Jan. 2011; C. Kifukieto leg.; study code: DJ 0083; BE RMCA INS. Iso.059345 • soldier, worker; Duale; 4°20′ S, 16°5′ E; Jan. 2011; C. Kifukieto leg.; study code: DJ 0141; BE RMCA INS.Iso.059346 • soldier, worker; Bombo-Luméné; 4°25.94′ S, 16°2.83′ E; 22 Apr. 2017; C. Kifukieto leg.; study code: DJ 0459; GenBank nos MN646723 (*COI*), MN685926 (*COII*), MN685987 (*28S*), PQ679184 (mitogenome); BE RMCA INS.Iso.059320.

**Historical review**

This species is described here. Although several samples were present in museum collections under the names of *C. gibbifrons*, *C. fungifaber*, or *C. fungifaber* var. *elongata*, the species was not recognized until Josens & Deligne (2019: 42–44) placed it within the *finitimus* valve pattern group.

**Description**

**Imago**

The description of the imagines is based on 14 *Isognathotermes phalloides* sp. nov. imagines (five female alates, six male alates, two queens, and one king) from nine colonies; only nine individuals concerning the wings.

Colour. **Head capsule**: well sclerotised, very dark (C6–C8), paler in long preserved samples; fontanelle concolorous with or slightly paler than head capsule. Postclypeus C5–C7, often paler (one level) than head capsule. Antennae C4–C6. **Thorax**: pronotum C5–C7 as postclypeus, generally one level paler than head capsule; meso- and metanotum C5–C7. Legs C4–C5; tibia concolorous with or slightly (one level) darker than femur. Wings hyaline with brown to grey tinge (Cf2–Cf4), anterior veins darker. **Abdomen**: tergites C5–C6. Sternites appreciably paler in middle (C3–C4) with both sides darker (C4–C5); posterior sternites darker (C4–C5) than anterior.

Setation. **Head capsule**, with some prominent setae set amongst a high density of short, fine setae forming a dense mat. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and shorter ones in middle; meso- and metanotum with fine, pale setae, arranged in a medio-longitudinal strip, generally visible at 40× or 80×; frequently some larger setae on the posterior lobe of metanotum. **Legs** very pilose, furnished (among numerous fine setae) with 8–10 stronger setae on fore coxa and 5–6 on trochanter; tibia pilose fore, mid, and hind tibia furnished with 20–30 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 11, Fig. 54). **Size**: the imagines of *I. phalloides* sp. nov. are among the smallest of the genus *Isognathotermes* (Fig. 26). **Head capsule**: compound eyes nearly round; ocelli

shortly oval to oval, removed from eyes by a distance about equal to 0.9–1.5 ocellus small diameter; fontanelle generally a tiny round or elongate marking. Antennae: 16 articles on alate individuals, shortened by amputation by three to four articles in queens and kings. Labrum: cupola shaped. **Left mandible** with apical tooth on average shorter than in most other species of the genus (Fig. 27) but always more prominent than first marginal; marginal teeth three in number but second one only suggested by an undulation of edge between first and third marginal teeth; only the apical tooth is acute in unworn specimens; premolar tooth with proximal end obscured or partly obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth always more prominent than first marginal; marginal teeth two in number; first marginal

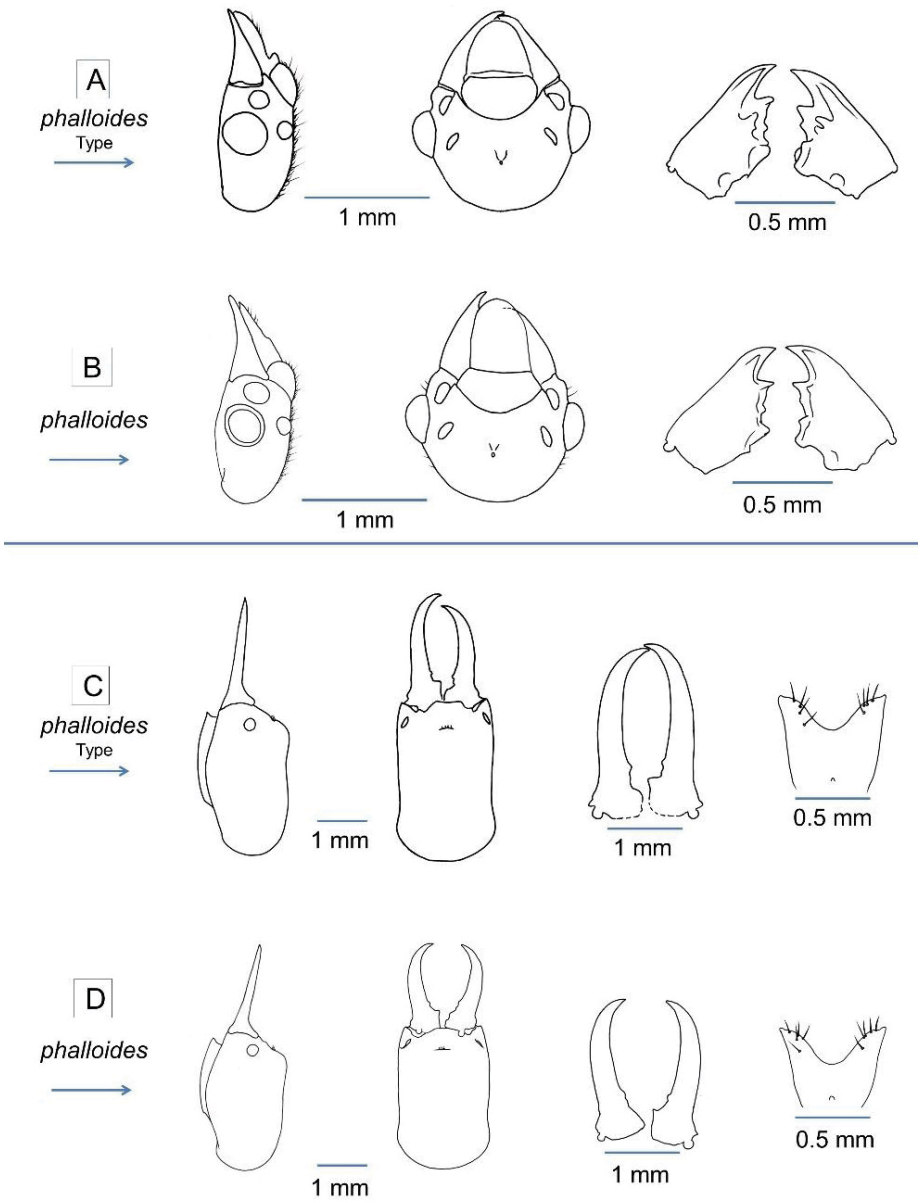


**Fig. 54.** *Isognathotermes phalloides* Josens & Deligne sp. nov.: imago and soldier. **A**. Lateral and dorsal views of the head capsule, and dorsal view of mandibles of an alate male from the type colony of *I. phalloides* (DJ 0087), and dorsal view of this imago's mandibles. **B**. The same of an alate female from a non-type colony of *I. phalloides* (DJ 0879). **C**. Lateral and dorsal views of the head capsule, ventral view of mandibles, and dorsal view of labrum of a soldier from the type colony of *I. phalloides* (DJ 0087). **D**. The same of a soldier from a non-type colony of *I. phalloides* (DJ 0879).

**Table 11.** *Isognathotermes phalloides* Josens & Deligne sp. nov.: ranges of significant measures in the three castes, in alphabetical orders of the "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 23) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.34–0.41 | 0.40 |
| | | Head: width across the eyes | IHdW | 1.38–1.54 | 1.45 |
| | | Left mandible: A-m1 distance | IMlAmD | 0.17–0.21 | 0.19 |
| | | Ocellus: large diameter | IOc*D* | 0.12–0.17 | 0.15 |
| | | Postclypeus: width | IPcW | 0.65–0.77 | 0.69 |
| | | Pronotum: maximal width | IPnW | 1.18–1.39 | 1.29 |
| | | Hind tibia: length | IT3L | 1.58–1.85 | 1.73 |
| | | Wing: length (n= 12) | IWgL | 12.4–13.9 | 13.4 |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.05–1.54 | 1.28 |
| Soldiers (n = 48) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.00–0.07 | 0.05 |
| | | Head: length | SHdL | 2.42–3.21 | 3.05 |
| | | Head: width | SHdW | 1.74–2.15 | 1.96 |
| | | Left mandible: lesser sagitta | SMlc | 0.19–0.33 | 0.25 |
| | | Left mandible: ventral length | SMlL | 1.99–2.36 | 2.30 |
| | | Hind tibia: length | ST3L | 1.48–1.82 | 1.61 |
| | Indices | Head elongation index | SHdL/SHdW | 1.33–1.66 | 1.56 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.09–0.15 | 0.11 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.77–1.09 | 1.01 |
| Workers (n = 27) | Raw measures (mm) | Head: width | WHdW | 1.06–1.27 | 1.18 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.15–0.19 | 0.17 |
| | | Left mandible: total length | WMlL | 0.49–0.58 | 0.56 |
| | | Hind tibia: length | WT3L | 1.17–1.40 | 1.38 |
| | | Valve: PC average length | WVP-AvL | 0.46–0.62 | 0.55 |
| | | Valve: PC average width | WVP-AvW | 0.06–0.09 | 0.07 |
| | | Valve: SC average length | WVS-AvL | 0.36–0.48 | 0.45 |
| | | Valve: SC average width | WVS-AvW | 0.17–0.28 | 0.26 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 5.90–10.1 | 7.24 |

* Abbreviations: see definitions in Material and methods.

tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a carina. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 2–4 and 9–12 branches, respectively.

**Soldier**

Colour. **Head capsule** generally tending towards faded palette (Cf4–Cf5) becoming darker (e.g., Cf5–Cf6) in long preserved samples; there is always a gradient from a darker frons to a paler back, frequently abrupt giving in some cases the impression that the head capsule is bicolorous (as in Fig. 13). Antennae and labrum one or two levels paler than frons. Mandibles dark (C7–C8) generally with an

abrupt clearing on their bases (two palette levels) which is generally paler than frons. **Thorax** and legs generally concolorous with head capsule (C3–C5) or somewhat paler. **Abdomen** grey to red-brown owing to digestive bolus, sometimes with a yellowish tinge on tergites.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Labrum** always with 4–5 large setae on each lobe. **Thorax**: pro- and mesonotum with a small number of setae mainly located on margins. **Legs**: fore coxa bears 4–7 spines on carina but none on ventral side; trochanter generally with 1–4 spines and some lined-up setae; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of 8–12 spines along their shaft. **Abdomen**: tergites with some large setae, mainly on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 11, Fig. 54). **Size**: the soldiers of *I. phalloides* sp. nov. are medium sized in the genus *Isognathotermes* (Fig. 28). **Head capsule**: always clearly sclerotised, appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a narrowing (sometimes strong) near posterior fourth; from antennal sockets sides converge towards bases of mandibles; posterior side regularly rounded or sometimes with three short straight or even concave parts; **upper profile** concave. Angle between extended mandibles and frons always a little obtuse; frons generally without any anterior hump. Gulamentum in ventral view always constricted in its posterior half, with sides of anterior part forming an acute widening or a kind of ear on each side. Antennae: of 15, rarely 14, articles. **Labrum**: always deeply bifurcate and wider than long, with sides generally lyre-shaped; lobes angular, with fine, whitish or translucent tips; anterior margin concave. **Mandibles**: sabre-like with a medium-sized curvature in the genus *Isognathotermes*; inner edges generally smooth with one distinct but very small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible generally more curved than left. **Thorax**: pronotum sellate, as wide as 57–63% of head width, with generally entire anterior and posterior margins. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in second half of abdomen. **Caecum** always rather well developed (as in the worker), best seen in ventral view, near centre of abdomen, as a typical finger-like process, extended forward and sometimes swollen distally or capped (Figs 52, 56). Arrangement of enteric valve cushions showing trilateral symmetry, the odd cushions being about 20% longer than the even cushions, with a pilosity becoming abruptly very dense showing the place where a crest would be expected (in comparison with the worker's EVA).

**Worker**

Colour. **Head capsule** pale (C1–C3) turning grey in long preserved samples. Antennae: proximal articles pale (C2–C3), distal articles always one to two levels darker (C4–C5). **Thorax**, nota, and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect, scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa always carinated, bearing one fine seta and furnished with 3–6 spines on carina and 0–3 on ventral side; fore trochanter with 5–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of 8–15 spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 11, Fig. 55). **Size**: the workers of *I. phalloides* sp. nov. are small sized in the genus *Isognathotermes* (Fig. 30). **Head capsule**: weakly sclerotised (except mandibles).

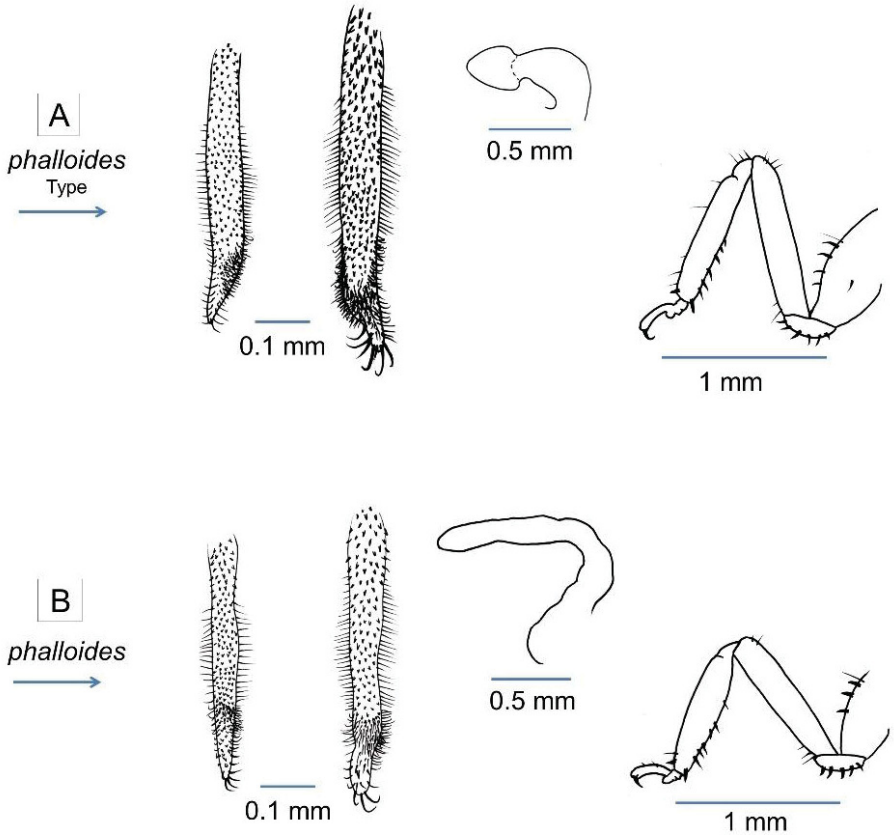


**Fig. 55.** *Isognathotermes phalloides* Josens & Deligne sp. nov.: soldier and worker. PC1s of soldier's and worker's enteric valves, caecum and foreleg of this worker. **A**. From the type colony of *I. phalloides* (DJ 0087), in both cases the distal end of PC1 is somewhat twisted. **B**. From a non-type colony of *I. phalloides* (DJ 0879), in both cases, here also, the distal end of PC1 is somewhat twisted.


**Fig. 56.** Capped caecum of a worker of *Isognathotermes phalloides* Josens & Deligne sp. nov. (DJ 0090), the front is on the left-hand side.

Antennae of 14–14.5 articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal tooth well developed but with a blunt tip even when fresh, second marginal tooth faint (visible as an undulated edge and disappearing in worn mandibles), third marginal tooth with a blunt tip; premolar tooth with its proximal end partly hidden under molar prominence; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 66–73% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in second half of abdomen. Arrangement of enteric valve cushions of the *finitimus* pattern with triradial symmetry: the odd PCs, in their downstream part, bear a higher density of rather short bristles on a globular bulge (*finitimus* EVA, Fig. 5); supporting bristles are numerous: 19–32 on each side of the odd PCs; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum always rather well developed, best seen in ventral view, near centre of abdomen, as a typical finger-like process, extended forward and sometimes swollen distally or seeming to be capped (Fig. 56).

**Chorology-ecology**

This species is linked with the forest galleries of the south-western Congolian forest savanna mosaic ecoregion (Fig. 53).

**Molecular data**

Herein, one mitogenome of *I. phalloides* sp. nov. is published alongside this work (GenBank accession: see Supp. file 3 and ‘Material examined’).

The representative of *I. phalloides* sp. nov. exhibited a dissimilarity of up to 2.26% with samples of *I. phallicaecalis* sp. nov. – the other species exhibiting a phalloid caecum –, and up to 2.43% with samples of *I. similifinitimus* sp. nov. (see Supp. file 4).

This sample was previously published under the label “phal” (DJ 0459), inserted within the species *I. severus* based on a phylogeny reconstructed from the *COII* gene (Hellemans *et al.* 2021). Herein, the same sample was re-sequenced for its mitogenome. The phylogeny based on *COII* extracted from mitogenomes again placed this sample within the species *I. severus* (Supp. file 2). However, the phylogenetic reconstruction from full mitogenomes places this species as sister to a clade containing *finitimus* + *minitabundus* + *ugandensis* + *severus* (Fig. 33), with low support values (SH-aLRT = 70.7; UFB = 82). Further analyses leveraging more samples and nuclear loci will be required to better ascertain its phylogenetic position.

### ***Isognathotermes planifrons*** (Sjöstedt, 1924)

Figs 26–31, 33, 57–59, distribution map: Fig. 47; Table 12

*Cubitermes planifrons* Sjöstedt, 1924b: 255–256.
*Cubitermes fungifaber* var. *elongata* Sjöstedt, 1924b: 256. S**yn. nov**.
*Cubitermes loubetsiensis* Sjöstedt, 1924c: 493. S**yn. nov**.
*Mirotermes* (*Cubitermes*) *gaigei* Emerson, 1928: 516–517, fig. 59. S**yn. nov**.

*Mirotermes* (*Cubitermes*) *loubetsiensis* – Emerson 1928: 515–516, text-fig. 58, pl XXX.
*Cubitermes planifrons* – Sjöstedt 1926: 243–244. — Snyder 1949: 162. — Ruelle 1992: 500. — Krishna *et al.* 2013: 1931. — Josens & Deligne 2019: 60–61.

*Cubitermes* sp. affinis *subarquatus* "spB" – Roy *et al*. 2006: 4–5.
*Isognathotermes planifrons* – Hellemans *et al.* 2021: 233.

**Diagnosis**

This species is difficult to identify from its morphology since it is located near *I. finitimus* and *I. phalloides* sp. nov. It is obviously easier to identify from its *COII* sequence: *I. planifrons* makes a clade well apart from the *finitimus* clade (Hellemans *et al.* 2021: 231).

Best recognition, if molecular data are not available, by a combination of worker's EVA, soldier's mandibles curvature, and geographic origin.

The worker has a *finitimus* EVA (Fig. 5) and is among the medium-sized workers of the genus *Isognathotermes* (Fig. 30) but with a rather small-sized enteric valve (Fig. 31).

The soldier has, on average and along with that of *I. fungifaber*, the highest left mandible apical curvature index; it is among the medium-sized soldiers of *Isognathotermes* (Fig. 28); on the odd PCs of its enteric valve, the pilosity becomes very dense showing the place where a bulge exists in the worker's valve, its *finitimus* pattern is therefore recognizable.

The imago is, on average, medium sized in the genus *Isognathotermes* (Fig. 26) with, on average, larger eyes and ocelli than *I. finitimus*.

This species is also defined by its ecology and chorology: it has always been found in evergreen forests from Gabon to CAR, up to 1000 km from the Atlantic coast (Fig. 47).

Some samples of *I. planifrons* are like *I. fungifaber*, but they have different EVAs.

Some samples of *I. planifrons* are like *I. phalloides* sp. nov.; (Fig. 22) they have similar EVAs, but they have different caeca and geographical distributions.

Many samples of *I. planifrons* are like *I. finitimus*, (Fig. 22) they have similar EVAs and caeca; but their geographical distributions are different, but in CAR (Figs 38, 47).

**Etymology**

The epithet *planifrons* from the Latin *planus* (flat) and *frons* (forehead) refers to the soldier's head morphology (not protruding frons).

**Material examined**

Seventy-seven samples from 29 locations. Of the 41 old museum samples examined, only one, the type, was identified as *C. planifrons* (and subsequently renamed "*C. fungifaber*"); six samples were labelled as *C. banksi*, two as *C. bulbifrons*, one as *C. finitimus*, three as *C. fungifaber*, one as *C. fungifaber* var. *elongata*, six as *C. gaigei*, one as *C. loubetsiensis*, one as *C. subarquatus*, six as *Cubitermes* sp. and 13 not identified.

This species also includes *C.* aff. *subarquatus* "spB" (in Roy *et al.* 2006).

**Syntypes of *Cubitermes planifrons* Sjöstedt, 1924**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker; Mukimbungu; 5°8.5′ S, 14°2.3′ E; 25 Oct. 1904; K.E. Laman leg.; study code: DJ 0296; initially *C. planifrons* → *C. fungifaber*; AMNH.

Krishna *et al.* (2013: 1931) report imagines in the AMNH syntype but the sample that was examined did not contain any. They also mention that another syntype subsample is deposited in NHRM, not examined.

**Paratypes from type colony of *Cubitermes fungifaber* var. *elongata* Sjöstedt, 1924**
DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker; Mukimbungu; 5°8.5′ S, 14°2.3′ E; ca 1904; K.E. Laman leg.; study code: DJ 0270; initially *C. fungifaber* var. *elongata*; AMNH

Krishna *et al.* (2013: 1931) mention that another syntype subsample is deposited in NHRM (not examined).

**Paratypes of *Mirotermes* (*Cubitermes*) *gaigei* Emerson, 1928**
CAMEROON • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0274; initially *C. gaigei* → *C. fungifaber*; AMNH • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0288; initially *C. gaigei* → *C. fungifaber*; AMNH.

**Paratypes of *Cubitermes loubetsiensis* Sjöstedt, 1924**
CONGO REPUBLIC • soldier; Loubetsi; 3°12′ S, 12°10′ E; 1924; Nilsson leg.; study code: DJ 0611; initially *C. loubetsiensis* → *C finitimus*; AMNH • soldier; Loubetsi; 3°12′ S, 12°10′ E; [no date]; Kranz leg.; study code: DJ 0281; initially *C. loubetsiensis*; NHMM.

**Other material examined**

ANGOLA • soldier, worker, ♀ (alate); Quimucanda; 8°5.14′ S, 15°7.43′ E; 28 Nov. 2024; J. Šobotnik leg.; study code: DJ 0973; BE_RMCA_INS.Iso.059898.

CAMEROON • soldier, worker; Bipindi; 3°5′ N, 10°24.5′ E; 1903; G. Zenker leg.; study code: DJ 0961; initially *Eutermes zenkeri*; RBINS • soldier, worker, ♀ (queen); Bipindi; 3°5′ N, 10°24.5′ E; 1920; G. Zenker leg.; study code: DJ 0276; initially *C. fungifaber*; AMNH • soldier; 45 km from Abong-Mbang; 5°16′ N, 17°38′ E; 1 Jul. 1948; P.-P. Grassé and C. Noirot leg.; study code: DJ P195; MNHN EP9900 • soldier, worker, ♂ (alate); Réserve forestière de Nyong; 3°33′ N, 11°37′ E; 5 Dec. 1949; J. Birkett-Smith and J. Dahl leg.; study code: DJ 0678; initially *C. subarquatus*; NHMUK 13671991 • soldier; Eboufek; 3°30′ N, 11°53′ E; 1 Dec. 1962; G. Becker leg.; study code: DJ U066; initially *C. banksi*; NHMUK 13671829 • soldier; Akok; 3°53′ N, 11°57′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U096; initially *C. bulbifrons*; NHMUK 13671844 • soldier; Akok; 3°53′ N, 11°57′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U097; initially *C. bulbifrons*; NHMUK 13671841 • soldier; Bilik; 3°31′ N, 11°17′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U067; initially *C. banksi*; NHMUK 13671832 • soldier, ♂ (king); Bilik; 3°31′ N, 11°17′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U091; initially *C. banksi*; NHMUK 13671827 • soldier, worker; Bilik; 3°31′ N, 11°17′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ 0705; initially *C. banksi*; NHMUK 13671830 • soldier; Ebogo; 3°31′ N, 11°30′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U093; initially *C. banksi*; NHMUK 13671833 • soldier; Ebogo; 3°31′ N, 11°30′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U119; initially *C. gaigei*; NHMUK 13671904 • soldier, worker; Ebogo; 3°23′ N, 11°28′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ 0703; initially *C. banksi*; NHMUK 13671834 • soldier; Mbalmayo; 3°28′ N, 11°31′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ U118; initially *C. gaigei*; NHMUK 13671903 • ♀ (queen); Mbalmayo; 3°31′ N, 11°30′ E; ca 1995; P. Eggleton *et al.* leg.; study code: DJ 0724; initially *C. gaigei*; NHMUK • soldier, worker; Nsimi; 3°10′ N, 11°58′ E; Nov. 1996; M. Harry leg.; study code: DJ 0754; GenBank no PQ679239 (mitogenome); MNHN EP9901 • soldier, worker; Nsimi; 3°10′ N, 11°58′ E; Nov. 1996; M. Harry leg.; study code: DJ 0755; GenBank no PQ679178 (mitogenome); MNHN EP9902 • soldier; Dja forest; 3°20.63′ N, 12°43.03′ E; 30 Mar. 2015; J. Šobotnik leg.; study code: DJ B321; BE RMCA INS.Iso.059347 • soldier; Dja Rock; 3°20.73′ N, 12°42.84′ E; 30 Mar. 2015; J. Šobotnik leg.; study code: DJ B319; BE RMCA INS.Iso.059348 • soldier, worker; near Somalomo; 3°20.7′ N, 12°42.8′ E; 30 Mar. 2015; J. Šobotnik leg.; study code: DJ 0259; BE RMCA INS.Iso.059356 • soldier, worker; Ebogo; 3°22.95′ N, 11°27.718′ E; 22 May 2017; Y. Roisin leg.; study code: DJ 0509; BE RMCA INS.Iso.059361 • soldier, worker; Ebogo; 3°22.772′ N,

11°27.899′ E; 24 May 2017; Y. Roisin leg.; study code: DJ 0518; BE RMCA INS.Iso.059362 • soldier, worker, ♂ (king); Ebogo; 3°22.914′ N, 11°27.8′ E; 26 May 2017; Y. Roisin leg.; study code: DJ 0519; GenBank no PQ679176 (mitogenome); BE RMCA INS.Iso.059363 • soldier, worker; Yolo-Chimpa; 5°35.136′ N, 10°53.301′ E; 30 May 2017; Y. Roisin leg.; study code: DJ 0508; GenBank nos MN646726 (*COI*), MN685929 (*COII*), MN685990 (*28S*); BE RMCA INS.Iso.059364 • soldier, worker; Akometa; 3°28.194′ N, 11°32.814′ E; 6 Jun. 2017; Y. Roisin leg.; study code: DJ 0507; GenBank nos MN646725 (*COI*), MN685928 (*COII*), MN685989 (*28S*), PQ679210 (mitogenome); BE RMCA INS.Iso.059365 • soldier, worker, ♂ (king), ♀ (queen); Ebogo; 3°22.935′ N, 11°27.793′ E; 7 Jun. 2017; Y. Roisin leg.; study code: DJ 0511; BE RMCA INS.Iso.059366 • soldier, worker; Nguinda; 4°15′ N, 12°11′ E; 23 Nov. 2023; J. Šobotnik leg.; study code: DJ 0954; GenBank no PV564654 (mitogenome); BE RMCA INS. Iso.059489 • soldier, worker; Nguinda; 4°15′ N, 12°11′ E; 25 Nov. 2023; J. Šobotnik leg.; study code: DJ 0951; GenBank no PV564644 (mitogenome); BE RMCA INS.Iso.059372 • soldier, worker; Nguinda; 4°15′ N, 12°11′ E; 25 Nov. 2023; J. Šobotnik leg.; study code: DJ 0953; GenBank no PV564645 (mitogenome); BE RMCA INS.Iso.059488 • soldier, worker; Nguinda; 4°15′ N, 12°11′ E; 3 Dec. 2023; J. Šobotnik leg.; study code: DJ 0950; GenBank no PV564653 (mitogenome); BE RMCA INS.Iso.059373 • soldier; Nguinda; 4°15′ N, 12°11′ E; 3 Dec. 2023; J. Šobotnik leg.; study code: DJ 0957; GenBank no PV564659 (mitogenome); BE RMCA INS.Iso.059155.

CENTRAL AFRICAN REPUBLIC • soldier; Boukoko; 3°54′ N, 17°55′ E; 21 Jun. 1948; P.-P. Grassé and C. Noirot leg.; study code: DJ P185; MNHN EP9898 • soldier; Boukoko; 3°54′ N, 17°55′ E; 21 Jun. 1948; P.-P. Grassé and C. Noirot leg.; study code: DJ P186; MNHN EP9899 • soldier, worker, ♀ (alate); Bounguélé; 3°57′ N, 16°45′ E; 12 May 2007; N. Sion leg.; study code: DJ 0931; BE RMCA INS.Iso.059355.

CONGO REPUBLIC • soldier; Ouesso; 1°37′ N, 16°1′ E; 27 Dec. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P168; MNHN EP9896 • soldier, worker; Dimonika; 4°12′ S, 12°20′ E; 21 Apr. 1983; C. Noirot leg.; study code: DJ 0930; MNHN EP9894 • soldier, worker, ♀ (queen); Loundoungou; 2°22.973′ N, 17°4.298′ E; 3 Dec. 2017; Y. Roisin leg.; study code: DJ 0526; GenBank nos MN646728 (*COI*), MN685931 (*COII*), MN685992 (*28S*); BE RMCA INS.Iso.059357 • soldier, worker; Loundoungou; 2°22.929′ N, 17°4.301′ E; 4 Dec. 2017; Y. Roisin leg.; study code: DJ 0524; GenBank no PQ679227 (mitogenome); BE RMCA INS.Iso.059358 • soldier, worker; Mokabi; 3°8.795′ N, 16°57.826′ E; 6 Dec. 2017; Y. Roisin leg.; study code: DJ 0523; GenBank nos MN646727 (*COI*), MN685930 (*COII*), MN685991 (*28S*); BE RMCA INS.Iso.059359 • soldier, worker; Mokabi; 3°9.022′ N, 16°58.214′ E; 8 Dec. 2017; Y. Roisin leg.; study code: DJ 0525; GenBank no PQ679194 (mitogenome); BE RMCA INS.Iso.059360 • soldier, worker; Loundoungou; 2°22.93′ N, 17°4.301′ E; Dec. 2018; S. Lenz leg.; study code: DJ 0767; GenBank no PV564648 (mitogenome); BE RMCA INS.Iso.059371.

DEMOCRATIC REPUBLIC OF THE CONGO • soldier; Mekambo; 1°1′ N, 13°56′ E; 8 Jan. 1957; P.-P. Grassé and C. Noirot leg.; study code: DJ P171; MNHN EP9897 • soldier; Forêt de Djidji; 0°13′ N, 11°48′ E; 26 Jan. 1957; P.-P. Grassé and C. Noirot leg.; study code: DJ P162; GenBank no PQ679182 (mitogenome); MNHN EP9895 • soldier; Route Makokou-Mekambo; 0°41′ N, 13°2′ E; 6 Jun. 1962; J. Deligne leg.; study code: DJ U099; initially *C. gaigei*; NHMUK 13671888 • soldier; Forêt des Abeilles; 0°19′ S, 12°7′ E; 1995; C. Bordereau (?) leg.; study code: DJ P218; MNHN EP9891 • soldier; Forêt des Abeilles; 0°19′ S, 12°7′ E; 1995; C. Bordereau (?) leg.; study code: DJ P219; MNHN EP9892 • soldier; Forêt des Abeilles; 0°19′ S, 12°7′ E; 1995; C. Bordereau (?) leg.; study code: DJ P221; MNHN EP9893 • soldier, worker; Forêt des Abeilles; 0°35′ S, 12°25′ E; 1995; C. Bordereau and A. Robert leg.; study code: DJ 0861; MNHN EP9889 • soldier, worker; Forêt des Abeilles; 0°19′ S, 12°7′ E; 1995; C. Bordereau and A. Robert leg.; study code: DJ 0863; MNHN EP9890 • soldier; La Lopé N.P.; 0°15′ S, 11°35′ E; 6 Mar. 1998; M. Harry leg.; study code: DJ P236; MNHN EP9910 • soldier; La Lopé N.P.; 0°9′ S, 11°36′ E; 7 Mar. 1998; M. Harry leg.; study code: DJ P227; MNHN EP9904 • soldier; La Lopé N.P.;

0°15′ S, 11°35′ E; 7 Mar. 1998; M. Harry leg.; study code: DJ P247; MNHN EP9915 • worker; La Lopé N.P.; 0°12.7′ S, 11°33.5′ E; 7 Mar. 1998; M. Harry leg.; study code: DJ 0632; GenBank nos DQ246542 (*COII*), DQ246524 (*ITS2*), PQ679220 (mitogenome); initially *C.* aff. *subarquatus* "spB" (cf. Roy *et al.* 2006); MNHN EP9919 • soldier; La Lopé N.P.; 0°9′ S, 11°36′ E; 9 Mar. 1998; M. Harry leg.; study code: DJ P229; MNHN EP9905 • soldier, worker; La Lopé N.P.; 0°15′ S, 11°35′ E; 9 Mar. 1998; M. Harry leg.; study code: DJ 0624; GenBank nos DQ127312 (*COII*), DQ246520 (*ITS2*), PQ679183 (mitogenome); initially *C.* aff. *subarquatus* "spB" (cf. Roy *et al.* 2006); MNHN EP9918 • soldier, worker; Doda (north of La Lopé N.P.); 0°4.5′ S, 11°25.5′ E; 10 Mar. 1998; M. Harry leg.; study code: DJ 0923; MNHN EP9903 • soldier; La Lopé N.P.; 0°12′ S, 11°33′ E; 11 Mar. 1998; M. Harry leg.; study code: DJ P233; MNHN EP9908 • soldier; La Lopé N.P.; 0°12′ S, 11°33′ E; 11 Mar. 1998; M. Harry leg.; study code: DJ P234; MNHN EP9909 • soldier; La Lopé N.P.; 0°15′ S, 11°35′ E; 11 Mar. 1998; M. Harry leg.; study code: DJ P248; MNHN EP9916 • soldier; La Lopé N.P.; 0°9′ S, 11°41′ E; 15 Mar. 1998; M. Harry leg.; study code: DJ P230; MNJN EP9906 • soldier; La Lopé N.P.; 0°9′ S, 11°41′ E; 15 Mar. 1998; M. Harry leg.; study code: DJ P231; MNHN EP9907 • soldier, ♀ (queen); La Lopé N.P.; 0°15′ S, 11°35′ E; 15 Mar. 1998; M. Harry leg.; study code: DJ P245; MNHN EP9914 • worker, ♂ (king); La Lopé N.P.; 0°15′ S, 11°35′ E; 15 Mar. 1998; M. Harry leg.; study code: DJ P250; MNHN EP9917 • soldier, ♀ (queen); La Lopé N.P.; 0°15′ S, 11°35′ E; 16 Mar. 1998; M. Harry leg.; study code: DJ P238; MNHN EP9912 • soldier; La Lopé N.P.; 0°15′ S, 11°35′ E; 16 Mar. 1998; M. Harry leg.; study code: DJ P240; MNHN EP9913 • soldier; La Lopé N.P.; 0°15′ S, 11°35′ E; 23 Mar. 1998; M. Harry leg.; study code: DJ P237; MNHN EP9911 • soldier, worker; Nkobissimo [= Nkolmengboua ?]; 2°14.3′ N, 11°29.25′ E; 15 Apr. 2017; G. Trembleau leg.; study code: DJ 0455; GenBank nos MN646724 (*COI*), MN685927 (*COII*), MN685988 (*28S*); BE RMCA INS.Iso.059354.

**Historical review**

Sjöstedt (1924b: 255–256) briefly described the soldier of this species under the name *Cubitermes planifrons*. Two years later, Sjöstedt (1926: 243–244) provided more detailed descriptions of all three castes, housing the species in the sub-family Termitinae. He included (1926: 218–226) *C. planifrons* in imagines' and soldiers' keys of *Cubitermes* species and inserted it in a "*fungifaber*-Gruppe" of species with a not protruding soldier's frons.

Snyder (1949: 162) catalogued this species under the name *Cubitermes planifrons* and housed it in the sub-family Termitinae.

This is one of the species that Ruelle (1992: 500) called "forgotten species".

Krishna *et al.* (2013: 1931) housed *Cubitermes planifrons* in the sub-family Cubitermitinae. Following Emerson's "card catalog", they mentioned that this species might become a junior synonym of *C. fungifaber*; however, this synonymy could not be accepted because *C. planifrons* and *C. fungifaber* belong to different valve pattern groups: Josens & Deligne (2019: 42–44) placed this species within the *finitimus* valve pattern group.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

*Cubitermes* aff. *subarquatus* "spB" was mentioned by Roy *et al.* (2006) in La Lopé National Parc, Gabon. On a genetical base, it was considered a cryptic species. Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes* as synonym of *I. planifrons*.

**Redescription**

**Imago**

Colour. **Head capsule**: well sclerotised, fresh samples very dark, C7–C8 (C6–C7 in long preserved imagines); fontanelle concolorous with or slightly paler than head capsule. Postclypeus C6–C7 slightly

paler (one level) than head capsule. Antennae C5–C6 without any difference between proximal and distal articles. **Thorax**: pronotum C6–C7 as postclypeus, generally one level paler than head capsule; meso- and metanotum C5–C6, concolorous with or somewhat paler than pronotum. Legs C3–C5; tibia usually slightly (one level) darker than femur. Wings hyaline with brown to grey tinge (Cf3–Cf4), anterior veins darker. **Abdomen**: tergites C6–C7. Sternites appreciably paler in middle (C2–C5) with both sides darker (C4–C6); posterior sternites darker (C4–C6) than anterior.

Setation. **Head capsule**, with some prominent setae set amongst a high density of short, fine setae forming a dense mat. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and shorter ones in middle; meso- and metanotum with some fine, pale setae, arranged in a medio-longitudinal strip, generally visible at 20–40×. **Legs** very pilose, furnished (among numerous fine setae) with some stronger setae: 6–10 on the carina of fore coxa and 1–4 on the ventral side of fore coxa and sometimes also some on trochanter; tibia pilose fore, mid, and hind tibia furnished with 15–30 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 12; Figs 26–27, 57). **Size**: the imagines of *I. planifrons* are, on average, among the medium-sized of the genus *Isognathotermes* (Fig. 26). **Head capsule**: compound eyes nearly round; ocelli nearly round to oval, removed from eyes by a distance about equal to 0.7–1.2 ocellus small diameter; fontanelle generally a tiny round marking. Antennae: 16 articles on alate individuals, always shortened by amputation in queens and kings. Labrum: cupola shaped. **Left mandible** with apical tooth on average rather small in comparison with other species of the genus (Fig. 27) and always more prominent than first marginal; marginal teeth three in number but second one only suggested by an undulation of edge between first and third marginal teeth; only the apical tooth is acute in unworn specimens; premolar tooth with proximal end obscured or partly obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth always more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a more or less sharp carina. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 3–4 and 10–11 branches respectively. **Gut**: enteric valve not studied.

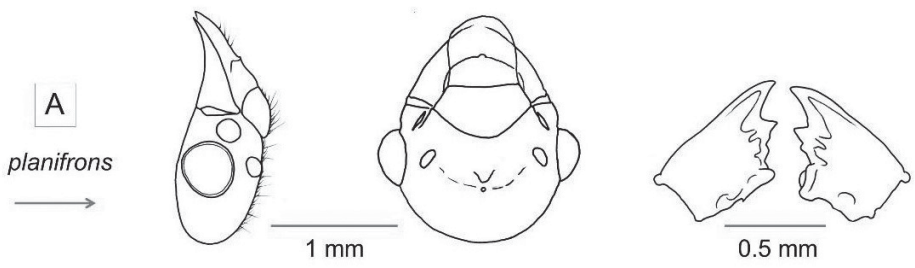


**Fig. 57.** *Isognathotermes planifrons* (Sjöstedt, 1924): imago. **A**. Lateral and dorsal views of the head capsule of the king from a non-type colony of *I. planifrons* (DJ 0511), and dorsal view of this imago's mandibles.

**Table 12.** *Isognathotermes planifrons* (Sjöstedt, 1924): ranges of significant measures in the three castes, in alphabetical orders of the "Code" column; 77 samples from 28 locations.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 14) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.41–0.47 | NA |
| | | Head: width across the eyes | IHdW | 1.49–1.67 | NA |
| | | Left mandible: A-m1 distance | IMlAmD | 0.19–0.23 | NA |
| | | Ocellus: large diameter | IOc*D* | 0.15–0.19 | NA |
| | | Postclypeus: width | IPcW | 0.72–0.81 | NA |
| | | Pronotum: maximal width | IPnW | 1.36–1.57 | NA |
| | | Hind tibia: length | IT3L | 1.30–2.00 | NA |
| | | Wing: length (n= 4) | IWgL | 13.6–14.0 | NA |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.21–1.73 | NA |
| Soldiers (n = 76) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.00–0.06 | 0.012 |
| | | Head: length | SHdL | 2.60–3.45 | 3.06 |
| | | Head: width | SHdW | 1.83–2.34 | 2.12 |
| | | Left mandible: lesser sagitta | SMlc | 0.19–0.35 | 0.28 |
| | | Left mandible: ventral length | SMlL | 2.13–2.62 | 2.40 |
| | | Hind tibia: length | ST3L | 1.50–1.89 | 1.73 |
| | Indices | Head elongation index | SHdL/SHdW | 1.35–1.63 | 1.44 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.08–0.15 | 0.12 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.79–1.37 | 0.93 |
| Workers (n = 42) | Raw measures (mm) | Head: width | WHdW | 1.08–1.30 | 1.21 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.16–0.20 | 0.18 |
| | | Left mandible: total length | WMlL | 0.55–0.64 | 0.59 |
| | | Hind tibia: length | WT3L | 1.18–1.48 | 1.31 |
| | | Valve: PC average length | WVP-AvL | 0.49–0.66 | 0.55 |
| | | Valve: PC average width | WVP-AvW | 0.05–0.10 | 0.08 |
| | | Valve: SC average length | WVS-AvL | 0.38–0.51 | 0.39 |
| | | Valve: SC average width | WVS-AvW | 0.18–0.27 | 0.24 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 5.48–9.57 | 6.27 |

* Abbreviations: see definitions in Material and methods.

**Soldier**

Colour. **Head capsule** generally tending towards deep palette (Cd4–Cd5) becoming fader in long preserved samples; there is always a gradient from a darker frons to a paler back (e.g., from C5 to C4), smooth and extended in 60% of the samples examined but more abrupt in the remaining 40% giving the impression that the head capsule is bicolorous (as in Fig. 13). Antennae and labrum sometimes concolorous or one level paler than head capsule. Mandibles dark (C6–C8) generally with an abrupt clearing on their bases (two palette levels) which is generally the same colour as frons. **Thorax** and legs paler than head capsule (C2–C4) somewhat darker in long preserved samples. **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal

extremity of distal articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Labrum** always with some large setae on lobes. **Thorax**: pro- and mesonotum with a small number of setae mainly located on margins. **Legs**: fore coxa bears at least one fine seta and not any spines in some (10%) samples examined but generally furnished with 1–4 spines on carina and no spines on ventral side; trochanter generally with some long lined-up setae, sometimes with five or six spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively (the latter sometimes weakly developed) and a row of 6–15 spines along their shaft. **Abdomen**: tergites with some large setae, mainly or only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 12; Figs 28, 58). **Size**: the soldiers of *I. planifrons* are medium sized in the genus *Isognathotermes* (Fig. 28). **Head capsule**: always clearly sclerotised; appreciably longer than wide. **Dorsal view**: lateral sides subparallel with a narrowing near posterior third or fourth; from antennal sockets sides converge more or less clearly towards bases of mandibles; posterior side regularly rounded or (in 56% of the samples examined) with a short straight part in the middle. Upper profile almost always slightly concave; angle between extended mandibles and frons always a little obtuse; frons generally (88%) without any anterior hump, rarely with a slight hump. Gulamentum in ventral view always constricted in its posterior half, with sides of anterior part either roundly convex or forming an acute widening or even (in 36% of the samples studied) a kind of ear on each side. Antennae: of 15 articles. **Labrum**: always deeply bifurcate and wider than long, with sides varying from lyre shaped (in 92% of the samples examined) to straight; lobes angular, frequently with fine, whitish or translucent tips; anterior margin concave. **Mandibles**: sabre-like, strongly curved (on average, *I. fungifaber*, and *I. planifrons*, have the highest left mandible apical curvature index in the genus *Isognathotermes*); inner edges generally smooth with one distinct but generally very small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible generally slightly more curved than left. **Thorax**: pronotum sellate, as wide as 56–64% of head width, with generally entire anterior and posterior margins. **Fore coxa** flanged ventrally resulting in a more or less sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in second half of abdomen. Arrangement of enteric valve cushions showing trilateral symmetry, the odd cushions being about 20% longer than the even cushions, generally without any crest or with crests very weakly developed. **Caecum** always rather small, best seen in ventral view, near centre of abdomen, shortly lobed.

**Worker**

Colour. **Head capsule** pale (C1–C3) turning grey in long preserved samples. Antennae: proximal articles pale (C2–C3), distal articles always one to two levels darker (C4–C5). **Thorax**, nota and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect, scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa carinated, bearing one fine seta and furnished with 3–5 spines on carina and generally 1, rarely 2 or 3 spines on ventral side; fore trochanter with 5–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively (the latter sometimes weakly developed) and a row of spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 12; Figs 30, 59). **Size**: the workers of *I. planifrons* are, on average, medium sized in the genus *Isognathotermes* with large overlapping on several other species (Fig. 30).

**Head capsule**: weakly sclerotised (except mandibles). Antennae of 14.5 articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal tooth well developed but with a blunt tip even when fresh, second marginal tooth faint (visible as an undulated edge and disappearing in worn mandibles), third marginal tooth with a blunt tip; premolar tooth with its proximal end generally hidden under molar prominence; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip

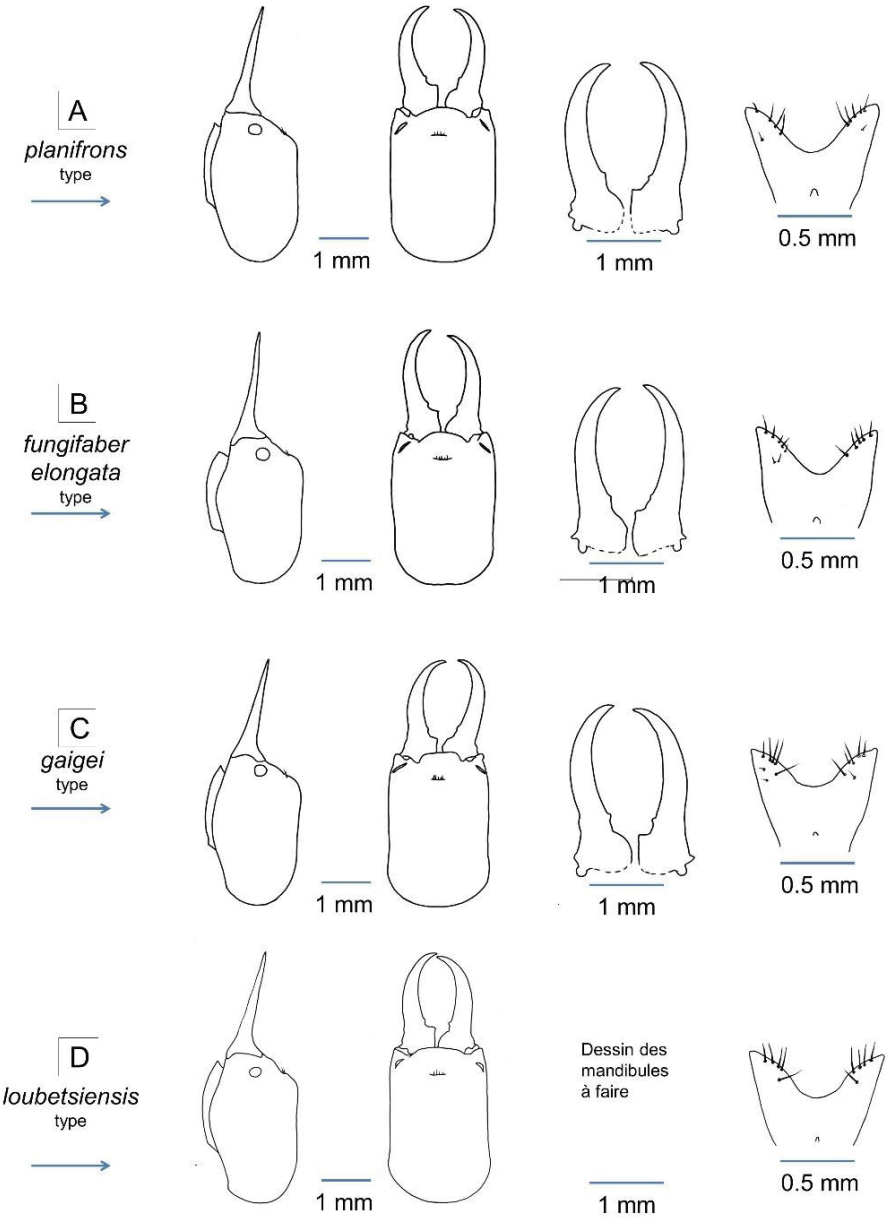


**Fig. 58.** *Isognathotermes planifrons* (Sjöstedt, 1924) and junior synonym species: soldiers. Lateral and dorsal views of a soldier's head capsule, ventral view of this soldier's mandibles, and dorsal view of this soldier's labrum. **A**. From the type colony of *Cubitermes planifrons* Sjöstedt, 1924 (DJ 0296). **B**. From the type colony of *Cubitermes fungifaber* var *elongata* Sjöstedt, 1924 (DJ 0270). **C**. From the type colony of *Mirotermes* (*Cubitermes*) *gaigei* Emerson, 1928 (DJ 0288). **D**. From the type colony of *Cubitermes loubetsiensis* Sjöstedt, 1924 (DJ 0611).

even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 63–76% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in second half of abdomen. Arrangement of enteric valve cushions of the *finitimus* pattern with triradial symmetry: the odd PCs, in their downstream part, are wide and bear at that place a high density of rather short bristles on a globular bulge; supporting bristles are generally numerous: 17–31 on each side of the odd PCs; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum always rather small, visible in ventral view, near centre of abdomen, shortly lobed (generally three small lobes).

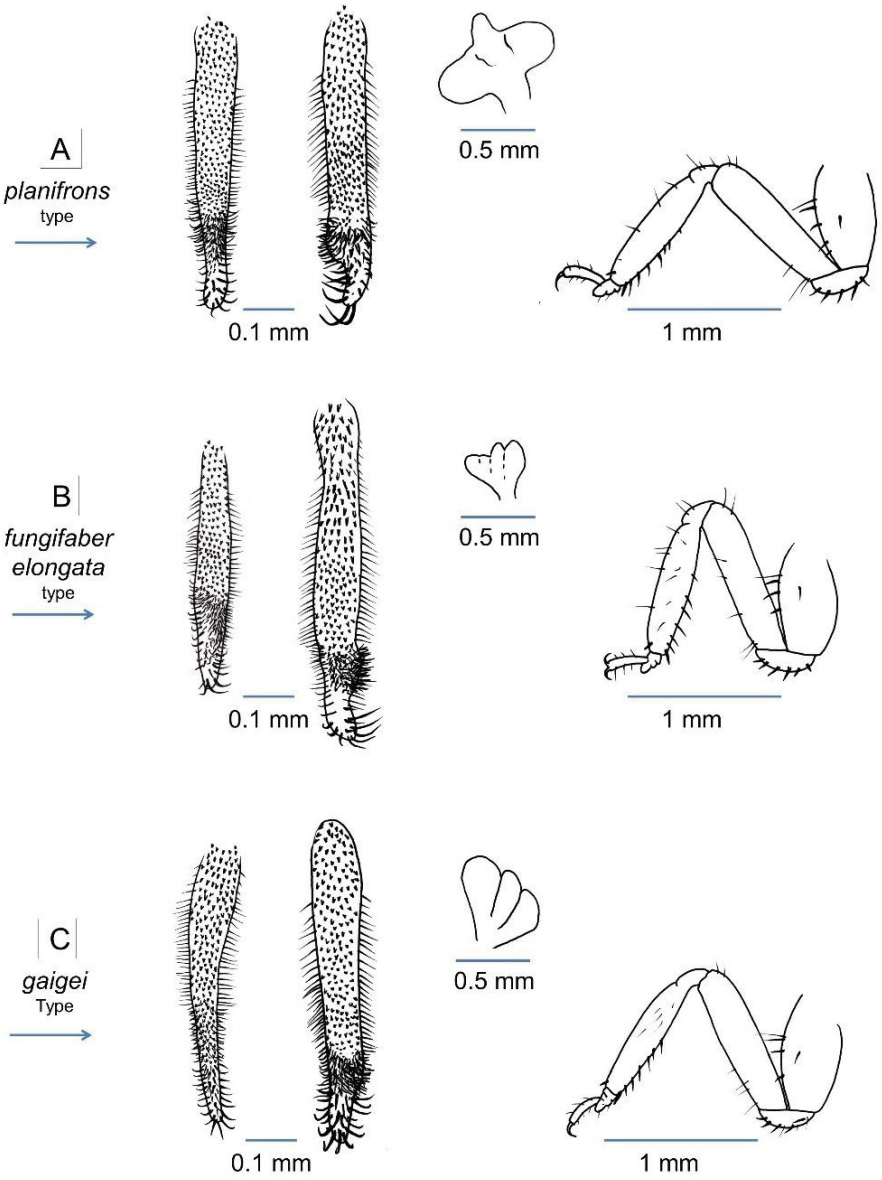


**Fig. 59.** *Isognathotermes planifrons* (Sjöstedt, 1924) and junior synonym species: soldiers and workers. PC1s of a soldier's and a worker's enteric valves, and worker's caecum and foreleg. **A**. From the type colony of *Cubitermes planifrons* Sjöstedt, 1924 (DJ 0296). **B**. From the type colony of *Cubitermes fungifaber* var *elongata* Sjöstedt, 1924 (DJ 0270). **C**. From the type colony of *Mirotermes* (*Cubitermes*) *gaigei* Emerson, 1928 (DJ 0288).

**Chorology-ecology**

The geographic distribution of *I. planifrons* is linked with humid, evergreen forest environments up to 800 km from the Atlantic coast: it includes the Atlantic equatorial coastal forests and the northwestern Congolian lowland forests ecoregions (Fig. 47). This distribution is partly similar to that of *I. fungifaber* (but with another EVA).

**Molecular data**

Sixteen mitogenomes of the morphological species *I. planifrons* are published alongside this work (GenBank accessions: see Supp. file 3 and 'Material examined'). The morphological species *I. planifrons* appears to be genetically heterogeneous, with sample DJ P141 differing from the others by a dissimilarity of over 2%, which probably makes it a cryptic species, but as it is currently unique, it has not yet been described and was moved as *I.* aff. *planifrons* in the Incertae sedis chapter. Surprisingly, two samples of *I. planifrons* (DJ 0754 and DJ 0755) as well as *I.* aff. *planifrons* (DJ P141) were collected almost in the same place (between Nsimi and Zoétélé, Cameroon).

After having discarded DJ P141 (which is slightly more similar to *I. phallicaecalis* sp. nov. and *I. phalloides* sp. nov.), the fifteen remaining mitogenomes exhibited a dissimilarity of up to 2.1% with each other (Supp. file 4). Our present sampling includes full mitogenomes from Gabonese samples previously published under the appellation *Cubitermes* aff. *subarquatus* "spB" by Roy *et al.* (2006). This species "spB" was already reassigned to *I. planifrons* by Hellemans *et al.* (2021) based on *COII* phylogeny (accession DQ127312).

***Isognathotermes rectimalatus*** Josens & Deligne sp. nov.
urn:lsid:zoobank.org:act:5D53B849-4EC2-4D5E-9C7E-93264E227BC8
Figs 26–31, 33, 60, distribution map: Fig. 53; Table 13

**Diagnosis**

The worker has a *finitimus* EVA (Fig. 5) and is among the large-sized workers of the genus *Isognathotermes* (Fig. 30) with large-sized enteric valve (Fig. 31); in particular, the odd PCs elongation index is very high (WVPOdd-Elg = 8.60–11.6).

The soldier is medium sized in the genus *Isognathotermes* (Fig. 28) and has almost straight mandibles with a low left mandible apical curvature index (SMlc/SMlL = 0.05–0.07), as in *I. minitabundus* and *I. ugandensis* (Fig. 29) but the latter have a *fungifaber* EVA.

The only known imago is medium sized, its compound eyes are also medium sized, but they are located far from the head margin and close to the ocelli.

This species is also defined by its ecology and chorology: it has been found only in Angolan woodlands (Fig. 53).

**Etymology**

The epithet *rectimalatus* from the Latin *rectus* (straight) and *malatus* (mandible) refers to the straight mandibles of the soldier.

**Material examined**

Six samples from two locations.

**Holotype**

ANGOLA • soldier; Mussende; 10°33.17′ S, 15°39.492′ E; 21 Sep. 2019; M. Hasson leg.; study code: DJ 0719; GenBank no PQ679198 (mitogenome); BE RMCA INS.Iso.059376.

**Paratypes**

ANGOLA • soldier, worker; same data as for holotype; BE RMCA INS.Iso.059938.

**Other material examined**

ANGOLA • soldier, worker; Mussende; 10°33.17′ S, 15°39.492′ E; Dec. 2018; M. Hasson leg.; study code: DJ 0771; GenBank no PQ679237 (mitogenome); BE RMCA INS.Iso.059379 • soldier, worker; Cangandala N.P.; 9°49.33′ S, 16°40′ E; 1 Mar. 2019; M. Viage leg.; study code: DJ 0864; GenBank no PQ679197 (mitogenome); BE RMCA INS.Iso.059374 • soldier, worker; Cangandala N.P.; 9°49.33′ S, 16°40′ E; 1 Mar. 2019; M. Viage leg.; study code: DJ 0867; GenBank no PQ679203 (mitogenome); BE RMCA INS.Iso.059375 • worker; Mussende; 10°33.17′ S, 15°39.492′ E; 13 Aug. 2019; M. Hasson leg.; study code: DJ 0710; GenBank no PQ679233 (mitogenome); BE RMCA INS.Iso.059377 • soldier, ♂ (alate); Mussende; 10°33.17′ S, 15°39.492′ E; 25 Oct. 2021; M. Hasson leg.; study code: DJ 0812; BE RMCA INS.Iso.059378.

**Historical review**

The species is described here. It was discovered by two of us (MV & MiH) in the Angolan Miombo.

**Description**

**Imago**

The imagines are very similar to those of *I. finitimus*.

Colour. **Head capsule**: well sclerotised, very dark (C7); fontanelle paler than head capsule. Postclypeus C5, paler than head capsule. Antennae C5. **Thorax**: pronotum C7 as head capsule; meso- and metanotum C6. Legs C4–C5; tibia slightly (one level) darker than femur. Wings hyaline with brown to grey tinge (Cf3), anterior veins darker. **Abdomen**: tergites C6. Sternites appreciably paler in middle (C3) with both sides darker (C5); posterior sternites darker (C5) than anterior.

Setation. **Head capsule**, with some prominent setae set amongst a high density of short, fine setae forming a dense mat. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and shorter ones in middle; meso- and metanotum without any visible setae, even at 100×. **Legs** very pilose, furnished (among numerous fine setae) with 6 stronger setae on fore coxa and 4–5 on trochanter; tibia pilose fore, mid, and hind tibia furnished with 20–35 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs, respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 13; Figs 26, 60). **Size**: the only known imago of *I. rectimalatus* sp. nov. is among the medium sized of the genus *Isognathotermes* (Fig. 26). **Head capsule**: compound eyes shortly oval; ocelli shortly oval, removed from eyes by a distance about equal to 0.7–0.8 ocellus small diameter; fontanelle generally a tiny round or elongate marking. Antennae: 16 articles on the single known alate. Labrum: cupola shaped. **Left mandible** apical tooth always more prominent than first marginal; marginal teeth three in number but second one only suggested by an undulation of edge between first and third marginal teeth; only the apical tooth is acute in unworn specimens; premolar tooth with proximal end obscured or partly obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth always more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and narrower than head width (including the eyes),

**Table 13.** *Isognathotermes rectimalatus* Josens & Deligne sp. nov.: ranges of significant measures in the three castes, in alphabetical orders of the "Code" column; six samples from two locations.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 1) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.42 | 0.42 |
| | | Head: width across the eyes | IHdW | 1.60 | 1.60 |
| | | Left mandible: A-m1 distance | IMlAmD | 0.21 | 0.21 |
| | | Ocellus: large diameter | IOc*D* | 0.18 | 0.18 |
| | | Postclypeus: width | IPcW | 0.82 | 0.82 |
| | | Pronotum: maximal width | IPnW | 1.34 | 1.34 |
| | | Hind tibia: length | IT3L | 1.93 | 1.93 |
| | | Wing: length (n= 1) | IWgL | 15.9 | 15.9 |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.51 | 1.51 |
| Soldiers (n = 5) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.04–0.09 | 0.05 |
| | | Head: length | SHdL | 3.04–3.41 | 3.15 |
| | | Head: width | SHdW | 2.06–2.34 | 2.30 |
| | | Left mandible: lesser sagitta | SMlc | 0.13–0.19 | 0.14 |
| | | Left mandible: ventral length | SMlL | 2.33–2.63 | 2.52 |
| | | Hind tibia: length | ST3L | 1.74–1.89 | 1.80 |
| | Indices | Head elongation index | SHdL/SHdW | 1.35–1.55 | 1.37 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.05–0.07 | 0.06 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.86–1.14 | 1.05 |
| Workers (n = 4) | Raw measures (mm) | Head: width | WHdW | 1.25–1.34 | NA |
| | | Left mandible: A-m1 distance | WMlAmD | 0.20–0.21 | NA |
| | | Left mandible: total length | WMlL | 0.59–0.65 | NA |
| | | Hind tibia: length | WT3L | 1.35–1.41 | NA |
| | | Valve: PC average length | WVP-AvL | 0.73–0.75 | NA |
| | | Valve: PC average width | WVP-AvW | 0.07–0.09 | NA |
| | | Valve: SC average length | WVS-AvL | 0.59–0.64 | NA |
| | | Valve: SC average width | WVS-AvW | 0.32–0.41 | NA |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 8.60–11.6 | NA |

* Abbreviations: see definitions in Material and methods.

straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** weakly flanged ventrally resulting in an unclear carina. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 3 and 9 branches, respectively.

**Soldier**

Colour. **Head capsule** C4–C5; frons C5–C6. Gulamentum somewhat darker than head. Antennae and labrum concolorous with head capsule. Mandibles dark (C7–C8) with an abrupt clearing on their bases (two palette levels) which is the same colour as frons. **Thorax**, nota and legs somewhat paler than head capsule (C3–C4). **Abdomen** grey to red-brown owing to digestive bolus, rarely with a yellow tinge on tergites.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal

extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50 × or more). **Labrum** with some large setae on lobes. **Thorax**: pro- and mesonotum with some setae mainly located on margins. **Legs**: fore coxa furnished with 1–3 spines on carina and 0–1 on ventral side; trochanter with 3–6 long lined-up spines; fore, mid-, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively; all tibiae furnished with a row of 9–15 spines. **Abdomen**: tergites with some large setae, mainly on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 13, Figs 28, 60). **Size**: the soldiers of *I. rectimalatus* sp. nov. are medium sized in the genus *Isognathotermes* (Fig. 28). **Head capsule**: clearly sclerotised and appreciably

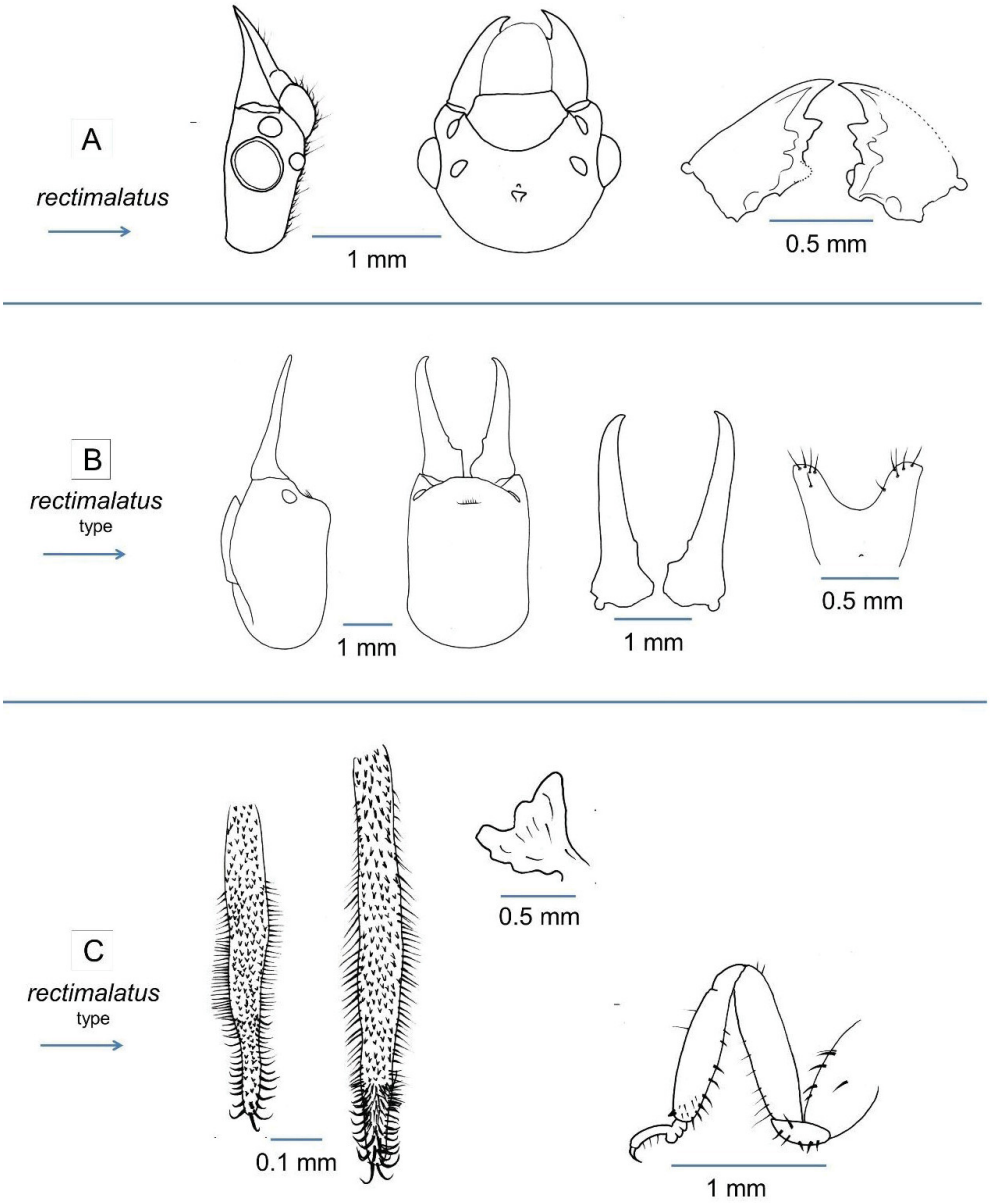


**Fig. 60.** *Isognathotermes rectimalatus* Josens & Deligne sp. nov.: imago, soldier, and worker. **A**. Lateral and dorsal views of the head capsule, and dorsal view of mandibles of an alate male from a non-type colony of *I. rectimalatus* (DJ 0812). **B**. Lateral and dorsal views of the head capsule; ventral view of mandibles; and dorsal view of labrum of a soldier from the type colony of *I. rectimalatus* (DJ 0771). **C**. PC1s of soldier's and worker's enteric valves; caecum and foreleg of this worker from the type colony of *I. rectimalatus*.

longer than wide. **Dorsal view**: lateral sides mostly subparallel with a slight narrowing near posterior third; from antennal sockets sides converge clearly towards bases of mandibles; posterior side regularly convex. **In profile**: upper profile concave; frons: fontanelle overhanged by a sketched frontal hump. Gulamentum in ventral view constricted in its posterior half, with sides of anterior part forming an acute widening with a kind of ear on each side. Antennae of 15 articles. **Labrum**: deeply bifurcate and wider than long, with sides lyre-shaped; lobes angular or truncated, with fine, whitish or translucent tips; anterior margin concave. **Mandibles**: sabre-like, almost straight at the base and slightly curved distally; left mandible apical curvature index very low (SMlc/SMlL < 0.075); inner edges smooth with one distinct but very small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. **Thorax**: pronotum sellate, clearly narrower than head, sometimes with a slight notch in anterior margin and entire posterior margin. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions showing trilateral symmetry: the odd cushions are 19% longer than the even cushions, with humps weakly developed; secondary cushions wide at the upstream end narrowing noticeably downstream with a homogeneous spine scattering. **Caecum** rather small, best seen in ventral view, near centre of abdomen, lobed (three small lobes).

**Worker**

Colour. **Head capsule** pale (C1–C3). Antennae: proximal articles pale (C2), distal articles two levels darker (C4). **Thorax**, nota and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa carinated, bearing one fine seta and furnished with 2–4 spines on carina and 0–2 on ventral side; fore trochanter with 7–9 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of 8–16 spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 13, Figs 30–31, 60). **Size**: the workers of *I. rectimalatus* sp. nov. are medium to large sized in the genus *Isognathotermes* (Fig. 30). **Head capsule** weakly sclerotised (except mandibles). Antennae 14–14.5 articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed (WMlAmD > 0.19 mm) with a sharp tip when fresh; marginal teeth three in number, first marginal well developed but with a blunt tip even when fresh, second marginal faint (visible as an undulated edge), third marginal with a blunt tip; the premolar tooth is best seen than in most other species; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal well developed with a sharp tip when fresh; second marginal smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 63–70% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions of the *finitimus* pattern with triradial symmetry: the odd PCs, in their downstream part, are wide and bear at that place a very high density of rather short bristles on a globular bulge; supporting bristles are generally numerous: 25–33 on each side of the odd PCs; worker's valve very large (WVP-AvL > 0.72 mm, Fig. 31) odd PCs elongation index very high (WVPOdd-Elg > 8.5); secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum rather small, visible in ventral view, near centre of abdomen, shortly lobed (three small lobes).

**Chorology-ecology**

This species is only known from Angola; its geographic distribution is linked with the Angolan Miombo woodland ecoregion (Fig. 53).

**Molecular data**

The five mitogenomes of *I. rectimalatus* sp. nov. exhibited less than 2% dissimilarity with each other (Supp. file 4: GenBank accessions: see supplementary Supp. file 3 and 'Material examined'). After *I. acristatus* sp. nov., the species *I. rectimalatus* sp. nov. was established as sister to all remaining *Isognathotermes* members (Fig. 33).

***Isognathotermes severus*** (Silvestri, 1914)
Figs 26–31, 33, 61–63, distribution maps: Figs 45, 49; Table 14

*Cubitermes severus* Silvestri, 1914: 92–93, fig. LIV.
*Cubitermes severus* var. *modestior* Silvestri, 1914: 93–94, fig. LV. S**yn. nov**.
*Cubitermes silvestrii* Sjöstedt, 1925: 54. S**yn. nov**.

*Cubitermes severus* – Sjöstedt 1926: 250–251. — Snyder 1949: 163. — Krishna *et al.* 2013: 1936. — Josens & Deligne 2019: 60–61.
*Isognathotermes severus* – Hellemans *et al.* 2021: 233.

**Diagnosis**

This is the *Isognathotermes* species with the largest geographic distribution: from Gambia to CAR (Figs 45, 49).

The worker has a *fungifaber* EVA but in 12% of the samples examined, it has an EVA intermediate between the *fungifaber* and *finitimus* patterns; it is among the medium-sized workers of the genus *Isognathotermes* (Fig. 30). Its premolar tooth on left mandible is generally better seen than in most other species.

The soldier is, on average, among the medium-sized soldiers in the genus *Isognathotermes* (Figs 21, 28) and its EVA, generally without any crest, looks like a *muneris* EVA; its head is generally bulbous but this is shared with *I. minitabundus* and *I. ugandensis* (and with *I. bulbifrons* that has a *finitimus* EVA).

The imago is, on average, among the middle- to large-sized imagines in the genus *Isognathotermes* (Fig. 26).

Confusion may occur mainly with *I. fungifaber* in West Africa and with *I. ugandensis* in central Africa. (see discussion about the ambiguities between *I. severus* and *I. ugandensis ugandensis*). This species has been found in various ecosystems (see chorology).

**Etymology**

The epithet *severus* means 'serious, earnest' in Latin.

**Material examined**

One hundred fifty-seven samples from 88 locations. Of the 101 old museum samples examined, 42 were initially labelled as *Cubitermes severus*, two as *C. severus* var. *modestior*, one as *C. fungifaber*, 15 as *C. gaigei*, six as *C. silvestrii*, four as *C. speciosus*, six as *C. ugandensis*, one as *Cubitermes* sp. and 24 not identified.

**Syntypes of *Cubitermes severus* Silvestri, 1914**
GUINEA • soldier, worker, ♀ (queen); Kakoulima; 9°46′ N, 13°27′ W; Aug. 1912; F. Silvestri leg.; study code: DJ 0608; initially *C. severus*; IEAP • soldier, worker, ♀ (queen); Camayenne; 9°31.83′ N, 3°41.17′ W; 16 Oct. 1912; F. Silvestri leg.; study code: DJ 0609; initially *C. severus*; IEAP • soldier, worker; Kakoulima; 9°46′ N, 13°27′ W; before 1904; F. Silvestri leg.; study code: DJ 0292; initially *C. severus*; AMNH • soldier, worker; Camayenne; 9°31.8′ N, 13°41.5′ W; 16 Oct. 1912; F. Silvestri leg.; study code: DJ 0293; initially *C. severus*; AMNH

**Syntypes of *Cubitermes severus* var. *modestior* Silvestri, 1914**
GUINEA • soldier, worker, ♂ (king); Kindia; 10°3′ N, 12°52′ W; 20 Aug. 1912; F. Silvestri leg.; study code: DJ 0294; initially *C. severus* var. *modestior*; AMNH • soldier, worker, ♀ (queen); Kindia; 10°3′ N, 12°52′ W; 20 Aug. 1912; F. Silvestri leg.; study code: DJ 0341; initially *C. severus* var. *modestior*; IEAP.

Krishna *et al.* (2013: 1927) mention that another subsample is deposited in PPRI (not examined).

**Syntypes of *Cubitermes silvestrii* Sjöstedt, 1925**
GUINEA • soldier, worker; Kakoulima; 9°46′ N; 13°27′ W), Fr. Guinea [= Guinea]; ca 1912; F. Silvestri leg.; study code: DJ 0302; initially *C. silvestrii*; AMNH.

Krishna *et al.* (2013: 1937) mention that another subsample is deposited in NHRM (not examined).

**Other material examined**

BENIN • soldier, worker; Birni (forêt classée); 10°1′ N, 1°32′ E; Nov. 2016; L.E. Loko leg.; study code: DJ 0402; GenBank no PQ679191 (mitogenome); BE RMCA INS.Iso.059446 • soldier, worker, ♀ (queen); Birni (forêt classée); 10°1′ N, 1°32′ E; Nov. 2016; L.E. Loko leg.; study code: DJ 0403; GenBank nos MN646735 (*COI*), MN685940 (*COII*), MN686001 (*28S*); BE RMCA INS.Iso.059448 • soldier, worker; Birni (forêt classée); 10°1′ N, 1°32′ E; Nov. 2016; L.E. Loko leg.; study code: DJ 0404; GenBank no PQ679230 (mitogenome); BE RMCA INS.Iso.059445 • soldier, worker; Birni (forêt classée); 10°1′ N, 1°32′ E; Nov. 2016; L.E. Loko leg.; study code: DJ 0405; GenBank no PQ679200 (mitogenome); BE RMCA INS.Iso.059449 • soldier, worker; Birni (forêt classée); 10°1′ N, 1°32′ E; Nov. 2016; L.E. Loko leg.; study code: DJ 0406; GenBank no PQ679221 (mitogenome); BE RMCA INS.Iso.059447.

BURKINA FASO • soldier, worker; Bama; 11°21′ N, 4°23′ W; Feb. 2012; S. Traoré leg.; study code: DJ 0052; BE RMCA INS.Iso.059412.

CAMEROON • soldier, worker, ♂ (alate); Mont Guendérou; 7°10′ N, 14°14′ E; before 1914?; Riggenbach leg.; study code: DJ 0324; initially *C. silvestrii*; AMNH • soldier, worker, ♀ (alate), ♂ (alate); Ekoua; 3°52.6′ N, 12°15.5′ E; 28 Mar. 2015; J. Šobotnik leg.; study code: DJ 0249; GenBank no PQ679208 (mitogenome); BE RMCA INS.Iso.059401 • soldier, worker, ♀ (alate), ♂ (alate); Batié; 5°17′ N, 10°14.7′ E; 7 Apr. 2015; J. Šobotnik leg.; study code: DJ 0250; BE RMCA INS.Iso.059402 • soldier, worker, ♀ (alate), ♂ (alate); Koutaba; 5°39.3′ N, 10°46.4′ E; 8 Apr. 2015; J. Šobotnik leg.; study code: DJ 0251; GenBank no PQ679250 (mitogenome); BE RMCA INS.Iso.059403 • soldier, worker; Koutaba; 5°39.3′ N, 10°46.4′ E; 8 Apr. 2015; J. Šobotnik leg.; study code: DJ 0258; GenBank no PQ679229 (mitogenome); BE RMCA INS.Iso.059407 • soldier, worker, ♀ (alate), ♂ (alate); Boulourou; 4°48.8′ N, 11°0.1′ E; 10 Apr. 2015; J. Šobotnik leg.; study code: DJ 0252; BE RMCA INS. Iso.059404 • soldier, worker; Koutaba; 5°35.988′ N, 10°44.973′ E; 31 May 2017; Y. Roisin leg.; study code: DJ 0530; GenBank no PQ679166 (mitogenome); BE RMCA INS.Iso.059408 • soldier, worker; Mancha; 5°33.534′ N, 10°52.836′ E; 1 Jun. 2017; Y. Roisin leg.; study code: DJ 0510; BE RMCA INS. Iso.059409 • soldier, worker; Koutaba; 5°35.816′ N, 10°45.856′ E; 2 Jun. 2017; Y. Roisin leg.; study

code: DJ 0531; GenBank no PQ679168 (mitogenome); BE RMCA INS.Iso.059410 • soldier, worker; Kimi; 6°5′ N, 11°29′ E; 30 Nov. 2023; J. Šobotnik leg.; study code: DJ 0949; GenBank no PV564658 (mitogenome); BE RMCA INS.Iso.059405 • soldier, worker; Kimi; 6°5′ N, 11°29′ E; 30 Nov. 2023; J. Šobotnik leg.; study code: DJ 0952; GenBank no PV564651 (mitogenome); BE RMCA INS.Iso.059406.

CENTRAL AFRICAN REPUBLIC • soldier; Bouala; 6°22.8′ N, 15°37′ E; 8 Jan. 1914; Elbert leg.; study code: DJ U006; initially *C. severus*; NHMUK 13671956 • soldier, ♀ (alate); Bosoum; 6°19′ N, 16°22′ E; 1 May 1914; G. Tessmann leg.; study code: DJ U016; initially *C. severus*; NHMUK 13671955 • soldier; Boukoko; 3°54′ N, 17°55′ E; 2 Jul. 1948; P.-P. Grassé and C. Noirot leg.; study code: DJ P187; MNHN EP9939 • soldier; 20 km N of Bangui; 4°37′ N, 18°33′ E; Nov. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P174; MNHN EP9928 • soldier; 20 km N of Bangui; 4°36′ N, 18°31′ E; Nov. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P177; MNHN EP9931 • soldier; Bossembélé; 5°16′ N, 17°38′ E; 21 Nov. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P175; MNHN EP9929 • soldier; Bossembélé; 5°16′ N, 17°38′ E; 21 Nov. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P181; MNHN EP9935 • soldier; 70 km from Alindao; 5°30′ N, 20°49′ E; Dec. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P180; MNHN EP9934 • soldier; 70 km from Alindao; 5°30′ N, 20°49′ E; Dec. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P184; MNHN EP9938 • soldier; Bambari; 5°46′ N, 20°40′ E; Dec. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P178; MNHN EP9932 • soldier; Bambari; 5°46′ N, 20°40′ E; Dec. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P179; MNHN EP9933 • soldier; Bambari; 5°46′ N, 20°40′ E; Dec. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P182; MNHN EP9936 • soldier; Bambari; 5°46′ N, 20°40′ E; 4 Dec. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P183; MNHN EP9937 • soldier; Bambari; 5°46′ N, 20°40′ E; 13 Dec. 1956; P.-P. Grassé and C. Noirot leg.; study code: DJ P176; MNHN EP9930 • soldier; Bambari; 5°46′ N, 20°40′ E; 1975; P. Eggleton *et al.* leg.; study code: DJ U070; initially *C. ugandensis*; NHMUK 13671994 • soldier; near Bangui; 4°23′ N, 18°34.5′ E; 1975; Becker leg.; study code: DJ U111; initially *C. gaigei*; NHMUK 13671894 • soldier, worker, ♂ (alate); Boika (Mbaïki); 3°52′ N, 17°58′ E; 11 Apr. 2007; N. Sion leg.; study code: DJ 0934; GenBank no PV564656 (mitogenome); BE RMCA INS.Iso.059399 • soldier, worker; Mopiti (Mbaïki); 3°52′ N, 17°58′ E; 14 Apr. 2007; N. Sion leg.; study code: DJ 0932; GenBank no PV564660 (mitogenome); BE RMCA INS.Iso.059418 • soldier, worker; Mopiti (Mbaïki); 3°52′ N, 17°58′ E; 14 Apr. 2007; N. Sion leg.; study code: DJ 0933; BE RMCA INS.Iso.059417 • soldier, worker; Bondoé; 5°10.3′ N, 17°44.2′ E; 23 Apr. 2007; N. Sion leg.; study code: DJ 0004; BE RMCA INS.Iso.059400 • soldier, worker; Gbasabangui (Bangui); 4°22.5′ N, 18°34.75′ E; 3 May 2007; N. Sion leg.; study code: DJ 0935; GenBank no PV564646 (mitogenome); BE RMCA INS.Iso.059452 • soldier, worker; Bondoé; 5°10.3′ N, 17°44.2′ E; 27 May 2007; N. Sion leg.; study code: DJ 0001; BE RMCA INS.Iso.059450 • soldier, worker; near Bangui; 4°23′ N, 18°34.5′ E; 30 Oct. 2010; G. Josens leg.; study code: DJ 0367; BE RMCA INS.Iso.059414 • soldier, worker, ♀ (alate); Mbaïki; 3°55′ N, 18°0′ E; 24 Apr. 2018; S.P. Wango leg.; study code: DJ 0586; BE RMCA INS.Iso.059395 • soldier, worker, ♀ (alate); Mbaïki; 3°55′ N, 18°0′ E; 24 Apr. 2018; S.P. Wango leg.; study code: DJ 0587; GenBank no PQ679223 (mitogenome); BE RMCA INS.Iso.059388 • soldier, worker; Mbaïki; 3°55′ N, 18°0′ E; 24 Apr. 2018; S.P. Wango leg.; study code: DJ 0588; BE RMCA INS.Iso.059394 • soldier, worker; Mbaïki; 3°55′ N, 18°0′ E; 24 Apr. 2018; S.P. Wango leg.; study code: DJ 0595; BE RMCA INS.Iso.059389 • soldier, worker; Mbaïki; 3°55′ N, 18°0′ E; 24 Apr. 2018; S.P. Wango leg.; study code: DJ 0596; GenBank no PQ679247 (mitogenome); BE RMCA INS.Iso.059396 • soldier, worker, ♀ (alate); Bondoé; 5°10.3′ N, 17°44.2′ E; 26 Apr. 2018; S.P. Wango leg.; study code: DJ 0589; GenBank nos MN646738 (*COI*), MN685943 (*COII*), MN686004 (*28S*); BE RMCA INS.Iso.059393 • soldier, worker, ♀ (alate); Bondoé; 5°10.3′ N, 17°44.2′ E; 26 Apr. 2018; S.P. Wango leg.; study code: DJ 0590; GenBank no PQ679244 (mitogenome); BE RMCA INS.Iso.059390 • soldier, worker, ♂ (alate); Bondoé; 5°10.3′ N, 17°44.2′ E; 26 Apr. 2018; S.P. Wango leg.; study code: DJ 0591; GenBank no PQ679206 (mitogenome); BE RMCA INS.Iso.059392 • soldier, worker; Bondoé; 5°10.3′ N, 17°44.2′ E; 26 Apr. 2018; S.P. Wango leg.; study code: DJ 0594; GenBank no PQ679201 (mitogenome); BE RMCA INS.Iso.059391 • soldier, worker,

♂ (king); Bangui ?; 4°21′ N, 18°30′ E; 3 May 2007; N. Sion leg.; study code: DJ 0936; GenBank no PV564647 (mitogenome); BE RMCA INS.Iso.059398.

CHAD • soldier, worker; Moundou; 8°24′ N, 16°24′ E; 23 May 1948; P.-P. Grassé and C. Noirot leg.; study code: DJ 0431; MNHN EP9923.

CÔTE D'IVOIRE • soldier; 6 km E of Odienné; 9°30′ N, 7°30′ W; Dec. 1938; P.-P. Grassé leg.; study code: DJ P154; MNHN EP9925 • soldier; 6 km E of Odienné; 9°30′ N, 7°30′ W; Dec. 1938; P.-P. Grassé leg.; study code: DJ P155; MNHN EP9926 • soldier; Odienné; 7°15′ N, 7°14′ W; Dec. 1938; P.-P. Grassé leg.; study code: DJ P156; MNHN EP9927 • soldier; Mont Tonkui; 7°24′ N, 7°9′ W; 18 Mar. 1947; C. Noirot leg.; study code: DJ P338; MNHN EP9953 • soldier; Ferkessédougou; 9°35′ N, 5°12′ W; 2 Oct. 1947; C. Noirot leg.; study code: DJ P192; MNHN EP9940 • soldier; Bouaké–Mbayakro road; 7°40′ N, 4°54′ W; 8 Oct. 1947; C. Noirot leg.; study code: DJ P332; MNHN EP9947 • soldier, worker; Youhouli; 5°25′ N, 4°29′ W; 7 Sep. 1953; M. Lüscher leg.; study code: DJ 0330; initially *C. severus*; AMNH • soldier; Yapo; 5°44′ N, 4°5′ W; 26 May 1960; C. Noirot leg.; study code: DJ P323; MNHN EP9861 • soldier, ♀ (alate); Kpouébo (Orumbo Boka); 6°21′ N, 4°53.7′ W; 30 Oct. 1960; C. Noirot leg.; study code: DJ P346; MNHN • soldier, ♂ (alate); Adiaké; 5°27′ N, 3°15.5′ W; 15 Apr. 1963; C. Noirot leg.; study code: DJ P349; MNHN • soldier; Dabou; 5°19′ N, 4°20′ W; 10 Jun. 1964; P. Bodot leg.; study code: DJ U014; initially *C. severus*; NHMUK 13671954 • soldier; Dabou; 5°19′ N, 4°20′ W; 10 Jun. 1964; P. Bodot leg.; study code: DJ U015; initially *C. severus*; NHMUK 13671953 • worker; Taï; 5°52′ N, 7°20′ W; 1970; C. Kerdelhué leg.; study code: DJ 0749; GenBank no PQ679224 (mitogenome); MNHN EP9942 • soldier, worker; Taï; 5°52′ N, 7°20′ W; 1970; C. Kerdelhué leg.; study code: DJ 0750; GenBank no PQ679242 (mitogenome); MNHN EP9943 • soldier, worker, ♂ (alate); Pakobo (Lamto research centre); 6°12′ N, 4°59′ W; 8 Mar. 2010; K. Dosso leg.; study code: DJ 0017; BE RMCA INS.Iso.059385 • soldier, worker; Pakobo (Lamto research centre); 6°12′ N, 4°59′ W; 8 Mar. 2010; K. Dosso leg.; study code: DJ 0066; BE RMCA INS.Iso.059386 • soldier, worker; Pakobo (Lamto research centre); 6°12′ N, 4°59′ W; 8 Mar. 2010; K. Dosso leg.; study code: DJ 0069; BE RMCA INS.Iso.059387 • soldier, worker, ♀ (alate), ♂ (alate); Korhogo; 9°24′ N, 5°37′ W; 2013; T. Coulibaly leg.; study code: DJ 0044; BE RMCA INS.Iso.059411 • soldier; Korhogo; 9°24′ N, 5°37′ W; 2013; T. Coulibaly leg.; study code: DJ 0056; BE RMCA INS.Iso.059441 • soldier, worker; Youhouli; 5°26.433′ N, 4°29.351′ W; 18 Feb. 2015; G. Josens leg.; study code: DJ 0408; BE RMCA INS.Iso.059439 • soldier, worker; Youhouli; 5°26.417′ N, 4°29.333′ W; 18 Feb. 2015; G. Josens leg.; study code: DJ 0410; GenBank no PQ679209 (mitogenome); BE RMCA INS.Iso.059440 • soldier, worker; Pakobo (Lamto research centre); 6°12.56′ N, 4°58.584′ W; 21 Feb. 2015; G. Josens leg.; study code: DJ 0411; GenBank no PQ679169 (mitogenome); BE RMCA INS.Iso.059415 • soldier, worker; Taabo; 6°17.87′ N, 5°0.129′ W; 21 Feb. 2015; G. Josens leg.; study code: DJ 0409; GenBank nos MN646736 (*COI*), MN685941 (*COII*), MN686002 (*28S*); BE RMCA INS.Iso.059455 • soldier, worker; Katiola; 7°58.6′ N, 5°4′ W; 26 Feb. 2015; G. Josens leg.; study code: DJ 0260; BE RMCA INS.Iso.059413 • soldier, worker; Odienné; 9°26.252′ N, 7°34.935′ W; 26 Feb. 2015; G. Josens leg.; study code: DJ 0414; BE RMCA INS.Iso.059444 • soldier, worker, ♀ (queen); Man; 7°24.7′ N, 7°35.1′ W; 27 Feb. 2015; G. Josens leg.; study code: DJ 0261; BE RMCA INS.Iso.059416 • soldier, worker, ♂ (king), ♀ (queen); Zéalé; 5°57.9′ N, 8°11.4′ W; 28 Feb. 2015; G. Josens leg.; study code: DJ 0262; BE RMCA INS.Iso.059442 • soldier, worker; Zéalé; 6°57.879′ N, 8°11.386′ W; 28 Feb. 2015; G. Josens leg.; study code: DJ 0415; GenBank no PQ679171 (mitogenome); BE RMCA INS. Iso.059443 • soldier, worker; Route Man–Duékoué; 6°50.051′ N, 7°24.53′ W; 1 Mar. 2015; G. Josens leg.; study code: DJ 0413; GenBank nos MN646737 (*COI*), MN685942 (*COII*), MN686003 (*28S*), PQ679236 (mitogenome); BE RMCA INS.Iso.059451.

GABON • soldier; La Lopé N.P.; 0°15′ S, 11°35′ E; 15 Mar. 1998; M. Harry leg.; study code: DJ P251; MNHN EP9945.

GAMBIA • soldier, ♂ (king); Tabo Kotor; 13°24′ N, 16°40′ W; 10 Sep. 1966; W.A. Sands leg.; study code: DJ U100; initially *C. gaigei*; NHMUK 13671897 • soldier, ♂ (king); Bathurst [= Banjul]–Yundum road; 13°28′ N, 16°38′ W; 12 Sep. 1966; W.A. Sands leg.; study code: DJ U103; initially *C. gaigei*; NHMUK 13671898 • soldier; Sanyangh–Gunjur road; 13°15′ N, 16°46′ W; 16 Sep. 1966; W.A. Sands leg.; study code: DJ U108; initially *C. gaigei*; NHMUK 13671885 • soldier, worker, ♀ (queen); Bathurst [= Banjul]; 13°13′ N, 16°19′ W; 18 Sep. 1966; W.A Sands leg.; study code: DJ 0717; initially *C. gaigei*; NHMUK 13671896 • soldier; Bakau; 13°28′ N, 16°40′ W; 17 Nov. 1973; R.M.C. Williams and R.W. Lamb leg.; study code: DJ U007; initially *C. severus*; NHMUK 13671950 • soldier; Jambanjeli; 13°17′ N, 16°44′ W; 25 Nov. 1973; R.W. Lamb leg.; study code: DJ U018; initially *C. severus*; NHMUK 13671952 • soldier; Abuko game reserve; 13°24′ N, 16°39′ W; 5 Dec. 1973; R.M.C. Williams and R.W. Lamb leg.; study code: DJ U008; initially *C. severus*; NHMUK 13671951 • soldier, ♂ (king); Abuko game reserve; 13°24′ N, 16°39′ W; 5 Dec. 1973; R.M.C. Williams and R.W. Lamb leg.; study code: DJ U017; initially *C. severus*; NHMUK 13671949 • soldier, worker; Brikama (Nyambai Forest?); 13°18′ N, 16°40′ W; 1 Nov. 2013; A. Ndiaye leg.; study code: DJ 0220; BE RMCA INS.Iso.059397.

GHANA • soldier, ♀ (queen); Larabanga–Sawla road; 9°13′ N, 1°55′ W; 22 Feb. 1959; W.A. Sands leg.; study code: DJ U115; initially *C. gaigei*; NHMUK 13671882 • soldier; Bolgatanga; 10°34′ N, 0°50′ W; 9 Mar. 1959; W.A. Sands leg.; study code: DJ U030; initially *C. severus*; NHMUK 13671966 • soldier; Tumu; 11°5′ N, 2°17′ W; 16 Mar. 1959; W.A. Sands leg.; study code: DJ U027; initially *C. severus*; NHMUK 13671970 • soldier; Lawra; 10°39′ N, 2°52′ W; 18 Mar. 1959; W.A. Sands leg.; study code: DJ U031; initially *C. severus*; NHMUK 13671967 • soldier; Tamale–Yeji road; 8°55′ N, 0°30′ W; 27 Mar. 1959; W.A. Sands leg.; study code: DJ U024; initially *C. severus*; NHMUK 13671969 • soldier, ♀ (queen); Akumadan on Wenchi–Kumasi road; 7°28′ N, 1°58′ W; 1 Apr. 1959; W.A. Sands leg.; study code: DJ U101; initially *C. gaigei*; NHMUK 13671883 • soldier, ♀ (queen); Akumadan on Wenchi–Kumasi road; 7°28′ N, 1°58′ W; 1 Apr. 1959; W.A. Sands leg.; study code: DJ U102; initially *C. gaigei*; NHMUK 13671885 • soldier; Nakpanduri; 10°34′ N, 0°17′ W; 6 Jun. 1959; W.A. Sands leg.; study code: DJ U023; initially *C. severus*; NHMUK 13671968 • soldier; Ejura; 7°23′ N, 1°22′ W; 20 Oct. 1966; W.A. Sands leg.; study code: DJ U020; initially *C. severus*; NHMUK 13671971 • soldier, ♀ (alate); Kumasi–Sunyani; 6°53′ N, 1°52′ W; 12 Jul 1975; R.M.C. Williams leg.; study code: DJ U116; initially *C. gaigei*; NHMUK 13671895.

GUINEA • ♀ (alate), ♂ (alate); "La Mé forest"; 9°31.5′ N, 13°41.1′ W; 31 Jan. 1931; P.-P. Grassé leg.; study code: DJ 0429; initially *C. fungifaber* in MNHN; MNHN EP9921 • soldier; Camayenne; 9°31.5′ N, 13°41.1′ W; 1934; P.-P. Grassé leg.; study code: DJ 0427; MNHN EP9920 • soldier, worker, ♀ (queen); Camayenne; 9°31.5′ N, 13°41.1′ W; 1934; P.-P. Grassé leg.; study code: DJ 0430; MNHN EP9922 • soldier, ♂ (alate); Nzo; 7°41′ N, 8°19′ W; 25 Mar. 1947; C. Noirot leg.; study code: DJ P322; MNHN EP9924 • soldier, ♀ (alate); Nzo; 7°41′ N, 8°19′ W; 26 Mar. 1947; C. Noirot leg.; study code: DJ P343; MNHN • soldier, ♀ (queen); Nzo; 7°41′ N, 8°19′ W; 27 Mar. 1947; C. Noirot leg.; study code: DJ P342; MNHN • soldier; Nimba mountain; 10°0′ N, 13°0′ W; Apr. 1996; M. Harry leg.; study code: DJ 0751; MNHN EP9944 • soldier; Foulaya; 10°0′ N, 12°50′ W; 20 Jun. 1996; F.L. Guilavogui leg.; study code: DJ 0068; initially *C. severus* in RMCA; BE RMCA INS.Iso.059421 • soldier; Forécariah; 9°28′ N, 13°6′ W; 21 Jun. 1996; O. Diallo leg.; study code: DJ 0067; initially *C. severus* in RMCA; BE RMCA INS.Iso.059420 • soldier, worker; Haut-Niger N.P.; 10°14.43′ N, 10°27.67′ W; 22 Dec. 1996; M. Mei leg.; study code: DJ 0314; initially *C. severus*; MURS.

LIBERIA • soldier, ♀ (alate); unknown location; 7°0′ N, 10°0′ W; 12 Feb. 1975; G. Becker leg.; study code: DJ U009; initially *C. severus*; NHMUK 13671957.

NIGERIA • soldier, ♂ (alate); Enugu Township; 6°27′ N, 7°32′ E; 13 Feb. 1955; W.V. Harris leg.; study code: DJ U106; initially *C. gaigei*; NHMUK 13671893 • soldier; Kaduna; 10°15′ N, 7°50′ E;

15 Feb. 1957; W.A. Sands leg.; study code: DJ U025; initially *C. severus*; NHMUK 13671974 • soldier, ♂ (alate); Kwei Hill, Heipang; 9°39′ N, 8°50′ E; 29 Mar. 1957; W.A. Sands leg.; study code: DJ U026; initially *C. severus*; NHMUK 13671977 • soldier, worker, ♂ (alate); Ropp; 9°30′ N, 8°55.7′ E; 3 Apr. 1957; W.A. Sands leg.; study code: DJ 0545; initially *C. severus*; NHMUK • soldier, ♂ (alate); Bauchi–Gombe road; 10°17′ N, 9°56′ E; 7 May 1957; W.A. Sands leg.; study code: DJ U105; initially *C. gaigei*; NHMUK 13671890 • soldier; Donkin; 8°37′ N, 11°44′ E; 24 May 1957; W.A. Sands leg.; study code: DJ U028; initially *C. severus*; NHMUK 13671972 • soldier; Wamba; 9°31′ N, 8°37′ E; 23 Feb. 1958; W.A. Sands leg.; study code: DJ U022; initially *C. severus*; NHMUK 13671973 • soldier, ♂ (alate); Gboko–Otupko road; 7°17′ N, 8°54′ E; 26 Feb. 1958; W.A. Sands leg.; study code: DJ U032; initially *C. severus*; NHMUK 13671976 • soldier, ♀ (queen); Kabba–Ondo road; 7°34.75′ N, 5°48′ E; 2 Mar. 1958; W.A. Sands leg.; study code: DJ U107; initially *C. gaigei*; NHMUK 13671889 • soldier, ♂ (alate); Enugu–Onitsha road; 6°25′ N, 7°24′ E; 3 Mar. 1958; W.A. Sands leg.; study code: DJ U113; initially *C. gaigei*; NHMUK 13671892 • soldier, ♂ (alate); Enugu–Otukpo road; 6°45′ N, 7°28′ E; 5 Mar. 1958; W.A. Sands leg.; study code: DJ U112; initially *C. gaigei*; NHMUK 13671891 • soldier, worker; Dekina; 7°40.25′ N, 6°56′ E; 7 Mar. 1958; W.A. Sands leg.; study code: DJ 0659; initially *C. gaigei*; NHMUK 13671993 • soldier, ♀ (alate); Lokoja; 7°50′ N, 6°33′ E; 10 May 1958; W.A. Sands leg.; study code: DJ U029; initially *C. severus*; NHMUK 13671975 • soldier; Mayo Ndaga; 6°55′ N, 11°27′ E; ca 1975; J.T. Medler leg.; study code: DJ U021; initially *C. severus*; NHMUK 13671978.

SIERRA LEONE • soldier, worker, ♀ (alate); unknown location; 8°0′ N, 12°0′ W; 14 Jun. 1917; P.A. Buxton leg.; study code: DJ 0323; initially *C. silvestrii*; AMNH • soldier; Njala; 8°6′ N, 12°4′ W; 24 Aug. 1930; E. Hargreaves leg.; study code: DJ U019; initially *C. severus*; NHMUK 13671979 • soldier, worker; Njala; 8°10′ N, 12°24′ W; 24 Aug. 1930; E. Hargreaves leg.; study code: DJ 0325; initially *C. silvestrii*; AMNH • soldier, worker; Njala; 8°10′ N, 12°24′ W; 24 Aug. 1930; E. Hargreaves leg.; study code: DJ 0540; initially *C. silvestrii*; NHMUK • soldier, worker; Njala; 8°10′ N, 12°24′ W; Apr. 1936; E. Hargreaves leg.; study code: DJ 0546; initially *C. severus*; NHMUK • soldier, worker, ♂ (alate), ♀ (queen); Njala; 8°10′ N, 12°24′ W; 29 May 1947; F.A. Squire leg.; study code: DJ 0326; initially *C. silvestrii*; AMNH • soldier; Freetown airport; 8°37′ N, 13°11′ W; Jan. 1955; W.V. Harris leg.; study code: DJ U011; initially *C. severus*; NHMUK 13671960 • soldier; Njala; 8°6′ N, 12°4′ W; 27 Jan. 1955; W.V. Harris leg.; study code: DJ U013; initially *C. severus*; NHMUK 13671964 • soldier; Freetown; 8°25′ N, 13°13′ W; Feb. 1955; W.V. Harris leg.; study code: DJ U002; initially *C. severus*; NHMUK 13671959 • soldier; Freetown; 8°25′ N, 13°13′ W; Feb. 1955; W.V. Harris leg.; study code: DJ U003; initially *C. severus*; NHMUK 13671961 • soldier, worker, ♀ (queen); Freetown; 8°28′ N, 13°15′ W; 27 May 1956; J.K. Ocloo and R.M.C. Williams leg.; study code: DJ 0544; initially *C. severus*; NHMUK • soldier; Freetown; 8°28′ N, 13°15′ W; 8 Jan. 1958; W. Wilkinson leg.; study code: DJ U005; initially *C. severus*; NHMUK 13671965 • soldier; Freetown; 8°28′ N, 13°15′ W; 8 Jan. 1958; W. Wilkinson leg.; study code: DJ U012; initially *C. severus*; NHMUK 13671960 • soldier; "Bo residential"; 7°57′ N, 11°44′ W; 10 Jan. 1958; W. Wilkinson leg.; study code: DJ U010; initially *C. severus*; NHMUK 13671963 • soldier; Makeni; 8°53′ N, 12°2′ W; 24 Sep. 1966; W.A. Sands leg.; study code: DJ U004; initially *C. severus*; NHMUK 13671958.

TOGO • soldier; Kloto; 6°57.17′ N, 0°34.21′ E; 8 Dec. 2018; G. Goergen leg.; study code: DJ BB01; BE RMCA INS.Iso.059380 • soldier; Kloto; 6°57.17′ N, 0°34.21′ E; 8 Dec. 2018; G. Goergen leg.; study code: DJ BB02; BE RMCA INS.Iso.059381 • soldier; Kloto; 6°57.17′ N, 0°34.21′ E; 8 Dec. 2018; G. Goergen leg.; study code: DJ BB03; BE RMCA INS.Iso.059383 • soldier; Kloto; 6°57.17′ N, 0°34.21′ E; 8 Dec. 2018; G. Goergen leg.; study code: DJ BB04; BE RMCA INS.Iso.059384 • soldier; Kloto; 6°57.17′ N, 0°34.21′ E; 8 Dec. 2018; G. Goergen leg.; study code: DJ BB05; BE RMCA INS. Iso.059382 • soldier, worker; Kloto; 6°57.15′ N, 0°34.2′ E; 8 Dec. 2018; G. Goergen leg.; study code: DJ 0635; BE RMCA INS.Iso.059454 • soldier, worker; Kloto; 6°57.15′ N, 0°34.2′ E; 8 Dec. 2018; G. Goergen leg.; study code: DJ 0636; BE RMCA INS.Iso.059453 • soldier; PN Fazao-Malfakassa, Bonako;

9°10.08′ N, 0°57′ E; 17 Feb 2025; Y. Roisin leg.; study code: DJ Y383; BE RMCA INS.Iso.059952 • soldier; Route Atakpamé–Badou; 7°32.4′ N, 1°0′ E; 19 Feb 2025; Y. Roisin leg.; study code: DJ Y381; BE RMCA INS.Iso.059950 • soldier; Route Atakpamé–Badou; 7°33.24′ N, 1°0.54′ E; 19 Feb 2025; Y. Roisin leg.; study code: DJ Y382; BE RMCA INS.Iso.059951.

**Historical review**

The first mention of an *Isognathotermes* species in the literature probably dates back to Smeathman (1781): of two mushroom-shaped nest-building species, "The largest species, the *Termes atrox*, in its perfect state measures one inch and three-tenths from the extremities of the wings on the one side to the extremities to the other". As Smeathman collected in Sierra Leone, this dimension (~33 mm) is entirely compatible with the wing dimensions of *I. severus* found in West Africa. However, Smeathman's material could not be traced even in the early 20th century (Sjöstedt 1926: 218) and is therefore considered lost and unavailable for a systematic revision.

Silvestri (1914: 92–93) described this species under the name *Cubitermes severus*. He provided a description of queen, soldier, and worker together with measurements and figures. In the same paper, he described *Cubitermes severus* var. *modestior* (1914: 93–94); he mentioned that the soldiers and imagines are like the typical form (= *Cubitermes severus*) but smaller.

Sjöstedt (1926: 250–251) housed *C. severus* in the sub-family Termitinae and provided a first description of alates. Sjöstedt (1926: 238–239) considered that *C. severus* var. *modestior* deserved to be elevated to the species level. He referred to it under the name *C. modestior*, housed it in the sub-family Termitinae, and included it in a "*glebae*-Gruppe" of small *Cubitermes* species. He also included *C. severus* in his soldier's key of *Cubitermes* species and inserted it in a "*bulbifrons*-Gruppe" of species with an upwards humped frons.

Snyder (1949: 163) catalogued *C. severus* and *C. modestior* and housed them in the sub-family Termitinae.

Krishna *et al.* (2013: 1936) housed *C. severus* and *C. modestior* in the sub-family Cubitermitinae.

Josens & Deligne (2019: 39–42) placed these species within the *fungifaber* valve pattern group.

Hellemans *et al.* (2021: 233) placed these species in the restored genus *Isognathotermes*.

The small size of *I. modestior* might suggest a very young colony, but this is excluded with a physogastric queen; this small size could also be the result of environmental conditions. As *I. modestior* is known from a single nest, without the aid of sequencing (old sample), there is still some doubt as to its status (abnormal sample or distinct species?). On the basis of morphology alone, since the type material of *I. modestior* (Silvestri, 1914) is now included among the smallest specimens of *I. severus*, it is now considered a junior synonym of *Isognathotermes severus* (Silvestri, 1914).

**Redescription**

**Imago**

Colour. **Head capsule**: well sclerotised, fresh samples very dark, C6–C8 (but C4–C6 in long preserved imagines); fontanelle concolorous with head capsule or paler (up to two levels). Postclypeus C6–C7 slightly paler than head capsule. Antennae C4–C6 without any difference between proximal and distal articles. **Thorax**: pronotum C6–C7 (paler in long preserved samples), as postclypeus, generally somewhat paler than head capsule; meso- and metanotum C4–C7, sometimes somewhat paler than pronotum. Legs C3–C5; tibia usually slightly (one level) darker than femur. Wings hyaline with brown

to grey tinge (Cf2–Cf4), anterior veins darker. **Abdomen**: tergites C5–C7. Sternites appreciably paler in middle (C3–C4) with both sides darker (C4–C6); posterior sternites darker (C4–C6) than anterior.

Setation. **Head capsule**, with some prominent setae set amongst a high density of short, fine setae forming a dense mat. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and shorter ones in middle; meso- and metanotum with some fine, pale setae, arranged in a medio-longitudinal strip, generally visible at 40×, sometimes only at 80×. **Legs** very pilose, furnished (among numerous fine setae) with some stronger setae: 7–12 on the carina of fore coxa and 0–8 on the ventral side of fore coxa; fore trochanter with some strong setae; tibia pilose fore, mid, and hind tibia furnished with 10–30 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 14; Figs 26, 61). **Size**: the imagines of *I. severus* are, on average, medium to large sized in the genus *Isognathotermes* (Fig. 26). **Head capsule**: compound eyes round to shortly oval; ocelli shortly to strongly oval, removed from eyes by a distance equal to 0.4–1.3 ocellus small diameter; fontanelle generally a tiny round or elongate marking. Antennae: 16 articles on alate individuals, always shortened by amputation by two to four articles in queens and kings. Labrum: cupola shaped, wider than long. **Left mandible** with apical tooth on average medium sized in the genus and always more prominent than first marginal; marginal teeth three in number but second one only suggested by an undulation of edge between first and third marginal teeth; only the apical tooth is acute in unworn specimens; premolar tooth with proximal end obscured or partly obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth always more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly

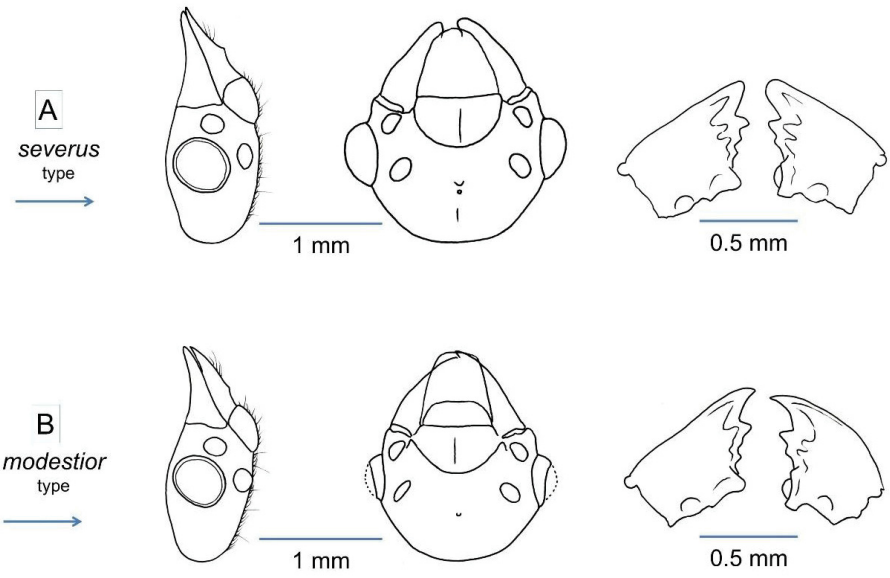


**Fig. 61.** *Isognathotermes severus* (Silvestri, 1914) and junior synonym species: imagines. Lateral and dorsal views of an imago's head capsule, and dorsal view of this imago's mandibles. **A**. Of the queen from type colony of *Cubitermes severus* Silvestri, 1914 (DJ 0609). **B**. Of the king from type colony of *Cubitermes severus* var. *modestior* Silvestri, 1914 (DJ 0294).

**Table 14.** *Isognathotermes severus* (Silvestri, 1914): ranges of significant measures in the three castes, in alphabetical orders of the "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 61) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.34–0.58 | 0.48 |
| | | Head: width across the eyes | IHdW | 1.49–1.79 | 1.71 |
| | | Left mandible: A-m1 distance | IMlAmD | 0.18–0.26 | 0.20 |
| | | Ocellus: large diameter | IOc*D* | 0.15–0.23 | 0.22 |
| | | Postclypeus: width | IPcW | 0.70–0.86 | 0.79 |
| | | Pronotum: maximal width | IPnW | 1.31–1.60 | 1.50 |
| | | Hind tibia: length | IT3L | 1.66–2.27 | 1.97 |
| | | Wing: length (n=31) | IWgL | 12.2–17.3 | NA |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.00–1.76 | 1.12 |
| Soldiers (n = 161) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.00–0.09 | 0.05 |
| | | Head: length | SHdL | 2.43–3.29 | 2.96 |
| | | Head: width | SHdW | 1.76–2.31 | 2.02 |
| | | Left mandible: lesser sagitta | SMlc | 0.14–0.31 | 0.19 |
| | | Left mandible: ventral length | SMlL | 2.07–2.58 | 2.33 |
| | | Hind tibia: length | ST3L | 1.52–1.93 | 1.75 |
| | Indices | Head elongation index | SHdL/SHdW | 1.22–1.57 | 1.47 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.06–0.13 | 0.08 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.79–1.24 | 0.90 |
| Workers (n = 92 | Raw measures (mm) | Head: width | WHdW | 1.06–1.36 | 1.25 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.15–0.22 | 0.18 |
| | | Left mandible: total length | WMlL | 0.51–0.65 | 0.60 |
| | | Hind tibia: length | WT3L | 1.11–1.48 | 1.33 |
| | | Valve: PC average length | WVP-AvL | 0.51–0.85 | 0.67 |
| | | Valve: PC average width | WVP-AvW | 0.05–0.10 | 0.08 |
| | | Valve: SC average length | WVS-AvL | 0.42–0.70 | 0.55 |
| | | Valve: SC average width | WVS-AvW | 0.22–0.43 | 0.30 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 6.78–12.7 | 8.85 |

* Abbreviations: see definitions in Material and methods.

elevated. **Fore coxa** flanged ventrally resulting in a carina. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 2–4 and 8–13 branches, respectively. **Gut** (only studied in some cases): enteric valve weakly developed and hardly comparable with workers' and soldiers' valves; odd PCs are slightly longer than even PCs. Caecum present as a small amorphous button.

**Soldier**

Colour. **Head capsule** generally tending towards deep palette (Cd3–Cd6); there is always a gradient from a darker frons to a paler back, smooth and extended in 72% of the samples examined but more abrupt in the remaining 28% giving in some cases the impression that the head capsule is bicolorous (as in Fig. 13). Antennae and labrum concolorous with or one level paler than head capsule. Mandibles dark (C6–C8) generally with an abrupt clearing on their bases (two palette levels) which is generally the same

colour as frons. **Thorax** and legs paler than head capsule (C2–C4). **Abdomen** grey to red-brown owing to digestive bolus, sometimes with a yellow tinge on tergites.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Labrum** always with 5–8 large setae on each lobe. **Thorax**: pro- and mesonotum with a small number of setae mainly located on margins. **Legs**: fore coxa bears at least one fine seta and generally 0–3 spines on carina and generally not any spine (rarely 1–2) on ventral side; trochanter generally with some long lined-up setae, sometimes with 6–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively (the latter sometimes weakly developed) and a row of 6–17 strong setae or spines along their shaft. **Abdomen**: tergites with some large setae, mainly or only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 14; Fig. 62). **Size**: the soldiers of *I. severus* are medium sized in the genus *Isognathotermes* (Figs 21, 28). **Head capsule**: always clearly sclerotised; appreciably longer

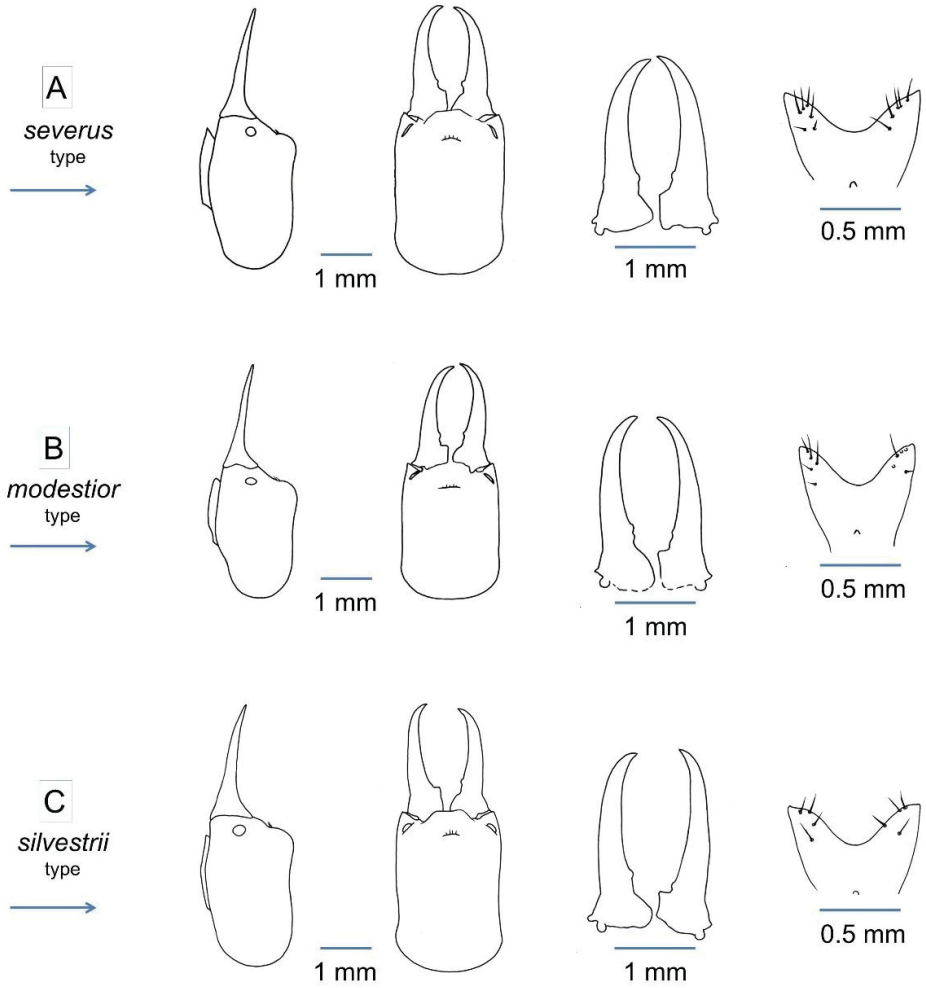


**Fig. 62.** *Isognathotermes severus* (Silvestri, 1914) and junior synonym species: soldiers. Lateral and dorsal views of a soldier's head capsule; ventral view of its mandibles; and dorsal view of its labrum. **A**. From the type colony of *Cubitermes severus* Silvestri, 1914 (DJ 0609). **B**. From the type colony of *Cubitermes severus* var. *modestior* Silvestri, 1914 (DJ 0294). **C**. From the type colony of *Cubitermes silvestrii* Sjöstedt, 1925 (DJ 0302).

than wide. **Dorsal view**: lateral sides mostly subparallel always with a narrowing near posterior third or fourth, from antennal sockets sides converge clearly towards bases of mandibles; posterior side regularly rounded or sometimes with a short straight or even concave part in the middle. Upper profile almost always slightly to strongly concave; angle between extended mandibles and frons varies from right to obtuse; frons generally with a sketched or small anterior hump (without any hump in 10% of the samples examined). Gulamentum in ventral view always constricted in its posterior half, with sides of anterior part either roundly convex or forming an acute widening or even a kind of ear on each side. Antennae: 14.5–15 articles). **Labrum**: always deeply bifurcate and wider than long, with sides varying from lyre-shaped (in 85% of the samples examined) to convex; lobes angular, frequently with fine, whitish or translucent tips; anterior margin concave. **Mandibles**: sabre-like generally strongly curved; inner edges generally smooth with one distinct but very small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible equally or slightly more curved than left. **Thorax**: pronotum sellate, as wide as 54–64% of head width, with generally entire anterior and posterior margins. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in second half of abdomen. **Caecum** always rather small, best seen in ventral view, near centre of abdomen, lobed, rarely (in 6% of the samples examined) with a lobe expanded somewhat forward. Arrangement of enteric valve cushions showing trilateral symmetry, the odd cushions being about 16% longer than the even cushions, generally without any crest (*muneris* EVA pattern) or with crests very weakly developed.

**Worker**

Colour. **Head capsule** pale (C1–C3) turning grey in long preserved samples. Antennae: proximal articles pale (C2–C3), distal articles always one to two levels darker (C4–C5). **Thorax**, nota, and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect, scattered setae. Labrum with few, robust, scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50 × or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa always carinated, bearing one fine seta and furnished with 3–5 spines on carina and 0–4 on ventral side; fore trochanter with 5–8 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively (the latter sometimes weakly developed) and a row of 6–15 spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 14, Fig. 63). **Size**: the workers of *I. severus* are, on average, medium sized in the genus *Isognathotermes* (with large overlapping on several other species: Fig. 30). **Head capsule**: weakly sclerotised (except mandibles). Antennae of 14 or 14.5 (rarely 15) articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal tooth well developed but with a blunt tip even when fresh, second marginal tooth faint (visible as an undulated edge and disappearing in worn mandibles), third marginal tooth with a blunt tip; premolar tooth with its proximal end generally (in 70% of the samples examined) well visible; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 57–73% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in second half of abdomen. Arrangement of enteric valve cushions of the *fungifaber* pattern with triradial symmetry: the odd PCs, in their downstream part, are rather narrow and bear crests that are generally as high as or higher than they are wide, with long and strong bristles; however, rather frequently (in 11 cases out of 92), including the syntype from Kakoulima (but not the syntype from

Camayenne), the EVA is intermediate between the *fungifaber* and the *finitimus* patterns; supporting bristles are generally numerous: 15–25 on each side of the odd PCs; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum always rather small, visible in ventral view, near centre of abdomen, generally with two or three (up to five) short lobes, rarely (in 5% of the samples examined) with a lobe expanded forward.

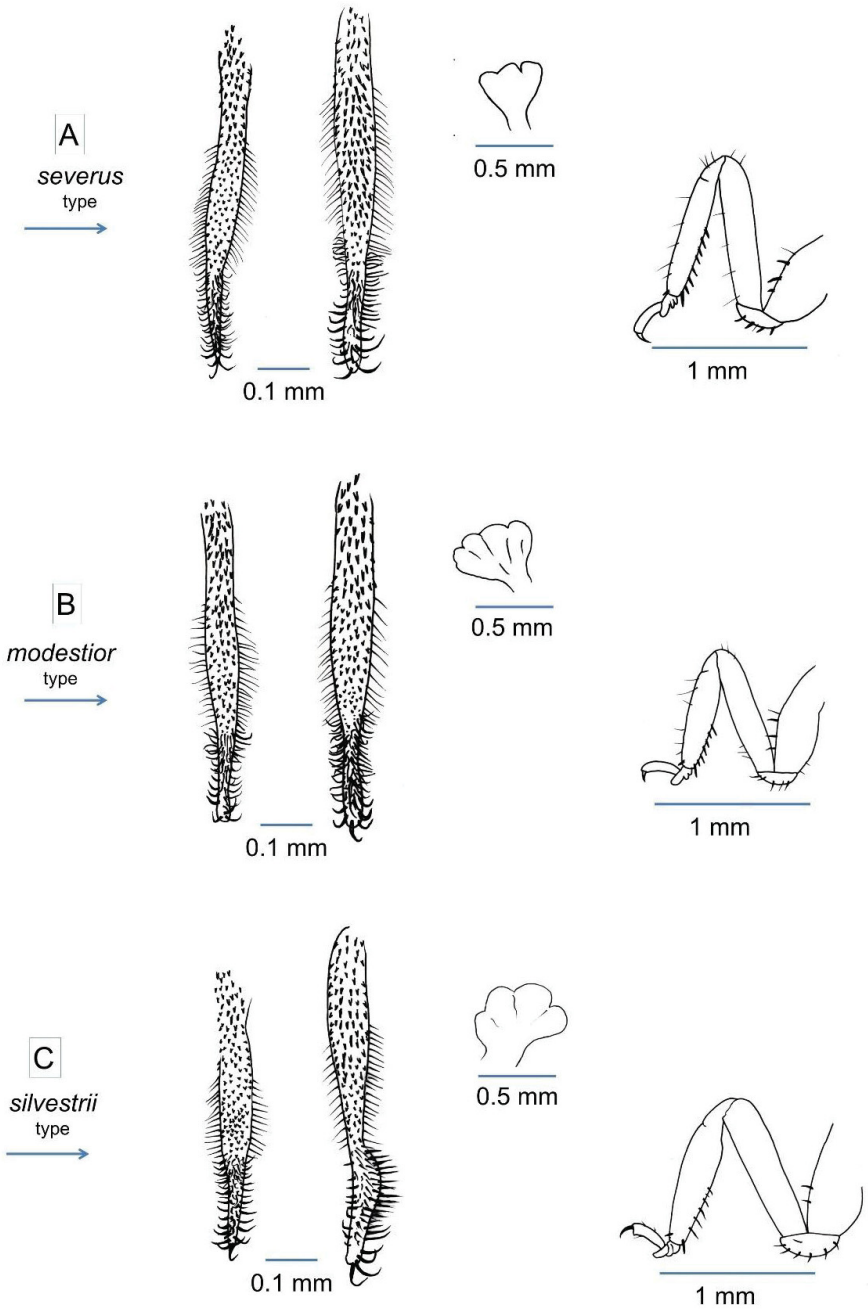


**Fig. 63.** *Isognathotermes severus* (Silvestri, 1914) and junior synonym species: soldiers and workers. PC1s of soldier's and worker's enteric valves, worker's caecum and foreleg. **A**. From the type colony of *Cubitermes severus* Silvestri, 1914 (DJ 0609). **B**. From the type colony of *Cubitermes severus* var. *modestior* Silvestri, 1914 (DJ 0294). **C**. From the type colony of *Cubitermes silvestrii* Sjöstedt, 1925 (DJ 0302), the downstream end of the worker's PC1 is twisted.

**Chorology-ecology**

The geographic distribution of *I. severus* is linked with the Sudanian savanna, the Guinean forest-savanna mosaic, and the northern Congolian forest-savanna mosaic ecoregions. Some samples were also found in evergreen forests in RCI and in southwest CAR and were certified by their mitogenomes.

This species shows an extended repartition from Gambia to CAR. It seems to be in competition with *I. fungifaber* (Figs 45, 49, see the general discussion).

**Molecular data**

Twenty mitogenomes of *I. severus* are published alongside this work (GenBank accessions: see Supp. file 3 and 'Material examined'). Despite the disparity in the origin of the samples (from RCI to CAR), mitogenomes exhibit less than 1.2% dissimilarity with each other (Supp. file 4).

***Isognathotermes similifinitimus*** Josens & Deligne sp. nov.
urn:lsid:zoobank.org:act:2CC856EC-F98A-4CA6-B7CE-C4458464CA43
Figs 26–31, 33, 64, distribution map: Fig. 47; Table 15

**Diagnosis**

The worker has a *finitimus* EVA and looks a little more like *I. finitimus* than *I. planifrons*.

The soldier also looks a little more like *I. finitimus* than *I. planifrons*.

The imago, however, clearly looks more like *I. planifrons*.

The specimens now assigned to *I. similifinitimus* sp. nov. were first considered to be close to *I. planifrons*; besides their mixed morphology, they were found outside the geographic range of *I. planifrons*.

*Isognathotermes similifinitimus* sp. nov. is a cryptic species that can be distinguished for sure only with molecular tools: it is therefore possible that some of the samples previously identified as *I. finitimus* (that could not be sequenced) belong in fact to *I. similifinitimus.*

In terms of its ecology and chorology, this species is up to now only known from the Congolese forest south of Kisangani, DRC.

**Etymology**

The name *similifinitimus* (from the Latin *similis*, 'similar' and *finitimus* from the species *I. finitimus*) refers to the morphology that is like that of *I. finitimus*.

**Material examined**

Two complete samples from one location.

**Holotype**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier; Yoko; 0°17.62′ N, 25°17.77′ E; 8 Jun. 2010; B. Le Ru leg.; study code: DJ 0744; GenBank no PQ679199 (mitogenome); BE RMCA INS.Iso.059457.

**Paratypes**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker, ♀ (queen); same data as for holotype; BE RMCA INS.Iso.059939.

**Other material examined**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker, ♂ (king), ♀ (queen); Yoko; 0°17.62′ N, 25°17.98′ E; 8 Jun. 2010; B. Le Ru leg.; study code: DJ 0745; GenBank no PQ679249 (mitogenome); BE RMCA INS.Iso.059456.

**Historical review**

This species is described here; only two samples are available which may seem too little for describing a new species but both samples are complete (imago, soldier, worker, and mitogenome).

It was discovered by one of us (BLR) in an evergreen forest south of Kisangani, DRC.

**Description**

**Imago**

Colour. **Head capsule**: well sclerotised, dark, C6–C7; fontanelle concolorous with head capsule. Postclypeus concolorous with head capsule. Antennae C5–C6 without any difference between proximal and distal articles. **Thorax**: pronotum C6–C7, concolorous with head capsule; meso- and metanotum C6–C7, as pronotum. Legs C3–C4. **Abdomen**: tergites C6–C7. Sternites appreciably paler in middle (C3–C4) with both sides darker (C4–C6); posterior sternites darker (C4–C6) than anterior.

Setation. **Head capsule** with some prominent setae, mainly near the eyes, and a higher density of shorter, finer setae everywhere. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and many shorter ones in middle; meso- and metanotum with some fine, pale setae, arranged in a medio-longitudinal strip, visible at 20×, with or without two larger setae on metanotum. **Legs** very pilose, furnished (among numerous fine setae) with some strong setae: 10–15 on the carina of fore coxa and 2 on the ventral side of fore coxa; tibia pilose; fore, mid, and hind tibia furnished with 10–30 strong setae and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 15; Figs 26, 64). **Size**: the imagines of *I. similifinitimus* sp. nov. are medium sized in the genus *Isognathotermes*; as shown in Fig. 26. **Head capsule**: compound eyes nearly round; fontanelle a tiny round to elongate marking; ocelli nearly round to oval, removed from eyes by a distance about equal to 0.8–0.9 ocellus small diameter. Labrum: cupola shaped. **Left mandible** with apical tooth always longer and more prominent than first marginal; marginal teeth three in number but second one only suggested by a slight undulation of edge between first and third marginal teeth; premolar tooth with proximal end obscured by molar prominence in dorsal view; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth longer and more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip; second marginal tooth smaller and with a blunt tip; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a sharp carina.

**Soldier**

Colour. **Head capsule** C4–C6; there is, in one of the two samples, a strong gradient from a darker frons to a paler back (e.g., from C6 to C4) giving the impression that the head capsule is bicolorous (as in Fig. 13). Gulamentum, antennae, and labrum concolorous with head. Mandibles dark (C7–C8) generally with an abrupt clearing on their bases (two palette levels) which is generally the same colour as frons. **Thorax**, nota C4 and legs paler (C2–C3). **Abdomen** grey owing to digestive bolus, with a yellow tinge on tergites.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or

more). **Labrum** always with 5–6 large setae on each lobe. **Thorax**: pro- and mesonotum with some setae mainly located on margins. **Legs**: fore coxa furnished with 1–2 spines on carina and not any one on ventral side; trochanter with some long setae, and 4–5 lined-up spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively; all tibiae furnished with a row of 7–15 spines. **Abdomen**: tergites with some large setae, only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 15; Figs 28, 64). **Size**: the soldiers of *I. similifinitimus* sp. nov. are medium sized in the genus *Isognathotermes*; (Fig. 28). **Head capsule** (Fig. 64): always clearly sclerotised and appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a slight narrowing near posterior third or fourth; from antennal sockets sides converge clearly towards bases of mandibles. Upper profile clearly concave; frons: flat without any hump. Gulamentum in ventral view always constricted in its posterior half, with sides of anterior part forming a kind of ear on each side. Antennae: of 15 articles. **Labrum**: deeply bifurcate and wider than long, with sides lyre-shaped; lobes

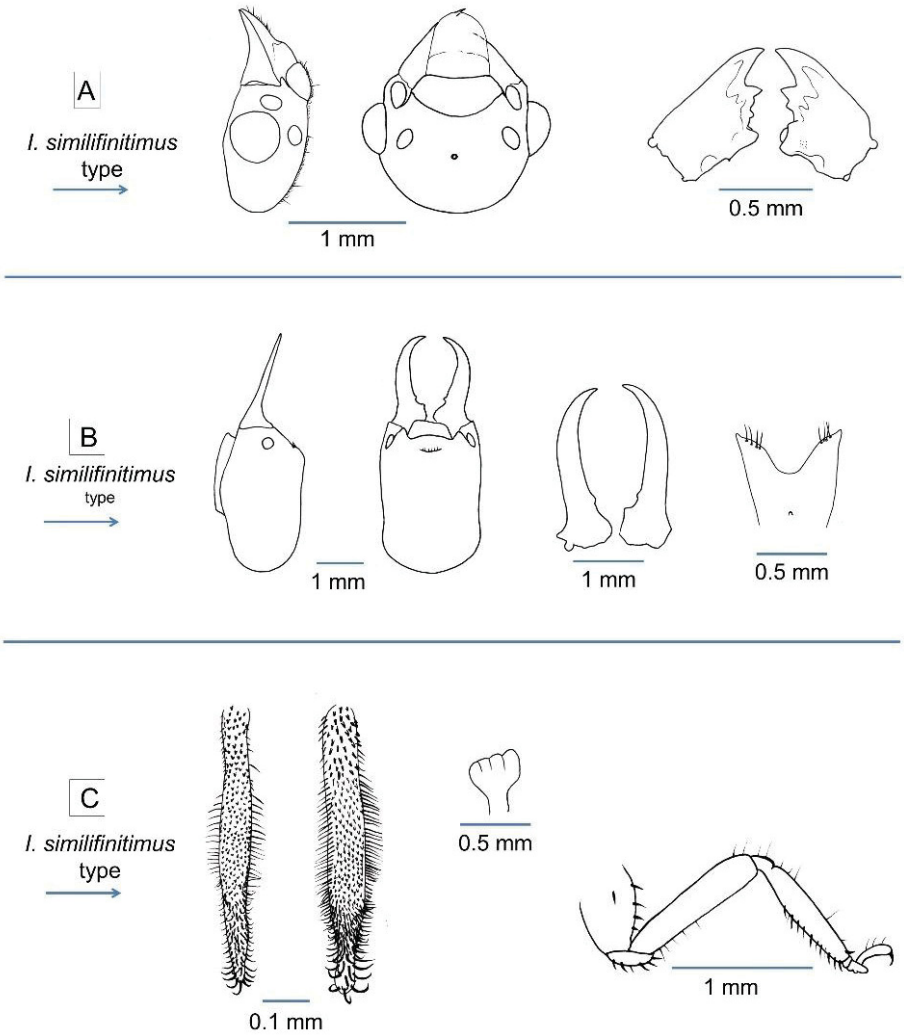


**Fig. 64.** *Isognathotermes similifinitimus* Josens & Deligne sp. nov.: soldier and worker. **A**. Lateral and dorsal views of the head capsule of the queen from the type colony of *I. similifinitimus* (DJ 0744), and dorsal view of its mandibles. **B**. Lateral and dorsal views of the head of a soldier from the same type colony; ventral view of its mandibles and dorsal view of its labrum. **C**. PC1s of soldier's and worker's enteric valves from the same type colony; caecum and foreleg of this worker.

**Table 15.** *Isognathotermes similifinitimus* Josens & Deligne sp. nov.: ranges of significant measures in the three castes, in alphabetical orders of the "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 2) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.41–0.45 | 0.45 |
| | | Head: width across the eyes | IHdW | 1.52–1.60 | 1.60 |
| | | Left mandible: A-m1 distance | IMlAmD | 0.21–0.22 | 0.22 |
| | | Ocellus: large diameter | IOc*D* | 0.18–0.20 | 0.18 |
| | | Postclypeus: width | IPcW | 0.70–0.79 | 0.79 |
| | | Pronotum: maximal width | IPnW | 1.45–1.49 | 1.49 |
| | | Hind tibia: length | IT3L | 1.83–1.95 | 1.95 |
| | | Wing: length (n= 0) | IWgL | NA | NA |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.38–1.57 | 1.57 |
| Soldiers (n = 2) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.02–0.06 | 0.06 |
| | | Head: length | SHdL | 2.97–3.30 | 3.30 |
| | | Head: width | SHdW | 2.00–2.20 | 2.20 |
| | | Left mandible: lesser sagitta | SMlc | 0.19–0.27 | 027 |
| | | Left mandible: ventral length | SMlL | 2.33–2.38 | 2.38 |
| | | Hind tibia: length | ST3L | 1.61–1.79 | 1.79 |
| | Indices | Head elongation index | SHdL/SHdW | 1.47–1.52 | 1.52 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.08–0.11 | 0.11 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.84–1.01 | 1.01 |
| Workers (n = 3) | Raw measures (mm) | Head: width | WHdW | 1.16–1.24 | 1.24 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.17–0.20 | 0.19 |
| | | Left mandible: total length | WMlL | 0.55–0.62 | 0.59 |
| | | Hind tibia: length | WT3L | 1.33–1.47 | 1.40 |
| | | Valve: PC average length | WVP-AvL | 0.60–0.65 | 0.65 |
| | | Valve: PC average width | WVP-AvW | 0.07–0.08 | 0.08 |
| | | Valve: SC average length | WVS-AvL | 0.48–0.56 | 0.52 |
| | | Valve: SC average width | WVS-AvW | 0.23–0.29 | 0.25 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 7.20–8.81 | 8.81 |

* Abbreviations: see definitions in Material and methods.

angular, with translucent to whitish tips; anterior margin concave. **Mandibles**: sabre-like, regularly curved; inner edges smooth with one distinct but very small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. **Thorax**: pronotum sellate, clearly narrower than head, with a slight notch in anterior margin and entire posterior margin. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions showing trilateral symmetry: the odd cushions are 14 to 18% longer than the even cushions, with humps hardly developed, moreover, the pilosity becoming abruptly very dense shows

the place where a hump is expected; secondary cushions wide at the upstream end narrowing noticeably downstream with a homogeneous spine scattering. **Caecum** rather small, best seen in ventral view, near centre of abdomen, lobed (three small lobes).

**Worker**

Colour. **Head capsule** pale (C2–C3). Antennae: proximal articles pale (C2), distal articles two levels darker (C4). **Thorax**, nota and legs pale (C1–C3). **Abdomen** grey owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50 × or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa carinated, bearing one fine seta and furnished with 5 spines on carina and 2 on ventral side; fore trochanter with 6–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 15; Figs 30, 64). **Size**: the workers of *I. similifinitimus* sp. nov. are, on average, medium sized in the genus *Isognathotermes* (but with large overlapping with several other species: Fig. 30). **Head capsule** weakly sclerotised (except mandibles). Antennae: 14.5 articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal well developed but with a blunt tip even when fresh, second marginal faint (visible as an undulated edge), third marginal with a blunt tip; premolar tooth with its proximal end hidden under molar prominence; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal well developed with a sharp tip when fresh; second marginal smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 72% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions of the *finitimus* pattern with triradial symmetry: the odd PCs, in their downstream part, are wide and bear at that place a very high density of rather short bristles on a globular bulge; supporting bristles are numerous: 25–27 on each side of the odd PCs; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum rather small, visible in ventral view, near centre of abdomen, shortly lobed (three or four small lobes).

**Chorology-ecology**

To date, this species is only known from two samples collected in an evergreen forest near Kisangani, DRC, in the northeastern Congolian lowland forests ecoregion (Fig. 47).

**Molecular data**

Two mitogenomes of *I. similifinitimus* sp. nov. are published alongside this work (GenBank accessions: see Supp. file 3 and ‘Material examined’), with a dissimilarity of 1.48% between them, even though they come from the same locality (Supp. file 4). The phylogenetic reconstructions based on full mitogenomes indicated that this species is paraphyletic with respect to *I. phallicaecalis* sp. nov. (Fig. 33), to which mitogenomes were up to 1.50% dissimilar. In this case, the separation of the two species is not justified by molecular dissimilarity but by the different types of caeca.

***Isognathotermes ugandensis*** (Fuller, 1923)
Figs 26–31, 33, 65–69, distribution map: Fig. 49; Tables 16–17

*Cubitermes ugandensis* Fuller, 1923: 191–192.
*Cubitermes antennalis* Sjöstedt, 1924c: 493.

*Mirotermes* (*Cubitermes*) *antennalis* – Emerson 1928: 513–515, text-fig. 57, pl XXXIII.
*Cubitermes ugandensis* – Sjöstedt 1926: 251–252, table 10 b1–b2. — Snyder 1949: 165. — Williams 1966: 107–108, figs 15, 31, 47, 64, 82. — Bouillon & Vincke 1971: 269. — Krishna *et al.* 2013: 1942. — Josens & Deligne 2019: 60–61.
*Cubitermes antennalis* – Williams 1966: 107–108. — Krishna *et al.* 2013: 1943.
*Cubitermes ugandensis* – Hellemans *et al.* 2021: 233.
*Isognathotermes antennalis* – Hellemans *et al*. 2021: 233.
*Isognathotermes ugandensis* – Hellemans *et al*. 2021: 233.

With four new subspecies:
*Isognathotermes ugandensis burundii* Josens & Deligne subsp. nov.
*Isognathotermes ugandensis kenyae* Josens & Deligne subsp. nov.
*Isognathotermes ugandensis malawii* Josens & Deligne subsp. nov.
*Isognathotermes ugandensis ugandensis* Josens & Deligne subsp. nov.

**Diagnosis**

This species is very close to *I. minitabundus* and *I. severus*.

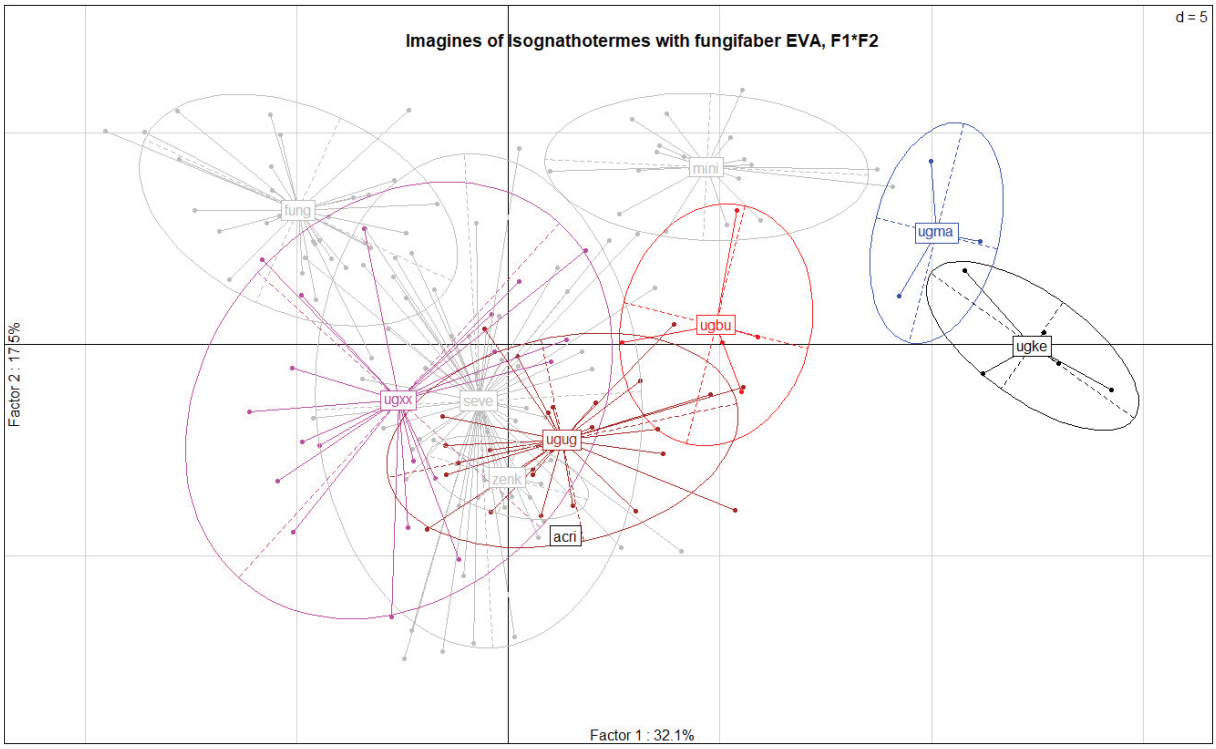


**Fig. 65.** PCA on imagines' morphology involving the species of *Isognathotermes* Sjöstedt, 1926 with a *fungifaber*-type EVA; the first axis is linked to size, especially that of the mandibles and thorax (the largest on the right), the second axis to the dimensions of the eyes and ocelli (the largest at the bottom). Abbreviations: acri = *I. acristatus* sp. nov.; fung = *I. fungifaber*; mini = *I. minitabundus*; seve = *I. severus*; ugbu = *I. ugandensis burundii* ssp. nov.; ugke = *I. ugandensis kenyae* ssp. nov.; ugma = *I. ugandensis malawii* ssp. nov.; ugug = *I. ugandensis. ugandensis* ssp. nov.; ugxx = *I. ugandensis* formerly known as *I. antennalis*; zenk = *I. zenkeri*.

The worker (all four subspecies) has a *fungifaber* EVA but in 6% of the samples examined, it has an EVA intermediate between the *fungifaber* and *finitimus* patterns. Its valve is, on average, somewhat larger than that of *I. minitabundus* (Fig. 31). It is among the medium- to large-sized workers of the genus *Isognathotermes* (Fig. 30). As in *I. minitabundus*, the premolar tooth of the left mandible is more apparent than in most other species.

The soldier (all four subspecies) is among the medium- to large-sized soldiers in the genus *Isognathotermes* (Fig. 28), on average somewhat larger than *I. severus*. It has the left mandible slightly curved to almost straight and obviously less curved than the right mandible as in *I. minitabundus* but more asymmetrical than in *I. severus* (SMlc/SMrc = 0.68–1.02, vs 0.51–1.03 in *I. minitabundus* and 0.79–1.24 in *I. severus*). Its head is generally clearly bulbous, but this is shared with *I. severus* (and also with *I. bulbifrons* which has a *finitimus* EVA).

The imago is among the medium- to large-sized imagines of the genus *Isognathotermes* (Figs 26, 65). The premolar tooth on left mandible is more apparent than in most other species (but this is shared with *I. severus* and *I. minitabundus*).

Contrary to usual, the morphology of imagines is more heterogeneous than that of soldiers and workers (Figs 65–69), and this heterogeneity is linked to origin and altitude (Fig. 66), revealing clear subgroups that are hardly detectable in soldiers or workers. Pending more comprehensive molecular data (most of the available samples being too old to be sequenced), we propose to distinguish four subspecies based on overall size (first PCA factor) and eye and ocelli dimensions (second PCA factor).

**Etymology**

The name *ugandensis* (from Uganda and Latin desinence -*ensis*, from) clearly refers to the country (Uganda) of the type locality.

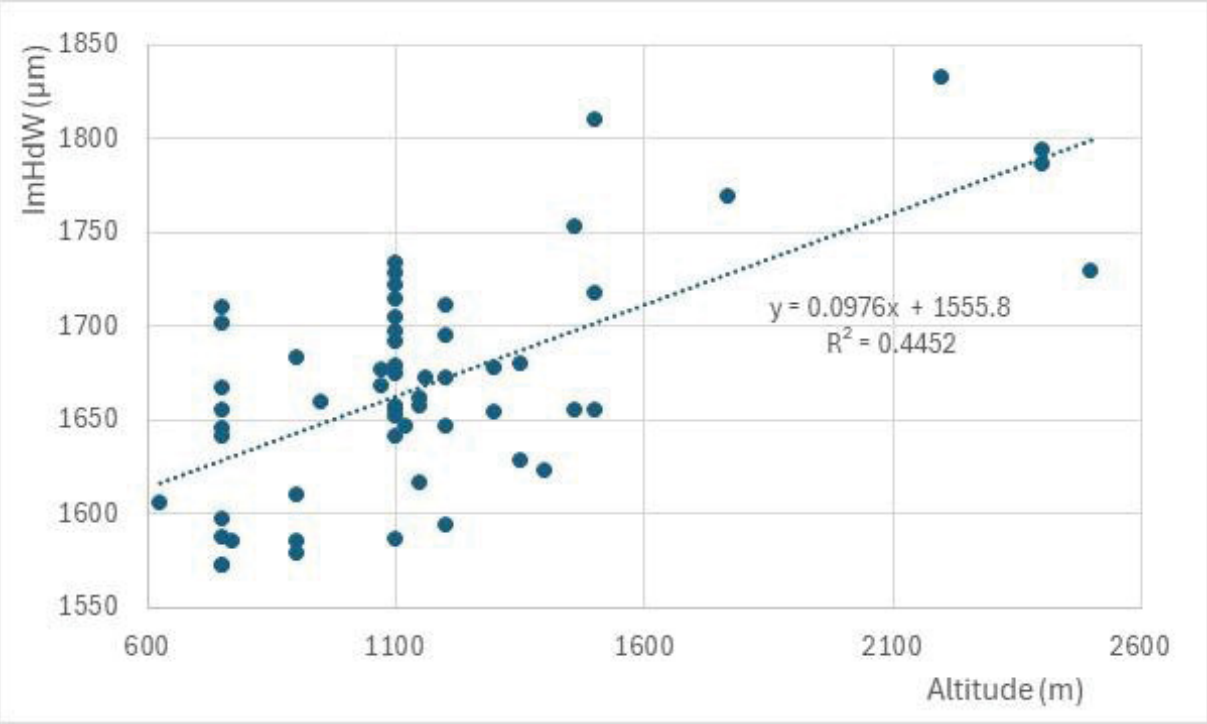


**Fig. 66.** Correlation between imago size (ImDdW = imagines' head width) and altitude (all *I. ugandensis* samples, n = 58, r = 0667, p<0.01).

**Material examined**

See hereafter the material examined of *Isognathotermes ugandensis ugandensis* and other subspecies.

**Historical review**

Fuller (1923: 191–192) described this species under the name *Cubitermes ugandensis*. He provided descriptions of alate, imago, and soldier.

Sjöstedt (1926: 251–252) provided a redescription of alate imago and soldier, together with figures of the soldier's head, and a short first description of the worker. Sjöstedt (1926: 249–250) included *Cubitermes ugandensis* in imagines' and soldiers' keys of *Cubitermes* species and inserted it in a "*bulbifrons*-Gruppe" of species with an upwards humped soldier's frons.

Snyder (1949: 165) catalogued *Cubitermes ugandensis* in the sub-family Termitinae.

Williams (1966: 107–108) provided a detailed redescription of imago and soldier along with measurements and figures. He stated that the alate imago described by Fuller (1923) and Sjöstedt (1926) belonged to *Ophiotermes ugandaensis*.

Williams (1966: 108) considered *C. ugandensis* as a senior synonym of *C. antennalis*.

Emerson, in his unpublished "card catalog", named six samples (from three nests) "*Cubitermes basilewskyi*" in honour of Pierre Basilewsky who collected this material in Rwanda, but it was neither described nor published (nomen nudum). Two such subsamples preserved in RMCA were examined by Williams in 1968 and considered to be *Cubitermes ugandensis*; confirmed in this study as *I. u. burundii*.

Bouillon & Vincke (1971: 269) described the enteric valve of *C. ugandensis* as belonging to the first of three types, the "simple type" without any spatula.

Krishna *et al.* (2013: 1942) housed *Cubitermes ugandensis* in the sub-family Cubitermitinae.

Josens & Deligne (2019: 39–42) placed this species within the *fungifaber* valve pattern group.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

Here, we divide the species *I. ugandensis* into four subspecies that could later become true species. The problem at this stage of our knowledge is that molecular data is still scarce; these taxa can therefore only be recognised by the morphology of the imagines (which are missing from almost half the samples) and by their geographical origin.

**Redescription**

The redescription concerns the species; the distinction between subspecies is based mainly on the imagines' sizes and origins: see diagnosis.

**Imago**

Colour. **Head capsule**: well sclerotised, fresh samples very dark, C6–C8 (C6–C7 in long preserved imagines); fontanelle concolorous or almost so with head capsule. Postclypeus C5–C7 concolorous or slightly paler (one level) than head capsule. Antennae C4–C7 without any difference between proximal and distal articles. **Thorax**: pronotum C5–C7, as postclypeus, concolorous or slightly (one level) paler than head capsule; meso- and metanotum C5–C6, sometimes somewhat paler than pronotum. Legs C3–C5; tibia concolorous with femur or somewhat (one level) darker. Wings hyaline with brown to grey tinge (Cf2–Cf3), anterior veins darker. **Abdomen**: tergites C6–C7. Sternites appreciably paler in middle (C3–C4) with both sides darker (C4–C5); posterior sternites darker (C4–C5) than anterior.

Setation. **Head capsule**, with some prominent setae set amongst a high density of short, fine setae forming a dense mat. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and shorter ones in middle; meso- and metanotum with some fine, pale setae, arranged in a medio-longitudinal strip, generally visible at 40–80×, these fine setae do not extend over the posterior margin. **Legs** very pilose, furnished (among numerous fine setae) with some stronger setae: 7–12 on the carina of fore coxa and 1–6 on the ventral side of fore coxa and on trochanter; tibia pilose, fore, mid, and hind tibia furnished with 15–30 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Tables 16–17; Fig. 67). **Size**: the imagines of *I. ugandensis* are among the medium- to large-sized species of the genus *Isognathotermes* (as *I. minitabundus*) (Fig. 26). The imagines' size is one of the criteria that distinguish the subspecies (see diagnosis). **Head capsule**: compound eyes oval; ocelli shortly to moderately oval, removed from eyes by a short distance with an eye to ocellus minimal distance index: IEyOcD/IOc*d* = 0.54–1.58 somewhat larger than in *I. severus* (0.39–1.29) and smaller than in *I. minitabundus* (1.10–1.70); fontanelle generally a tiny round or elongate marking. Antennae: 16 articles on alate individuals, shortened by amputation by some articles in king and queen. Labrum: cupola shaped, wider than long. **Left mandible** with apical tooth medium to small sized (IMlAmD = 0.19–0.27 mm: Fig. 27) and always more prominent than first marginal; marginal teeth three in number; second marginal appearing as an undulated edge, reduced but still present in worn mandibles, third marginal tooth with a blunt tip; premolar tooth generally well visible (best seen than in most other species); only the apical tooth is acute in unworn specimens; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth always more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a carina. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 2–5 and 9–12 branches, respectively. **Gut** not studied.

**Soldier**

Colour. **Head capsule** generally tending towards deep palette (Cd4–Cd6) becoming fader and somewhat darker in long preserved samples; there is generally a smooth gradient from a darker frons to a paler back. Antennae and labrum generally one to two palette levels paler than head capsule. Mandibles dark (C6–C8) generally with an abrupt clearing on their bases (one to two levels) which is generally the same colour as frons; in long preserved samples, this clearing tends to fade. **Thorax** and legs paler than head capsule (C3–C4) somewhat darker in long preserved samples. **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Labrum** always with 4–8 large setae on each lobe. **Thorax**: pro- and mesonotum with a small number of setae mainly located on margins. **Legs**: fore coxa bears at least one fine seta and 1–3 spines (exceptionally 6) on carina and not any spine on ventral side (rarely one); trochanter generally with some strong lined-up setae, or with 3–7 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively (the latter sometimes weakly developed) and a row of 7–18 spines along

their shaft. **Abdomen**: tergites with some large setae, mainly or only on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 16; Figs 28, 67). **Size**: the soldiers of *I. ugandensis* are part of the medium to larger soldiers in the genus *Isognathotermes* (Fig. 28). **Head capsule**: always clearly sclerotised; appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a clear narrowing near posterior third or fourth, from antennal sockets sides converge towards bases of mandibles; posterior side regularly convex or sometimes with short straight parts. Upper profile always

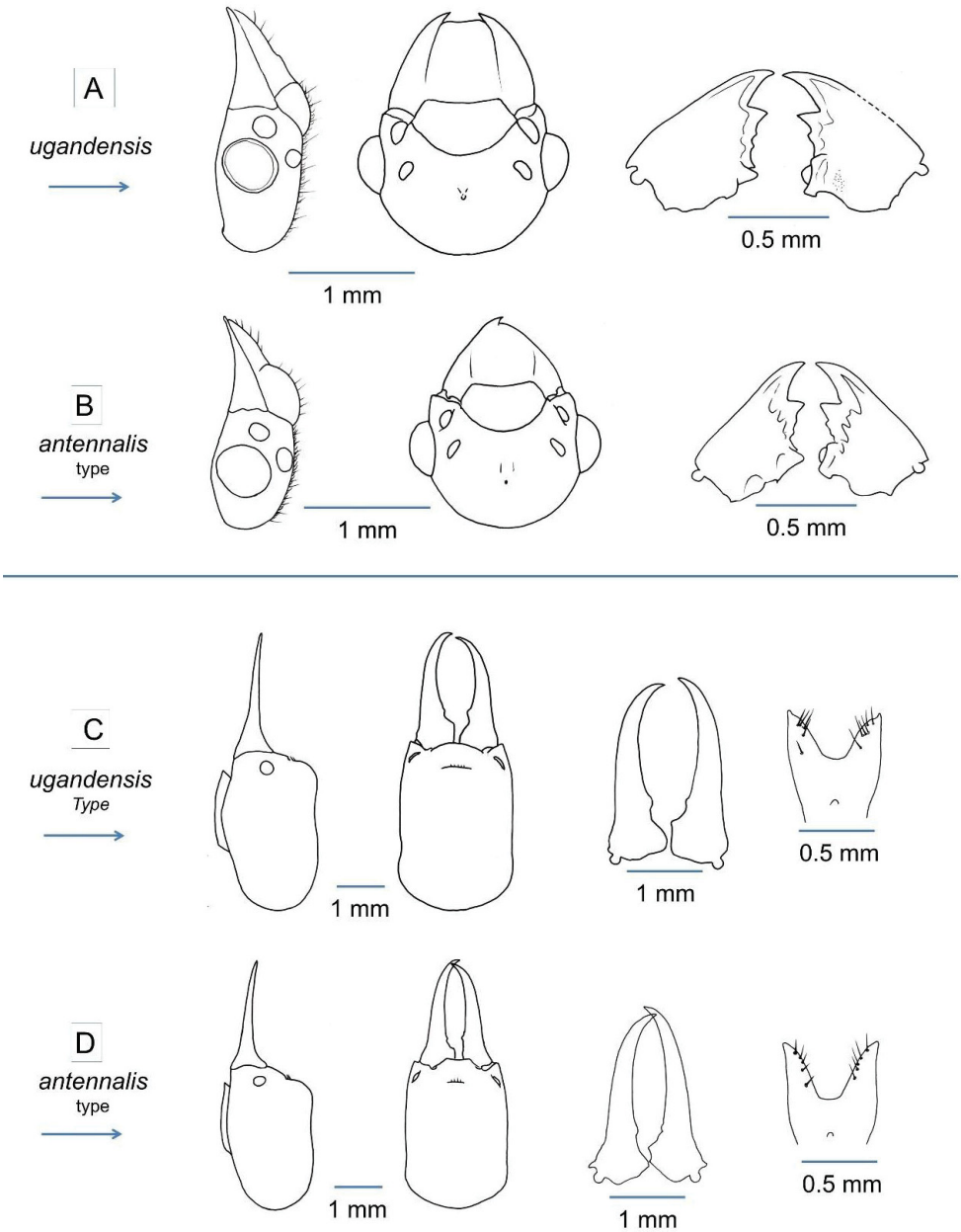


**Fig. 67.** *Isognathotermes ugandensis* (Fuller, 1923): imago and soldier. **A**. Lateral and dorsal views of the head capsule and dorsal view of the mandibles of an alate male of *I. ugandensis ugandensis* ssp. nov.; from a non-type colony (DJ 0570). **B**. Of an alate female from the type colony of *Cubitermes antennalis* Sjöstedt, 1924 (DJ 0031). **C**. Lateral and dorsal views of a soldier's head capsule, ventral view of its mandibles, and dorsal view of its labrum from the type colony of *Cubitermes ugandensis* Fuller, 1923 (DJ 0289). **D**. From the type colony of *Cubitermes antennalis* Sjöstedt, 1924 (DJ 0013).

**Table 16.** *Isognathotermes ugandensis* (Fuller, 1923): ranges of significant measures in the three castes, in alphabetical orders of the "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 59) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.39–0.57 | NA |
| | | Head: width across the eyes | IHdW | 1.57–1.84 | NA |
| | | Left mandible: A-m1 distance | IMlAmD | 0.19–0.27 | NA |
| | | Ocellus: large diameter | IOc*D* | 0.15–0.23 | NA |
| | | Postclypeus: width | IPcW | 0.68–0.93 | NA |
| | | Pronotum: maximal width | IPnW | 1.22–1.74 | NA |
| | | Hind tibia: length | IT3L | 1.47–2.31 | NA |
| | | Wing: length (n= 32) | IWgL | 13.7–19.4 | NA |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 0.93–1.71 | NA |
| Soldiers (n = 86) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.01–0.10 | 0.07 |
| | | Head: length | SHdL | 2.73–3.72 | 3.32 |
| | | Head: width | SHdW | 1.86–2.37 | 2.29 |
| | | Left mandible: lesser sagitta | SMlc | 0.12–0.27 | 0.23 |
| | | Left mandible: ventral length | SMlL | 2.15–2.74 | 2.56 |
| | | Hind tibia: length | ST3L | 1.57–1.88 | 1.86 |
| | Indices | Head elongation index | SHdL/SHdW | 1.35–1.62 | 1.45 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.06–0.10 | 0.09 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.68–1.02 | 0.83 |
| Workers (n = 45) | Raw measures (mm) | Head: width | WHdW | 1.11–1.42 | 1.17 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.16–0.22 | 0.19 |
| | | Left mandible: total length | WMlL | 0.53–0.67 | 0.58 |
| | | Hind tibia: length | WT3L | 1.10–1.49 | 1.35 |
| | | Valve: PC average length | WVP-AvL | 0.62–0.85 | 0.64 |
| | | Valve: PC average width | WVP-AvW | 0.06–0.12 | 0.07 |
| | | Valve: SC average length | WVS-AvL | 0.55–0.73 | 0.58 |
| | | Valve: SC average width | WVS-AvW | 0.30–0.45 | 0.33 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 5.57–12.1 | 10.4 |

* Abbreviations: see definitions in Material and methods.

rather strongly concave; angle between extended mandibles and frons obtuse; frons with sketched to clear anterior hump. Gulamentum in ventral view always constricted in its posterior half, with sides of anterior part generally forming an acute widening or even a kind of ear on each side. Antennae: of 14–15 articles. **Labrum**: always deeply bifurcate and wider than long, with sides varying from lyre-shaped (in 90% of the samples examined) to convex; lobes angular, generally with fine, whitish, or translucent tips; anterior margin concave. **Mandibles**: sabre-like and rather clearly asymmetrical (but a little less than in *I. minitabundus*), the left mandible is slightly curved and obviously less curved than the right mandible; inner edges generally smooth with one distinct but very small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible always clearly more curved than left. **Thorax**: pronotum sellate, as wide as 54–61% of

**Table 17.** New subspecies of *Isognathotermes ugandensis* (Fuller, 1923): significant measurement ranges in the imago caste.

| Mean altitude | 1015 m | 1350 m | 1560 m | 2200 m |
|---|---|---|---|---|
| Code * | Range *ugandensis* n = 45** | Range *burundii* n = 5 | Range *malawii* n = 5 | Range *kenyae* n = 3 |
| IEy*D* | 0.40–0.57 | 0.39–0.46 | 0.42–0.44 | 0.41–0.45 |
| IHdW | 1.57–1.74 | 1.62–1.72 | 1.65–1.78 | 1.72–1.84 |
| IMlAmD | 0.19–0.25 | 0.20–0.23 | 0.23–0.27 | 0.20–0.23 |
| IOc*D* | 0.15–0.23 | 0.15–0.18 | 0.15–0.18 | 0.15–0.18 |
| IPcW | 0.68–0.86 | 0.77–0.86 | 0.84–0.91 | 0.85–0.93 |
| IPnW | 1.22–1.60 | 1.41–1.55 | 1.58–1.71 | 1.61–1.74 |
| IT3L | 1.47–2.31 | 1.98–2.12 | 2.00–2.07 | 2.07–2.20 |
| IWgL | 13.6–18.1 | 15.6–17.5 | NA | 18.9–19.5 |
| IMlAmD/ IMlmmD | 1.10–1.64 | 1.02–1.34 | 1.18–1.71 | 0.93–1.20 |
| IEy*D*/IHdW | 0.25–0.34 | 0.24–0.28 | 0.24–0.27 | 0.23–0.25 |

* Abbreviations: see definitions in Material and methods.

** Including 14 individuals previously known as *I. antennalis*.

head width, with straight or indented anterior margin and posterior straight margin. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in second half of abdomen. **Caecum** always rather small, best seen in ventral view, near centre of abdomen, generally three-lobed. Arrangement of enteric valve cushions showing trilateral symmetry, the odd cushions being about 16% longer than the even cushions, generally without any crest or with crests very weakly developed.

**Worker**

Colour. **Head capsule** pale (C1–C3) turning grey in long preserved samples. Antennae: proximal articles pale (C2–C3), distal articles always one to two levels darker (C4–C5). **Thorax**, nota, and legs pale (C1–C3). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect, scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa always carinated, bearing one fine seta and furnished with 3–5 spines on carina and 0–2 on ventral side; fore trochanter with 6–7 spines, all except one lined up; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of 7–16 spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 16, Figs 30, 67). **Size**: the workers of *I. ugandensis* are part of the medium to larger workers in the genus *Isognathotermes* (but with large overlapping on several other species: Fig. 30). **Head capsule**: weakly sclerotised (except mandibles). Antennae of 14 or more often 14.5 articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal tooth well developed but with a blunt tip even when fresh, second marginal appearing as an undulated edge, reduced but still present in worn mandibles

(better seen than in other species), third marginal tooth with a blunt tip; premolar tooth generally well visible (also better seen than in other species); molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh and sometimes with a wavy inner edge near the base; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 60–68% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in second half of abdomen. Arrangement of enteric valve cushions of the *fungifaber* pattern with triradial symmetry: the odd PCs, in their downstream part, are rather narrow and bear crests that are as high as or higher than they are wide, with long and strong bristles (but in 6% of the samples examined, the EVA is intermediate between the *fungifaber* and *finitimus* patterns); 16–27 supporting bristles on each side of the odd PCs; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum always rather small, visible in ventral view, near centre of abdomen, generally with two short lobes.

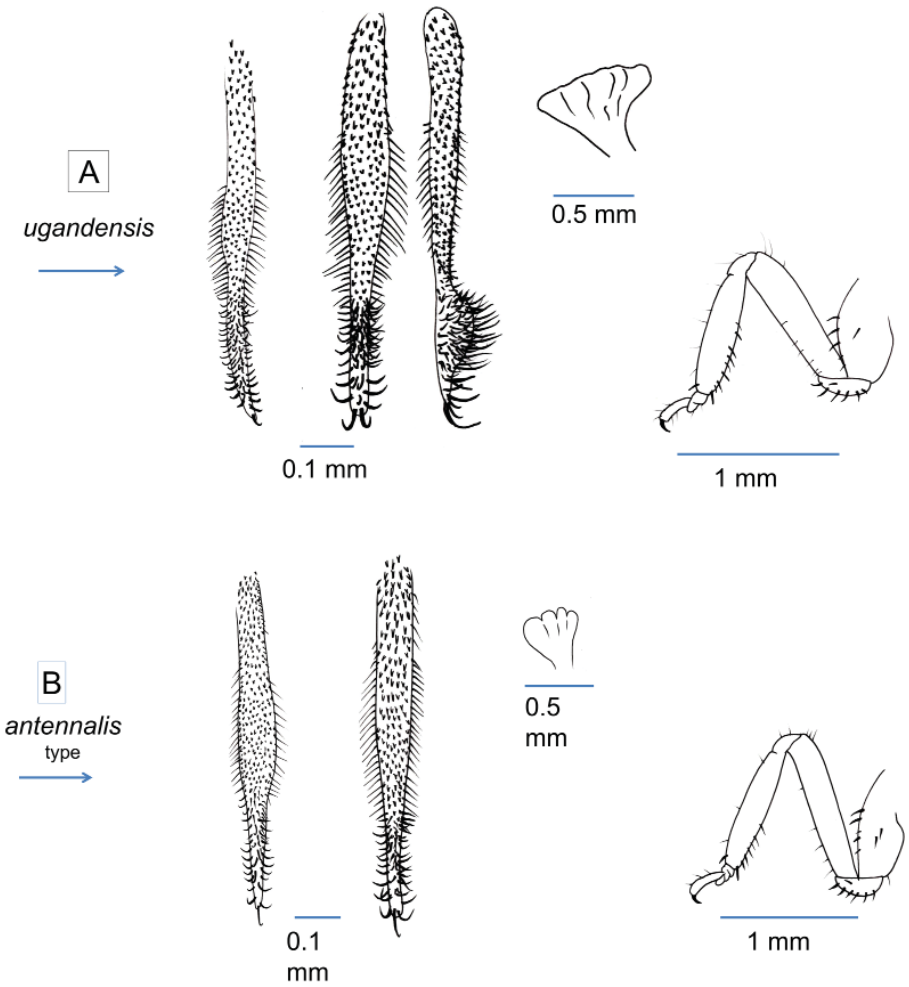


**Fig. 68.** *Isognathotermes ugandensis* (Fuller, 1923): soldier, and worker. **A**. PC1s of soldier's and worker's enteric valves (with another worker's PC in side view), caecum and foreleg of this worker from a non-type colony (DJ 0570). **B**. From the type colony of *Cubitermes antennalis* Sjöstedt, 1924 (DJ 0013).

**Chorology-ecology**

*Isognathotermes ugandensis* is the easternmost and southernmost species of the genus *Isognathotermes* (Fig. 49) its geographic distribution is linked with the Victoria basin forest-savanna mosaic, the east Sudanian savanna, the central Zambezian miombo woodlands, and the northern *Acacia-Commiphora* bushlands and thickets ecoregions. It settles at high altitudes: Williams (1966) mentioned that all his *C. ugandensis* samples had been collected between 1100 and 2400 m a.s.l. Here, we confirm and extend this range to 625–2500 m with a range of four subspecies.

**Molecular data**

Of the four considered subspecies, only two (*I. ugandensis burundii* subsp. nov., and *I. u. kenyae* subsp. nov.) were successfully sequenced. Six mitogenomes of *I. ugandensis* are published alongside this work (GenBank accessions: see Supp. file 3 and 'Material examined'). Overall, mitogenomes exhibited less than 1.3% dissimilarity with each other (see Supp. file 4), with *I. u. kenyae* (DJ 0599) being the most dissimilar. Our phylogenetic reconstructions placed *I. ugandensis* + *I. minitabundus* as sister to *I. finitimus* (Fig. 33; SHalrt /UFB = 99.3/93), with whom they are less than 2% dissimilar. Of note, *I. ugandensis* and *I. minitabundus* exhibit a *fungifaber* EVA which is distinctive from *I. finitimus*.

**Remarks**

The subdivision of *I. ugandensis* into four subspecies and the difficulty of incorporating *I. antennalis* into one of these subspecies betrays the vagueness that surrounds the *Isognathotermes* of East Africa. The morphological diversity of the imagines may result from genuine genetic differences, in which case the subspecies could become species, but it could also reflect phenotypic plasticity linked to altitude: only further molecular studies could resolve this question.

***Isognathotermes ugandensis ugandensis*** Josens & Deligne subsp. nov.
urn:lsid:zoobank.org:act:DDDE8D67-9E45-45F6-952D-EB3CF0D2EA71
Figs 65–69

**Diagnosis**

Soldiers and workers do not allow this subspecies to be distinguished from the other three.

The imago is close to that of *I. u. burundii* subsp. nov.; it is, on average, the smallest of the four subspecies, with, relatively speaking, the widest eyes ("ugug" in Fig. 65, Table 17).

*Isognathotermes u. ugandensis* is also the subspecies that comes from the lowest average altitude (625–1500 m, average = 1015 m); the samples come from Uganda, South Sudan, eastern CAR and Haut-Uele province, DRC). To date, no samples have been sequenced.

**Etymology**

The name refers to the country (Uganda) of the type locality.

**Material examined**

Sixty one old samples from 28 locations. Of the 61 old museum samples examined, 20 were initially labelled as *Cubitermes ugandensis*, 18 as *C. antennalis*, five as *C. speciosus*, and 18 as *Cubitermes* sp.

**Syntypes of *Cubitermes ugandensis* Fuller, 1923 = type of *Isognathotermes ugandensis ugandensis* subsp. nov.**

UGANDA • soldier, worker; near Entebbe?; 2°0′ N, 33°0′ E; 1921; H.L. Duke leg.; study code: DJ 0289; initially *C. ugandensis*; AMNH.

**Syntypes of *Cubitermes antennalis* Sjöstedt, 1924**
DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker, ♀ (alate), ♀ (queen); Moto; 2°54.47′ N, 29°24.85′ E; 1923; L. Burgeon leg.; study code: DJ 0013; initially *C. antennalis* in RMCA; BE RMCA

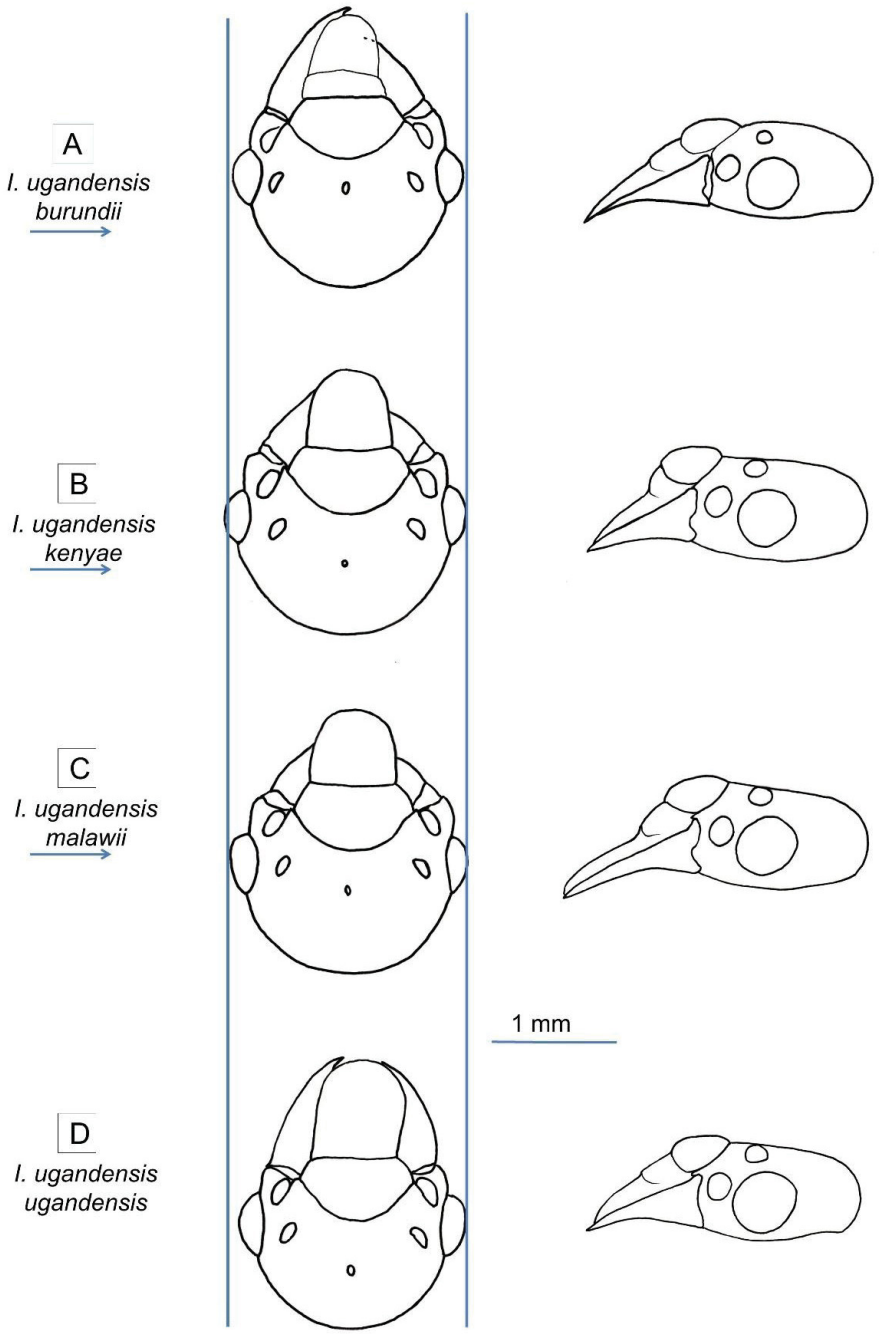


**Fig. 69.** Subspecies of *Isognathotermes ugandensis* (Fuller, 1923) imagines. **A**. Dorsal and lateral views of an alate female's head capsule from a colony of *I. ugandensis burundii* ssp. nov. (DJ 0368). **B**. Same views of an alate male's head capsule from a colony of *I. ugandensis kenyae* ssp. nov. (DJ 0669). **C**. Same views of an alate female's head capsule from a colony of *I. ugandensis malawii* ssp. nov. (DJ 0668). **D**. Same views of an alate male's head capsule from a colony of *I. ugandensis ugandensis* ssp. nov. (DJ 0570). The vertical lines show that the *kenyae* subspecies is larger and *ugandensis* smaller. Note the relative size of the eyes, which is smaller in the *burundii* and larger in the *ugandensis* subspecies.

INS.Iso.059422 • worker, ♀ (alate), ♂ (alate); Moto; 2°54.47′ N, 29°24.85′ E; 1923; L. Burgeon leg.; study code: DJ 0031; initially *C. antennalis* in RMCA; BE RMCA INS.Iso.059430.

Krishna *et al.* (2013: 1936) mention that another subsample is deposited in NHRM (not examined).

**Other material examined**

CENTRAL AFRICAN REPUBLIC • soldier, worker; Zemio; 5°2′ N, 25°7′ E; Mar. 1948; N.A Weber leg.; study code: DJ 0808; initially *C. antennalis* in AMNH; IZC 00321222 • soldier, worker, ♂ (alate); Djema; 6°5′ N, 25°12′ E; 6 Mar. 1948; N.A. Weber leg.; study code: DJ 0805; initially *C. antennalis* in AMNH; IZC 00321221.

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker, ♀ (alate); Garamba N.P.; 4°10′ N, 29°30′ E; 19 Mar. 1912; Lang-Chapin leg.; study code: DJ 0806; initially *C. antennalis*; AMNH, IZC 00321228 • soldier, worker, ♀ (queen); Garamba N.P.; 3°55′ N, 29°25′ E; Jul. 1912; Lang-Chapin leg.; study code: DJ 0736; initially *C. speciosus*; AMNH • soldier, worker; Garamba N.P.; 4°10′ N, 29°30′ E; Sep. 1912; Lang-Chapin leg.; study code: DJ 0809; initially *C. antennalis*; AMNH, IZC 00321227• soldier, worker; Manda; 4°0′ N, 24°54′ E; 2 Mar. 1925; H. Schouteden leg.; study code: DJ 0019; initially *C. ugandensis* in RMCA; BE RMCA INS.Iso.059434 • soldier; Manda; 4°0′ N, 24°54′ E; 27 Nov. 1925; H. Schouteden leg.; study code: DJ 0025; initially *C. ugandensis* in RMCA; BE RMCA INS.Iso.059435 • soldier, worker, ♀ (alate); Asa; 4°34′ N, 25°49′ E; 4 Mar. 1948; N.A. Weber leg.; study code: DJ 0804; initially *C. antennalis*; AMNH, IZC 00321224 • worker; Garamba N.P.; 4°20′ N, 29°15′ E; 25 Jan. 1950; G. Demoulin leg.; study code: DJ 0039; initially *C. antennalis* in RMCA; BE RMCA INS.Iso.059433 • soldier, worker, ♂ (king); Garamba N.P.; 3°55′ N, 29°25′ E; ca 1951; H. de Saeger *et al.* leg.; study code: DJ 0026; initially *C. antennalis* in RMCA; BE RMCA INS.Iso.059437 • soldier, ♂ (king); Garamba N. P.; 3°45′ N, 29°16′ E; ca 1951; H. De Saeger *et al.* leg.; study code: DJ U078; initially *C. ugandensis*; NHMUK 13672006 • soldier; Garamba N.P.; 3°55′ N, 29°25′ E; ca 1951; H. de Saeger *et al.* leg.; study code: DJ 0028; initially *C. antennalis* in RMCA; BE RMCA INS.Iso.059438 • worker, ♂ (alate); Garamba N.P.; 3°55′ N, 29°25′ E; ca 1951; H. de Saeger *et al.* leg.; study code: DJ 0029; initially *C. antennalis* in RMCA; BE RMCA INS.Iso.059425 • ♂ (alate); Garamba N.P.; 3°55′ N, 29°25′ E; ca 1951; H. de Saeger *et al.* leg.; study code: DJ 0033; initially *C. antennalis* in RMCA; BE RMCA INS. Iso.059423 • ♀ (alate); Garamba N.P.; 3°55′ N, 29°25′ E; ca 1951; H. de Saeger *et al.* leg.; study code: DJ 0035; initially *C. antennalis* in RMCA; BE RMCA INS.Iso.059424 • ♂ (king), ♀ (queen); Garamba N.P.; 3°55′ N, 29°25′ E; ca 1951; H. de Saeger *et al.* leg.; study code: DJ 0037; initially *C. antennalis* in RMCA; BE RMCA INS.Iso.059431 • ♂ (alate); Garamba N.P.; 3°55′ N, 29°25′ E; ca 1951; H. De Saeger *et al.* leg.; study code: DJ 0672; initially *C. ugandensis*; NHMUK 13672005 • soldier, worker; Garamba N.P.; 3°55′ N, 29°25′ E; 3 Feb. 1951; H. de Saeger *et al.* leg.; study code: DJ 0040; initially *C. antennalis* in RMCA; BE RMCA INS.Iso.059432 • soldier, worker; Garamba N.P.; 3°55′ N, 29°25′ E; 1 Oct. 1951; H. de Saeger *et al.* leg.; study code: DJ 0023; initially *C. antennalis* in RMCA; BE RMCA INS.Iso.059436 • soldier, worker, ♀ (queen); Garamba N.P.; 3°55′ N, 29°25′ E; 10 Nov. 1951; H. de Saeger *et al.* leg.; study code: DJ 0024; initially *C. antennalis* in RMCA; BE RMCA INS.Iso.059426.

"EAST AFRICA" (UGANDA?) • soldier; Mabira ?; 0°37′ N, 33°9′ E; no date; Oscar John leg., other label "collector almost certainly J. Sokolov in 1914 R.M.C.W."; study code: DJ U090; initially *C. speciosus*; NHMUK 13671990.

SOUTH SUDAN • soldier, worker, ♀ (alate), ♂ (alate); Madebe; 4°47′ N, 29°3′ E; 14 May 1937; J.G. Myers leg.; study code: DJ 0737; initially *C. speciosus*; AMNH.

UGANDA • soldier; Mityara, [= Mityana?]; 0°24′ N, 32°2′ E; Oct. 1926; H. Hargreaves leg.; study code: DJ N134; initially *C. ugandensis*; AMNH • soldier, ♀ (queen); Bugishu [Bugisu]; 1°6′ N,

34°11′ E; Feb. 1930; H. Hargreaves leg.; study code: DJ N133; initially *C. ugandensis*; AMNH • soldier; Kampala–Entebbe road; 0°11′ N, 32°32′ E; 2 Dec. 1934; H. Kirby leg.; study code: DJ N131; initially *C. ugandensis*; AMNH • soldier, worker, ♂ (king); Aduma; 3°0′ N, 31°0′ E; 1 Sep. 1934; Buxton and H. Kirby leg.; study code: DJ 0807; initially *C. antennalis*; AMNH, IZC 00321218 • soldier; Bugondo forest; 1°42′ N, 31°27′ E; 15 Dec. 1934; H. Kirby leg.; study code: DJ N130; initially *C. ugandensis*; AMNH • soldier, ♀ (alate); Kambrega Kiyezi; 1°13′ S, 29°53′ E; 1947; W.V. Harris leg.; study code: DJ U082; initially *C. ugandensis*; NHMUK 13671996 • soldier, ♂ (alate); Hoima; 1°26′ N, 31°21′ E; 4 Dec. 1948; W.V. Harris leg.; study code: DJ 0674; initially *C. ugandensis*; NHMUK 13671999 • soldier, ♀ (alate); Kiziba Bulemezi; 0°50′ N, 32°35′ E; 15 Apr. 1949; W.V. Harris leg.; study code: DJ U074; initially *C. ugandensis*; NHMUK 13672020 • soldier, worker, ♂ (alate); Kampala–Masake road; 0°3′ N, 32°5′ E; 4 Feb. 1955; W. Wilkinson leg.; study code: DJ 0570; initially *C. ugandensis*; NHMUK • soldier, ♀ (alate); Fort Portal–Masindi road; 0°44′ N, 30°41′ E; 12 Feb. 1955; R.M.C. Williams leg.; study code: DJ U083; initially *C. ugandensis*; NHMUK 13671995 • soldier, worker, ♂ (alate), ♂ (king); Fort Portal–Masindi road; 0°58′ N, 30°51′ E; 12 Feb. 1955; R.M.C. Williams leg.; study code: DJ 0571; initially *C. ugandensis*; NHMUK • soldier, worker, ♀ (alate); Kyenjojo–Mubende road; 0°33′ N, 30°54′ E; 14 Feb. 1955; R.M.C. Williams leg.; study code: DJ 0663; initially *C. ugandensis*; NHMUK 13671997 • soldier, ♀ (alate); Hoima–Fort Portal road; 1°11′ N, 31°2′ E; 17 Feb. 1955; R.M.C. Williams leg.; study code: DJ U071; initially *C. ugandensis*; NHMUK 13671998 • soldier, worker, ♂ (king); Hoima–Fort Portal road; 1°11′ N, 31°2′ E; 17 Feb. 1955; unknown leg.; study code: DJ 0683; initially *C. speciosus*; NHMUK 13671984 • soldier, ♂ (alate); Paidha–Pakwash road; 2°24′ N, 31°2′ E; 24 Feb. 1955; R.M.C. Williams leg.; study code: DJ U077; initially *C. ugandensis*; NHMUK 13672021 • soldier, ♀ (alate); Masindi–Kampala road; 1°37′ N, 31°45′ E; 27 May 1955; R.M.C. Williams leg.; study code: DJ U075; initially *C. ugandensis*; NHMUK 13672022 • soldier, worker, ♂ (alate); Mpigi–Masaka road; 0°10′ N, 32°16′ E; 25 Apr. 1955; R.M.C. Williams leg.; study code: DJ 0682; initially *C. speciosus*; NHMUK 13671983 • soldier, ♀ (alate); Kampala, Kawanda; 0°25′ N, 32°32′ E; 25 Jul. 1955; R.M.C. Williams leg.; study code: DJ U076; initially *C. ugandensis*; NHMUK 13672019 • soldier, ♂ (king), ♀ (queen); Kampala–Murchinson Falls road; 1°10′ N, 32°27′ E; 2 Sep. 1972; P. Vincke leg.; study code: DJ B253; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059474 • soldier, ♀ (alate), ♂ (king); Kampala–Murchinson Falls road; 1°10′ N, 32°27′ E; 2 Sep. 1972; P. Vincke leg.; study code: DJ B254; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059475 • soldier, ♂ (king), ♀ (queen); Kampala–Murchinson Falls road; 1°10′ N, 32°27′ E; 2 Sep. 1972; P. Vincke leg.; study code: DJ B255; initially *Cubitermes* sp. (+ *Ophiotermes*) in RMCA; BE RMCA INS.Iso.059479 • soldier; Kampala–Murchinson Falls road; 1°10′ N, 32°27′ E; 2 Sep. 1972; P. Vincke leg.; study code: DJ B256; initially "Big Cubi" in RMCA; BE RMCA INS.Iso.059471 • soldier, ♀ (queen); Kampala–Murchinson Falls road; 1°10′ N, 32°27′ E; 2 Sep. 1972; P. Vincke leg.; study code: DJ B257; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059481 • soldier; Kampala–Murchinson Falls road; 1°10′ N, 32°27′ E; 2 Sep. 1972; P. Vincke leg.; study code: DJ B258; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059472 • soldier, ♂ (king); Kampala–Murchinson Falls road; 1°10′ N, 32°27′ E; 2 Sep. 1972; P. Vincke leg.; study code: DJ B259; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059482 • soldier, ♂ (king); Kampala–Murchinson Falls road; 1°10′ N, 32°27′ E; 2 Sep. 1972; P. Vincke leg.; study code: DJ B260; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059484 • soldier; Luweero; 0°51′ N, 32°28′ E; 2 Sep. 1972; P. Vincke leg.; study code: DJ B252; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059473 • soldier, worker, ♀ (queen); Kampala–Murchinson Falls road; 1°10′ N, 32°15′ E; 2 Nov. 1972; P. Vincke leg.; study code: DJ 0905; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059419 • soldier, worker, ♂ (king); Kampala–Murchinson Falls road; 1°10′ N, 32°15′ E; 2 Nov. 1972; P. Vincke leg.; study code: DJ 0906; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059485 • soldier, worker, ♂ (king); Kampala–Murchinson Falls road; 1°10′ N, 32°15′ E; 2 Nov. 1972; P. Vincke leg.; study code: DJ 0907; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059487 • soldier, worker, ♀ (queen); Luweero; 0°51′ N, 32°28′ E; 2 Nov. 1972; P. Vincke leg.; study code: DJ 0928; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059476 • soldier, worker; near Luweero; 0°51′ N, 32°28′ E; 2 Nov. 1972;

P. Vincke leg.; study code: DJ 0900; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059486 • soldier, worker, ♀ (queen); near Luweero; 0°51′ N, 32°28′ E; 2 Nov. 1972; P. Vincke leg.; study code: DJ 0903; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059480 • soldier, worker, ♂ (king); near Luweero; 0°51′ N, 32°28′ E; 2 Nov. 1972; P. Vincke leg.; study code: DJ 0904; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059483 • soldier, worker; near Murchison Falls N.P.; 1°35′ N, 32°0′ E; 2 Nov. 1972; P. Vincke leg.; study code: DJ 0901; initially *Cubitermes* sp. in RMCA; BE RMCA INS. Iso.059478 • soldier, worker, ♀ (queen); near Murchison Falls N.P.; 0°51′ N, 32°28′ E; 2 Nov. 1972; P. Vincke leg.; study code: DJ 0902; initially *Cubitermes* sp. in RMCA; BE RMCA INS.Iso.059477.

**Description**

**Imago**

See the description of the imago of *I. ugandensis* (Fuller, 1923) with the particularity that the imago of *I. u. ugandensis* subsp. nov. is clearly the smallest of the four subspecies, with, relatively speaking, the widest eyes, best seen in a PCA ("ugug" in Fig. 65, Table 17), hence the highest IEyD/IHdW ratio (0.25–0.34 vs 0.23–0.28 for the other three subspecies).

Samples previously known as *I. antennalis* and synonymised with *I. ugandensis* (Williams 1966) are here assimilated to the subspecies *I. u. ugandensis* subsp. nov., because of the proximity of their geographical areas and morphological similarity of their imagines. However, not all individuals of *I. antennalis* should be considered synonyms of *I. u. ugandensis* as without molecular data, there is no reason to attribute certain samples to *I. ugandensis* rather than *I. severus*. And indeed the 'unusually' large size of the "ugxx" ellipse in Fig. 65 (*I. antennalis* samples) suggests a high "intrasubspecific" variability, probably linked with genetic heterogeneity.

**Soldier**

See the description of the soldier of *Isognathotermes ugandensis* (Fuller, 1923).

**Worker**

See the description of the worker of *Isognathotermes ugandensis* (Fuller, 1923).

**Chorology-ecology**

*Isognathotermes ugandensis ugandensis* subsp. nov. (including the samples previously identified as *I. antennalis*) is the subspecies that comes from the lowest altitude (625– 1500 m, average = 1015 m); it was found in Uganda, south-east CAR, South-Sudan, and north-east DRC. Its geographic distribution is linked with the northern Congolian forest-savanna mosaic, the Victoria basin forest-savanna mosaic, and the east Sudanian savanna ecoregions.

**Molecular data**

No genetic sequence is currently available.

***Isognathotermes ugandensis burundii*** Josens & Deligne subsp. nov.
urn:lsid:zoobank.org:act:085E6F35-0B31-4286-B03E-4B9411368E56
Figs 33, 65–66, 69

**Diagnosis**

This subspecies is best characterised by its mitogenome sequence.

Soldiers and workers do not allow this subspecies to be distinguished from the other three.

The imago of *I. u. burundii* subsp. nov. is close to that of *I. u. ugandensis* subsp. nov.; on average, it is somewhat larger with generally smaller eyes ("ugbu" in Fig. 65, Table 17); it can be found in Burundi, Rwanda, and Tanzania at a relatively low altitude (1200–1700 m, average = 1350 m).

**Etymology**

The name *burundii* (from Burundi) refers to the country of the type locality.

**Material examined**

Twenty one samples from 14 locations; of the 13 old museum samples examined, nine were initially labelled as *Cubitermes ugandensis* and four as *C. basilewskyi* (nomen nudum).

**Holotype**

BURUNDI • soldier; Ruvubu N.P.; 2°56.7′ S, 30°26.3′ E; Sep. 2014; B. Host leg.; study code: DJ 0396; GenBank no PQ679187 (mitogenome); BE RMCA INS.Iso.059458.

**Paratypes**

BURUNDI • soldier, worker, ♂ (alate); same data as for holotype; BE RMCA INS.Iso.059940.

**Other material examined**

BURUNDI • soldier, worker; Moso; 4°2′ S, 30°8′ E; 4 Jul. 1989; J. Ruelle (?) leg.; study code: DJ 0021; initially *C. ugandensis* in RMCA; BE RMCA INS.Iso.059467 • soldier, worker; Kibago; 4°18.152′ S, 29°55.73′ E; 25 Nov. 2013; Y. Roisin leg.; study code: DJ 0662; GenBank no PQ679212 (mitogenome) BE RMCA INS.Iso.059464 • soldier, worker; Gihofi–Giharo road pk75; 3°59.124′ S, 30°8.826′ E; 27 Nov. 2013; Y. Roisin leg.; study code: DJ 0661; GenBank nos MN646742 (*COI*), MN685948 (*COII*), MN686009 (*28S*), PQ679235 (mitogenome); BE RMCA INS.Iso.059465 • soldier, worker; Mahanga; 4°14.5′ S, 29°57.6′ E; 29 Nov. 2013; Y. Roisin leg.; study code: DJ 0091; GenBank no KY224661 (mitogenome) BE RMCA INS.Iso.059462 • soldier, worker; Ruvubu N.P.; 2°56.93′ S, 30°25.777′ E; 29 Nov. 2013; Y. Roisin leg.; study code: DJ 0660; GenBank nos MN685947 (*COII*), MN686008 (*28S*), PQ679215 (mitogenome); BE RMCA INS.Iso.059463 • soldier, worker; Rusigabangazi; 3°14.5′ S, 30°46.9′ E; 30 Nov. 2013; Y. Roisin leg.; study code: DJ 0107; BE RMCA INS.Iso.059461 • soldier, worker; Ruvubu N.P.; 2°56.7′ S, 30°26.3′ E; Sep. 2014; B. Host leg.; study code: DJ 0267; GenBank no PQ679217 (mitogenome) BE RMCA INS.Iso.059459 • soldier, worker, ♀ (alate); Ruvubu N.P.; 3°3.209′ S, 30°30.226′ E; Sep. 2014; B. Host leg.; study code: DJ 0368; BE RMCA INS.Iso.059460.

RWANDA • soldier, worker; Gabiro; 1°30.7′ S, 30°28′ E; 27 Dec. 1934; H. Kirby leg.; study code: DJ 0793; initially *C. basilewskyi* (unpublished); AMNH, IZC 00321237 • soldier, worker, ♀ (queen); Butare (←Astrida); 2.36°36′ S, 29°45′ E; 10 Jun. 1952; W.V. Harris leg.; study code: DJ 0675; initially *C. ugandensis*; NHMUK 13672007 • soldier; Gabiro; 1°30.5′ S, 30°28′ E; 8 Jul. 1952; W.V. Harris leg.; study code: DJ U079; initially *C. ugandensis*; NHMUK 13672008 • soldier, worker; Kinazi; 2°22′ S, 30°6′ E; 5–8 Jan. 1953; P. Basilewsky leg.; study code: DJ 0022; initially *C. ugandensis* in RMCA; BE RMCA INS.Iso.059468 • soldier, worker; Kinazi; 2°8.5′ S, 30°6′ E; 7 Jan. 1953; P. Basilewsky leg.; study code: DJ 0792; initially *C. basilewskyi* (unpublished); AMNH, IZC 00321235 • soldier, worker; Kinazi; 2°8.5′ S, 30°6′ E; 7 Jan. 1953; P. Basilewsly leg.; study code: DJ 0794; initially *C. basilewskyi* (unpublished); AMNH, IZC 00321234 • soldier, worker; Rukara; 1°50′ S, 30°28′ E; 4 Feb. 1953; P. Basilewsky leg.; study code: DJ 0791; initially *C. basilewskyi* (unpublished); AMNH, IZC 00321236 • soldier, worker; Rukara, near Mohasi lake; 1°50′ S, 30°27′ E; 5 Nov. 1953; P. Basilewsky leg.; study code: DJ 0020; initially *C. ugandensis* in RMCA; BE RMCA INS.Iso.059466.

TANZANIA • soldier, ♀ (alate); Bukoba; 1°20′ S, 31°48′ E; 1937; W.V. Harris leg.; study code: DJ U081; initially *C. ugandensis*; NHMUK 13672012 • soldier, worker, ♂ (alate); Geita–Uzinu road; 2°52′ S,

32°14′ E; Sep. 1937; W.V. Harris leg.; study code: DJ 0664; initially *C. ugandensis*; NHMUK 13672014 • soldier, ♀ (alate); Katoro; 3°0′ S, 31°55′ E; Sep. 1937; W.V. Harris leg.; study code: DJ U084; initially *C. ugandensis*; NHMUK 13672011 • soldier, worker, ♀ (alate); Mkwese; 5°38′ S, 34°49′ E; before 1959; P.B. Kemp leg.; study code: DJ 0667; initially *C. ugandensis*; NHMUK 13672013.

**Description**

*Isognathotermes ugandensis burundii* subsp. nov. is best characterised by its mitogenome sequence.

**Imago**

See the description of the imago of *I. ugandensis* (Fuller, 1923) with the particularity that, on average, the imago of *I. u. burundii* subsp. nov. is the second smallest of the four subspecies, best seen in a PCA ("ugbu" in Fig. 65, Table 17).

**Soldier**

See the description of the soldier of *Isognathotermes ugandensis* (Fuller, 1923).

**Worker**

See the description of the worker of *Isognathotermes ugandensis* (Fuller, 1923).

**Chorology – ecology**

*Isognathotermes ugandensis burundii* subsp. nov. was found in Burundi, Rwanda, and Tanzania at altitudes between 1200 and 1700 m (average = 1350 m). Its geographic distribution is linked with the central Zambezian miombo woodlands and the Victoria basin forest-savanna mosaic ecoregions.

**Molecular data**

Six mitogenomes of *I. ugandensis burundii* subsp. nov. are published alongside this work (GenBank accessions: see Supp. file 3 and 'Material examined').

Overall, *I. ugandensis burundii* subsp. nov. mitogenomes exhibited less than 1% dissimilarity with each other (see Supp. file 4), but 1.2% with *I. u. kenyae* subsp. nov. (DJ 0599).

***Isognathotermes ugandensis kenyae*** Josens & Deligne subsp. nov.
urn:lsid:zoobank.org:act:F149BC92-74B7-4ABE-8A1B-C277F33294EE
Figs 33, 65–66, 69

**Diagnosis**

This subspecies is best characterised by its mitogenome sequence.

Soldiers and workers do not allow this subspecies to be distinguished from the other three.

The imago is close to that of *I. u. malawii* subsp. nov. (but their geographical distributions are disjunct); it is, on average, the largest of the four subspecies (ugke, Fig. 65, Table 17) with the longest wings (IWgL = 18.9– 19.5 mm (vs 13.6–18.1 mm for two other subspecies, *I. u. malawii* is not yet available). It is also the subspecies that comes from the highest altitude (1500–2500 m, average = 2200 m); to date, all the samples have come from Kenya.

**Etymology**

The name *kenyae* (from Kenya) refers to the country of the type locality.

**Material examined**

Seven samples from five locations; all six old museum samples examined were initially labelled as *Cubitermes ugandensis*.

**Holotype**

KENYA • soldier; Mukuyuni; 0°1.612′ N, 36°0.303′ E; 13 Aug. 2015; J. Šobotnik leg.; study code: DJ 0599; GenBank no PQ679170 (mitogenome); BE RMCA INS.Iso.059469.

**Paratypes**

KENYA • soldier, worker; same data as for holotype; BE RMCA INS.Iso.059941.

**Other material examined**

"EAST AFRICA" (KENYA?) • worker, ♀ (alate); Molo?; 0°15′ S, 35°42′ E; 5 Jul. 1914; J. Sokolov (?) leg.; study code: DJ 0658; initially *C. ugandensis*; NHMUK.

KENYA • soldier; Thompson falls [= Nyahururu]; 0°2.75′ N, 36°22.25′ E; Mar. 1934; T. Anderson leg.; study code: DJ N132; initially *C. ugandensis*; AMNH • soldier, worker, ♀ (alate); Maji-Mazuri; 1°14′ S, 36°56′ E; 31 Mar. 1952; W.V. Harris leg.; study code: DJ 0666; initially *C. ugandensis*; NHMUK 13672002 • soldier, worker, ♂ (alate); Londiani–Makutano (road?); 0°2′ S, 36°20′ E; 18 Feb. 1954; R.M.C. Williams leg.; study code: DJ 0669; initially *C. ugandensis*; NHMUK 13672003 • soldier, worker, ♀ (alate); Londiani–Kisumu road; 0°15′ S, 35°30′ E; 19 Feb. 1954; R.M.C. Williams leg.; study code: DJ 0668; initially *C. ugandensis*; NHMUK 13672001 • soldier, ♀ (alate); Timboroa–Eldoret road; 0°9′ N, 35°28′ E; 12 May 1954; W.V. Harris leg.; study code: DJ U085; initially *C. ugandensis*; NHMUK 13672000.

**Description**

*Isognathotermes ugandensis kenyae* subsp. nov. is best characterised by its mitogenome sequence.

**Imago**

See the description of the imago of *I. ugandensis* (Fuller, 1923) with the particularity that the imago of *I. u. kenyae* subsp. nov. is clearly the largest of the four subspecies, best seen in a PCA ("ugke" in Fig. 65, Table 17). On average, the imago of this subspecies has the longest wings (IWgL = 18.9– 19.5 mm (vs 13.6–18.1 mm for two other subspecies, *I. u. malawii* subsp. nov. is not yet available).

**Soldier**

See the description of the soldier of *Isognathotermes ugandensis* (Fuller, 1923).

**Worker**

See the description of the worker of *Isognathotermes ugandensis* (Fuller, 1923).

**Chorology-ecology**

*Isognathotermes ugandensis kenyae* subsp. nov. is the subspecies found at the highest altitude (1500 to 2500 m, average = 2200 m) in the East African montane forest ecoregion of Kenya.

**Molecular data**

One sample of *I. ugandensis kenyae* subsp. nov. has recently been collected by one of us (JŠ) in Kenya, enabling its sequencing; it is published alongside this work (GenBank accessions: see Supp. file 3 and 'Material examined'). Its mitogenome exhibits 1.2% dissimilarity with *I. u. burundii* subsp. nov. samples (Supp. file 4).

***Isognathotermes ugandensis malawii*** Josens & Deligne subsp. nov.
urn:lsid:zoobank.org:act:025368E6-C9F7-46E7-88F5-7D7BE6A1DCAF
Figs 65–66, 69

**Diagnosis**

Soldiers and workers do not allow this subspecies to be distinguished from the other three.

The imago is close to that of *I. u. kenyae* subsp. nov. (but their geographical distributions are disjunct); it is, on average, the second largest of the four subspecies, best seen in a PCA ("ugma", Fig. 65); it is the subspecies with the greatest distance between the apical and the first marginal teeth (IMlAmD = 0.23–0.27 mm vs 0.20–0.25 mm for all three other subspecies, Table 17). It comes from a relatively high altitude (1460–1770 m, average = 1560 m), from Malawi and northern Zambia.

**Etymology**

The name *malawii* (from Malawi) refers to the country of the type locality.

**Material examined**

Eleven samples from eight locations; all old museum samples initially identified either as *Cubitermes minitabundus* (six samples) or *C. ugandensis* (five samples).

**Holotype**

MALAWI • soldier; Dowa-Lilongwe road; 13°39′ S, 33°51′ E; 13 Sep. 1953; W.A. Sands and W. Wilkinson leg.; study code: DJ 0699; initially *C. minitabundus*; NHMUK 13671919.

**Paratypes**

MALAWI • soldier, worker, ♀ (queen); same data as for holotype.

**Other material examined**

MALAWI • soldier, worker, ♀ (queen); Dedza; 14°22′ S, 34°19.5′ E; 4 Sep. 1953; W.A. Sands and W. Wilkinson leg.; study code: DJ 0688; initially *C. minitabundus*; NHMUK 13671917 • soldier, worker; Dedza; 14°23.5′ S, 34°18.5′ E; 2 Sep. 1953; W.A. Sands and W. Wilkinson leg.; study code: DJ 0698; initially *C. minitabundus*; NHMUK 13671918 • soldier, ♀ (queen); Dowa–Lilongwe road; 13°39′ S, 33°51′ E; 11 Sep. 1953; W.A. Sands and W. Wilkinson leg.; study code: DJ 0697; initially *C. minitabundus*; NHMUK 13671916 • soldier; Mzimba–Kasungu road; 12°16′ S, 33°38′ E; 18 Sep. 1953; W.A. Sands and W. Wilkinson leg.; study code: DJ U073; initially *C. ugandensis*; NHMUK 13672015 • soldier, worker; Nyika Plateau; 10°54′ S, 33°26′ E; 29 Sep. 1953; W.A. Sands and W. Wilkinson leg.; study code: DJ 0670; initially *C. ugandensis*; NHMUK 13672018 • soldier, worker; Nyika Plateau; 10°45′ S, 33°57′ E; 30 Sep. 1953; W.A. Sands and W. Wilkinson leg.; study code: DJ 0671; initially *C. ugandensis*; NHMUK 13672016 • soldier; Vipya Plateau, Ekwendeni; 11°23′ S, 33°54′ E; 20 Oct. 1953; W.A. Sands and W. Wilkinson leg.; study code: DJ U072; initially *C. ugandensis*; NHMUK 13672017.

ZAMBIA • soldier; Tunduma; 9°26′ S, 32°51′ E; 5 Aug. 1953; W.A. Sands and W. Wilkinson leg.; study code: DJ U080; initially *C. ugandensis*; NHMUK 13672009 • soldier, worker; Kasama–Mbala road; 10°2′ S, 31°15′ E; 23 Dec.1969; M.G. Bingham leg.; study code: DJ 0690; initially *C. minitabundus*; NHMUK 13671923 • soldier, worker; Mbala–Mpulungu road; 8°48′ S, 31°8′ E; 24 May 1970; J.R. Clover and Kistner leg.; study code: DJ 0689; initially *C. minitabundus*; NHMUK 13671924.

**Description**

**Imago**

See the description of the imago of *Isognathotermes ugandensis* (Fuller, 1923) with the particularity that the imago of *I. u. malawii* subsp. nov. is the second largest of the four subspecies, best seen in a PCA ("ugma" in Fig. 65, Table 17). This is the subspecies with the greatest distance between the apical and the first marginal teeth (IMlAmD = 0.23–0.27 mm vs 0.20–0.25 mm for all three other subspecies, Table 17).

**Soldier**

See the description of the soldier of *Isognathotermes ugandensis* (Fuller, 1923).

**Worker**

See the description of the worker of *Isognathotermes ugandensis* (Fuller, 1923).

**Chorology-ecology**

*Isognathotermes ugandensis malawii* subsp. nov. was found between altitudes of 1460 and 1770 m (average = 1560 m), in the central Zambezian miombo woodlands in Malawi and northern Zambia.

**Molecular data**

No genetic sequence is currently available.

***Isognathotermes zenkeri*** (Desneux, 1904)
Figs 26–31, 70, distribution map: Fig. 49; Table 18

*Termes Zenkeri* Desneux, 1904a: 148–149.

*Termes* (*Eutermes*) *Zenkeri* – Desneux 1904b: 46, pl. 2 fig. 12.
*Cubitermes* (*Termes*) *Zenkeri* – Wasmann 1911: 158.
*Mirotermes* (*Cubitermes*) *Zenkeri* – Sjöstedt 1913: 369, pl IX.
*Cubitermes Zenkeri* – Sjöstedt 1926: 236.
*Cubitermes zenkeri* – Snyder 1949: 166. — Bouillon & Vincke 1971: 269. — Ruelle 1975: 8. — Krishna *et al.* 2013: 1945. — Josens & Deligne 2019: 60–61.
*Isognathotermes zenkeri* – Hellemans *et al.* 2021: 233.

**Diagnosis**

The workers and soldiers of *I. zenkeri* are larger than those of the other species with a *fungifaber* EVA, but the imagines are almost indistinguishable from those of *I. severus* and *I. ugandensis*.

The worker has a *fungifaber* EVA; it is among the large-sized workers of the genus *Isognathotermes* (Fig. 30) with the largest apico-marginal distances in the genus (WMlAmD = 0.23–0.25 mm).

The soldier is among the large-sized soldiers of the genus *Isognathotermes* (Fig. 28); the mandibles are shorter than the head but longer than in other species of the genus (SMlL = 2.75–2.99 mm; SMlL/SHdL = 0.86–0.92), some soldiers of *I. bulbifrons* can have equally long mandibles but they have another EVA. Gulamentum with almost straight, parallel lateral edges, only slightly curved.

The imago is among the middle- to large-sized imagines of the genus *Isognathotermes* (Fig. 26) with the largest left and right apico-marginal distances; IMlAmD = 0.26–0.28 mm (Fig. 27); ocellus large, protruding and removed from eye by a distance shorter than 0.6 ocellus small diameter.

**Etymology**

This species was named in honour of G.A. Zenker who discovered this species and collected the type material.

**Material examined**

Five samples from one (?) location, all labelled as *Termes*, or *Eutermes*, or *Cubitermes zenkeri*.

**Syntypess of *Termes zenkeri* Desneux, 1904**

CAMEROON • soldier, worker, ♀ (alate); Bipindi? (3°5′ N, 10°24.5′ E); before 1904; G. Zenker leg.; study code: DJ 0283; initially *Termes zenkeri*; NHMM • soldier, worker, ♀ (alate); Cameroon, from Hill collection; [no date, no location]; G. Zenker (?) leg.; study code: DJ 0730; initially *Termes zenkeri*; AMNH • soldier, worker, ♀ (alate); Kamerun, from Holmgren collection; [no date, no location]; G. Zenker (?) leg.; study code: DJ 0731; initially *Termes zenkeri*; AMNH • soldier, worker, ♂ (alate); Bipindi (3°5′ N, 10°24.5′ E); 1903; G. Zenker leg.; study code: DJ 0962; initially *Eutermes zenkeri*; RBINS.

Krishna *et al.* (2013: 1945) mention that other type (sub)samples are deposited in NHRM, and in the Zoologisches Museum der Natur, Hamburg, Germany, not examined.

**Other material examined**

CAMEROON • soldier, worker, ♀ (alate), ♀ (queen); Bipindi? (3°5′ N, 10°24.5′ E); [no date]; G. Zenker leg.; study code: DJ 0321; initially *C. zenkeri*; AMNH. Five samples from one (?) location, all labelled as *Termes*, or *Eutermes*, or *Cubitermes zenkeri*.

**Historical review**

Desneux (1904a: 148–149) described this species under the name *Termes Zenkeri* (species name incorrectly published with a capital letter and only corrected in 1949). He provided a short description of alate imago, soldier, and worker along with a few measurements, mentioning some differences with *C. fungifaber*.

The species was later referred to under the name of *Termes* (*Eutermes*) *Zenkeri* by Desneux 1904b, *Cubitermes* (*Termes*) *Zenkeri* by Wasmann (1911: 158), *Mirotermes* (*Cubitermes*) *Zenkeri* by Holmgren (1912), and *Cubitermes Zenkeri* by Sjöstedt (1926: 236).

Sjöstedt (1926: 218–226) included the species in imagines' and soldiers' keys of *Cubitermes* species and inserted it in a "*Zenkeri*-Gruppe" of large *Cubitermes* species.

Snyder (1949: 166) catalogued *Cubitermes zenkeri* in the subfamily Termitinae while Krishna *et al.* (2013: 1945) housed it in the subfamily Cubitermitinae. Espousing the view of Ruelle (1975: 8) they considered *Cubitermes kemneri* as a junior synonym of *C. zenkeri*.

Bouillon & Vincke (1971: 269) described the enteric valve of *C. zenkeri* as belonging to the first of three types, the "simple type" without any spatula.

Josens & Deligne (2019: 39–42) placed this species within the *fungifaber* valve pattern group. Therefore, *C. zenkeri* cannot be the senior synonym of *C. kemneri* as the types of both species belong to different valve pattern groups, i.e., *fungifaber*- and *finitimus*-group respectively.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

This species is confusing: all the known samples seem to come from the same site (Bipindi, Cameroon) and the same collector (G. Zenker), and it has not been collected since, despite the numerous collecting campaigns that have been organised in Cameroon.

**Redescription**

**Imago**

Colour. **Head capsule**: well sclerotised, and very dark, C6–C7; fontanelle concolorous or almost so with head capsule. Postclypeus C5–C6, slightly paler than head capsule. Antennae C5, slightly paler than head capsule without any difference between proximal and distal articles. **Thorax**: pronotum C5–C6, as postclypeus, slightly paler than head capsule; meso- and metanotum C5–C6, concolorous with pronotum. **Legs** C4–C5; tibia concolorous with femur. Wings hyaline with brown to grey tinge (Cf3–Cf4), anterior veins darker. **Abdomen**: tergites C6. Sternites appreciably paler in middle (C3–C4) with both sides darker (C4–C6); posterior sternites darker (C4–C6) than anterior.

Setation. **Head capsule**, with some prominent setae set amongst a high density of short, fine setae forming a dense mat. Labrum and postclypeus with some prominent setae mixed with shorter ones. Antennae with some prominent setae, some more numerous smaller setae and, mainly distally on most articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: pronotum with prominent setae mainly on margins and shorter ones in middle; meso- and metanotum with some fine, pale setae, arranged in a medio-longitudinal strip, generally visible at 40–80×; some large setae sometimes present on metanotum. **Legs** very pilose, furnished (among numerous fine setae) with some stronger setae: 4–10 on the carina of fore coxa and 1–4 on the ventral side of fore coxa; tibia pilose fore, mid, and hind tibia furnished with 15–30 spines and bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively. **Abdomen**: tergites with many large and small setae. Sternites with long setae, erect or directed slightly forward, and many long and smaller setae directed backwards.

Structure (measurements in Table 18, Figs 26, 70). **Size**: the imagines of *I. zenkeri* are among the medium- to large-sized species of the genus *Isognathotermes* (Fig. 26) with the largest left and right apico-marginal distances (Fig. 27). **Head capsule**: compound eyes large and shortly oval; ocelli large, protruding and shortly to moderately oval, removed from eyes by a shorter distance than 0.6 ocellus small diameter; fontanelle generally a tiny round or elongate marking. Antennae: 16 articles on alate individuals, shortened by amputation by three articles in the queen. Labrum: cupola shaped, wider than long. **Left mandible** with apical tooth large sized in the genus and always more prominent than first marginal; marginal teeth three in number; second marginal appearing as an undulated edge, third marginal tooth with a blunt tip; only the apical tooth is acute in unworn specimens; premolar tooth partly hidden; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible** with apical tooth large sized in the genus and always more prominent than first marginal; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum appreciably wider than long and narrower than head width (including the eyes), straight to very weakly sellate with anterior lobe short and very slightly elevated. **Fore coxa** flanged ventrally resulting in a carina. **Wings**: R1 fused entirely with costal margin, sclerotised; Rs simple, sclerotised; M and Cu not or weakly sclerotised with 3–4 and 10–13 branches, respectively. **Gut** not studied.

**Soldier**

Colour. **Head capsule** C4–C6, darkened by age, with a smooth gradient from a darker frons to a paler back. Antennae and labrum approximately concolorous with head capsule. Mandibles dark (C7–C8) generally with an abrupt clearing on their bases (one palette level) which is generally the same colour as

frons. **Thorax** and legs paler than head capsule (C3–C5), darkened by age. **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** with few scattered setae; on frons a dense bunch of setae surrounds and overhangs fontanelle. Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of very fine, bent setae (visible only at high magnification, 50× or

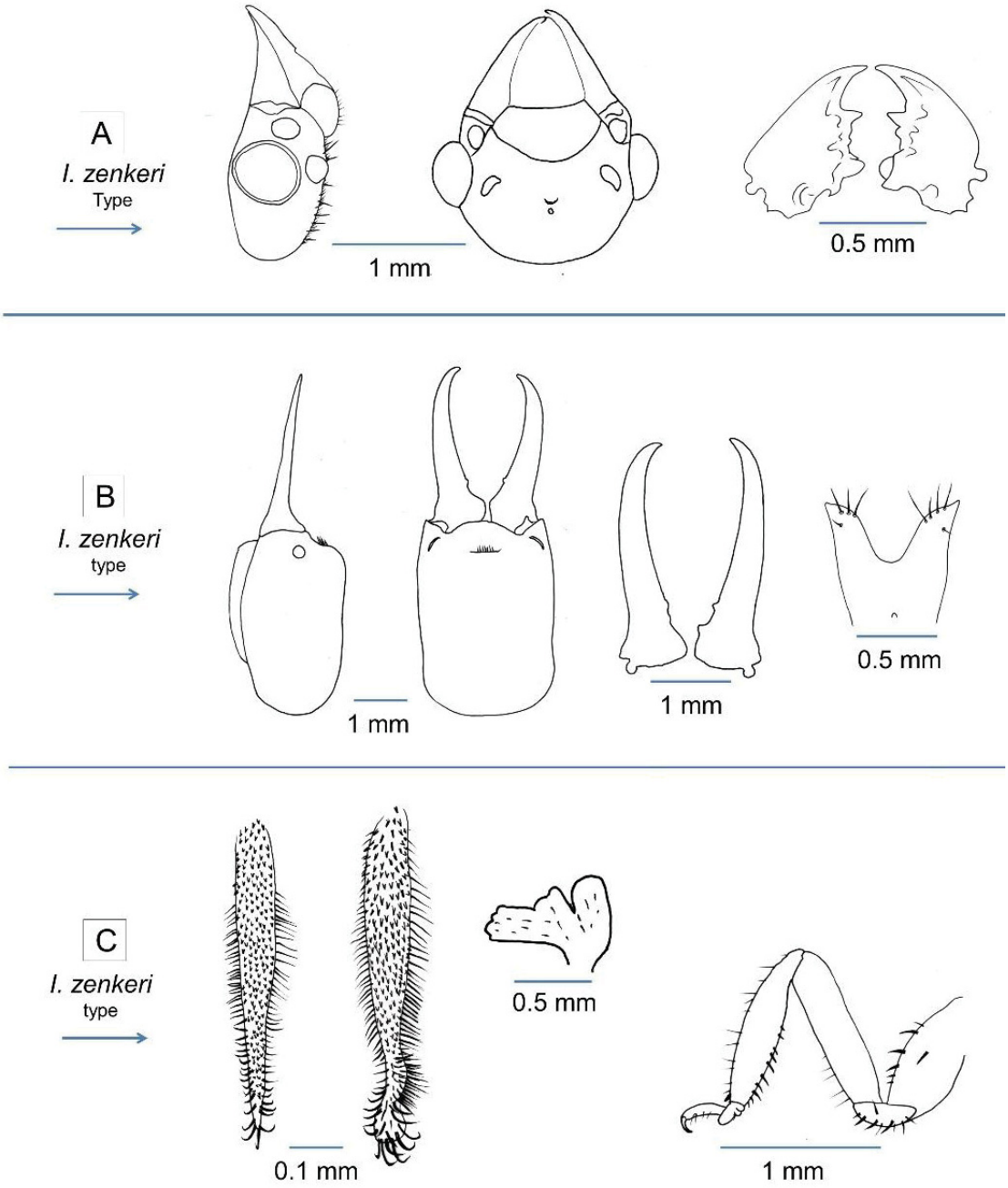


**Fig. 70.** *Isognathotermes zenkeri* (Desneux, 1904): imago, soldier, and worker. **A**. Lateral and dorsal views of the head capsule, and dorsal view of mandibles of an alate female from the type colony of *Termes zenkeri* Desneux, 1904 (DJ 0730). **B**. Lateral and dorsal views of the head capsule, ventral view of mandibles, and dorsal view of labrum of a soldier from the type colony. **C**. PC1s of soldier's and worker's enteric valves, caecum and foreleg of this worker from the type colony.

**Table 18.** *Isognathotermes zenkeri* (Desneux, 1904): ranges of significant measures in the three castes, in alphabetical orders of the "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Imagines (n = 6) | Raw measures (mm) | Eye: large diameter | IEy*D* | 0.49–0.53 | 0.52 |
| | | Head: width across the eyes | IHdW | 1.61–1.73 | 1.71 |
| | | Left mandible: A-m1 distance | IMlAmD | 0.26–0.28 | 0.28 |
| | | Ocellus: large diameter | IOc*D* | 0.21–0.23 | 0.22 |
| | | Postclypeus: width | IPcW | 0.78–0.86 | 0.84 |
| | | Pronotum: maximal width | IPnW | 1.53–1.65 | 1.59 |
| | | Hind tibia: length | IT3L | 1.45–2.08 | 2.03 |
| | | Wing: length (n= 3) | IWgL | 13.7–14.2 | 14.0 |
| | Index | Left apico-marginal index | IMlAmD/IMlmmD | 1.37–1.82 | 1.62 |
| Soldiers (n = 5) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.01–0.04 | 0.03 |
| | | Head: length | SHdL | 3.21–3.35 | 3.33 |
| | | Head: width | SHdW | 2.20–2.39 | 2.36 |
| | | Left mandible: lesser sagitta | SMlc | 0.21–0.26 | 0.23 |
| | | Left mandible: ventral length | SMlL | 2.75–2.99 | 2.96 |
| | | Hind tibia: length | ST3L | 1.70–1.92 | 1.84 |
| | Indices | Head elongation index | SHdL/SHdW | 1.39–1.46 | 1.41 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.08–0.08 | 0.08 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.92–1.14 | 1.01 |
| Workers (n = 5) | Raw measures (mm) | Head: width | WHdW | 1.17–1.31 | 1.25 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.23–0.25 | 0.24 |
| | | Left mandible: total length | WMlL | 0.64–0.69 | 0.66 |
| | | Hind tibia: length | WT3L | 1.38–1.48 | 1.42 |
| | | Valve: PC average length | WVP-AvL | 0.64–0.70 | 0.66 |
| | | Valve: PC average width | WVP-AvW | 0.09–0.10 | 0.09 |
| | | Valve: SC average length | WVS-AvL | 0.50–0.62 | 0.52 |
| | | Valve: SC average width | WVS-AvW | 0.27–0.42 | 0.29 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 6.39–8.27 | 7.40 |

* Abbreviations: see definitions in Material and methods.

more). **Labrum** always with 7–10 large setae on each lobe. **Thorax**: pro- and mesonotum with a small number of setae mainly located on margins. **Legs**: fore coxa bears at least one fine seta and 2–3 spines on carina and 0–1 spine on ventral side; trochanter with some strong lined-up setae, or with 5–6 spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively (the latter sometimes weakly developed) and a row of 9–14 spines along their shaft. **Abdomen**: tergites with some large setae, mainly on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 18; Figs 28, 70). **Size**: the soldiers of *I. zenkeri* are among the large-sized soldiers in the genus *Isognathotermes* (Fig. 29). **Head capsule**: always clearly sclerotised; appreciably longer than wide. **Dorsal view**: lateral sides mostly subparallel with a slight narrowing near

posterior third or fourth, from antennal sockets sides converge towards bases of mandibles; posterior side regularly convex or with a short straight part. Upper profile slightly concave; angle between extended mandibles and frons obtuse; frons with a slight anterior hump (Fig. 70). Gulamentum in ventral view with almost parallel sides, very weakly constricted in its posterior half; with sides of anterior part generally forming an acute widening or even a kind of ear on each side. Antennae: of 15 articles. **Labrum**: always deeply bifurcate and wider than long, with lyre-shaped sides; lobes angular, generally with fine, whitish, or translucent tips; anterior margin concave. **Mandibles**: sabre-like; inner edges smooth with one distinct but very small marginal tooth, near molar tooth on each mandible; mandibles shorter than head but the longest in relative value in the genus (85–90% of head length); entire surface of both mandibles smooth and glossy. Right mandible equally or slightly more curved than left. **Thorax**: pronotum sellate, as wide as about 60% of head width, with straight or indented anterior margin and posterior straight margin. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in second half of abdomen. **Caecum** always rather small, best seen in ventral view, near centre of abdomen, three-lobed. Arrangement of enteric valve cushions showing trilateral symmetry, the odd cushions being about 20% longer than the even cushions, generally without any crest.

**Worker**

Colour. **Head capsule** pale but darkened by age. Antennae: proximal articles pale (C2–C3), distal articles always one to two levels darker (C4–C5). **Thorax**, nota, and legs pale but darkened by age. **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect, scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50 × or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa always carinated, bearing one fine seta and furnished with 3–4 spines on carina and one on ventral side; fore trochanter with 6–7 spines, all except one lined up; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of 8–15 spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 18, Figs 30, 70). **Size**: the workers of *I. zenkeri* are part of the large-sized workers in the genus *Isognathotermes* (but with large overlapping on several other species: Fig. 30). **Head capsule**: weakly sclerotised (except mandibles). Antennae of 14 or 14.5 articles. Labrum: cupola shaped. **Left mandible**: apical tooth well developed, the largest in the genus, with a sharp tip when fresh; marginal teeth three in number, first marginal tooth well developed but with a blunt tip even when fresh, second marginal appearing as an undulated edge, third marginal tooth with a blunt tip; premolar tooth partly hidden underneath molar tooth; this latter bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed, the largest in the genus, with a sharp tip when fresh and sometimes with a wavy inner edge near the base; marginal teeth two in number; first marginal tooth well developed with a sharp tip when fresh; second marginal tooth smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate, as wide as 70–75% of head width. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in second half of abdomen. Arrangement of enteric valve cushions of the *fungifaber* pattern with triradial symmetry: the odd PCs, in their downstream part, are rather narrow and bear crests that are as high as or higher than they are wide, with long and strong bristles; 19–27 supporting bristles on each side of the odd PCs; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum with three lobes, either small or with one lobe somewhat extended forwards, visible in ventral view, near centre of abdomen,

**Chorology-ecology**

Only one collecting site is suspected in the Atlantic Equatorial coastal forest ecoregion of Cameroon (Fig. 49). Its precise origin is uncertain: in the original description, Desneux (1904a) only mentions that it came from "Kamerun" and that it was discovered by G. Zenker in a large nest (1 m high) at the base of a tall tree. Georg August Zenker was working at Jaunde [= Yaoundé] from 1889 to 1895 and was later domiciled at Bipindi from 1896 to 1922 (Wikipedia 2024a, German version), it is therefore believed that *Termes zenkeri* was found at Bipindi. However, this large and very characteristic species has never been found again despite numerous collections that were made in Cameroon, especially around Mbalmayo and in the region from Yaoundé to Kribi (including Bipindi). As Zenker collected in a vast region of Cameroon, it is quite possible that *I. zenkeri*, a species with a supposedly limited area, did not originate from Bipindi.

**Molecular data**

No genetic sequence is currently available.

## *Incertae sedis – species inquirenda*

This chapter contains a species already described (*I. congoensis* (Emerson, 1928)), but of uncertain matches; one potential species already named (*I. bredoi*) but not described (nomen nudum) and two potential species with unclear identity (a possible cryptic species of *I. planifrons* and an unknown species from Malawi). All these samples are classified "Incertae sedis" and "Species inquirenda".

### ***Isognathotermes bredoi*** (nomen nudum)

*Cubitermes bredoi* Mathur & Thapa, 1962 [nomen nudum]: 111.

*Cubitermes bredoi* – Krishna *et al*. 2013: 1915.

**Diagnosis**

The worker has a *fungifaber* EVA.

The PCA on soldiers' morphology places this sample at the intersection of the *severus* and *ugandensis* ellipses, and near the *acristatus* ellipse. However, the PCAs on workers' and soldiers' valves project this species onto the *fungifaber* ellipse. The enteric valve has poorly developed crests, which brings it closer to *I. acristatus* sp. nov. Therefore, this sample seems to be an intermediate between *I. ugandensis*, *I. fungifaber* and *I. acristatus*. This sample therefore deserves to be elevated to the rank of species, provided that other samples with the same characteristics can be found. Hence their provisional classification as *Incertae sedis*.

The imago is unknown.

**Etymology**

The name *Cubitermes bredoi* was given (not published) by A. E. Emerson in honour of Hans Bredo who collected the sample.

**Material examined**

Two subsamples from the same colony.

ZAMBIA (?) • soldier, worker; Swali; 8°45′ S, 29°20′ E; 25 May 1941; H. Bredo leg.; study code: DJ 0778; initially *C. bredoi* (unpublished); AMNH, IZC 00321243 • soldier, worker; Swali; 8°45′ S,

20°20′ E; 25 May 1941; H. Bredo leg.; study code: DJ 0779; initially *C. bredoi* (unpublished); AMNH, IZC 00321242.

**Historical review**

This putative species is known from a single nest sampled in 1941.

The sample has been named "*Cubitermes bredoi*" by A. Emerson in his unpublished "card catalog" but was not described. It was nevertheless quoted by Mathur & Thapa (1962), and was therefore mentioned as nomen nudum by Krishna *et al.* (1913: 1915) with an origin (Zimbabwe) which is likely incorrect.

This sample is not described here, its status remaining uncertain. We don't wish to describe a new species of which only one nest is known, and which could be an anomaly. Emerson got away with creating a new name, but he too did not describe a new species.

**Chorology-ecology**

The location (Swali or Suali) could not be found; it is assumed to be in Zambia, near the border with Katanga, DRC, where H. Bredo used to work and where there is a river bearing that name.

**Molecular data**

No genetic sequence is currently available.

***Isognathotermes congoensis*** (Emerson, 1928)
Figs 22, 28, 30–31, 36–37, distribution map: Fig. 38; Table 19

*Mirotermes* (*Cubitermes*) *congoensis* Emerson, 1928: 519–520, fig. 61.

*Cubitermes congoensis* – Snyder 1949: 158. — Krishna *et al.* 2013: 1918. — Josens & Deligne 2019: 60–61.
*Isognathotermes congoensis* – Hellemans *et al.* 2021: 233.

This species is suspected to be a junior synonym of *Isognathotermes bulbifrons*.

**Diagnosis**

The worker has a *finitimus* EVA and is among the smallest workers of the genus *Isognathotermes* (Fig. 30).

The soldier is among the smallest in the genus *Isognathotermes* (Fig. 28); the soldiers of *I. fungifaber* are sometimes as small but have a *fungifaber* EVA; the soldier of *I. phalloides* sp. nov. (also with a *finitimus* EVA) is sometime as small but has another, characteristic caecum.

The imago is unknown.

This species is also defined by its chorology: the two known samples come from forested regions up to about 200 km from the Atlantic coast (Fig. 38).

**Etymology**

The name *congoensis* (from Congo and the Latin desinence *-ensis*, 'from') clearly refers to the country of type locality ("Belgian Congo", now DRC).

**Material examined**

Three samples from two locations (probably from two colonies), all identified as *C. congoensis*.

**Table 19.** *Isognathotermes congoensis* (Emerson, 1928): ranges of significant measures in soldiers and workers (imagines are unknown), in alphabetical orders of the "Code" column.

| | | Variable * | Code * | Range | Type |
|---|---|---|---|---|---|
| Soldiers (n = 3) | Raw measures (mm) | Head: upper sagitta | SHdC | 0.01–0.06 | 0.03 |
| | | Head: length | SHdL | 2.35–2.52 | 2.49 |
| | | Head: width | SHdW | 1.74–1.79 | 1.78 |
| | | Left mandible: lesser sagitta | SMlc | 0.13–0.16 | 0.15 |
| | | Left mandible: ventral length | SMlL | 1.55–2.05 | 2.02 |
| | | Hind tibia: length | ST3L | 1.49–1.53 | 1.51 |
| | Indices | Head elongation index | SHdL/SHdW | 1.34–1.43 | 1.40 |
| | | Left mandible: apical curvature index | SMlc/SMlL | 0.06–0.10 | 0.07 |
| | | Mandibles: curvature symmetry | SMlc/SMrc | 0.76–1.38 | 0.87 |
| Workers (n = 3) | Raw measures (mm) | Head: width | WHdW | 1.06–1.08 | 1.07 |
| | | Left mandible: A-m1 distance | WMlAmD | 0.16–0.19 | 0.17 |
| | | Left mandible: total length | WMlL | 0.51–0.54 | 0.53 |
| | | Hind tibia: length | WT3L | 1.20–1.22 | 1.21 |
| | | Valve: PC average length | WVP-AvL | 0.55–0.58 | 0.57 |
| | | Valve: PC average width | WVP-AvW | 0.06–0.08 | 0.07 |
| | | Valve: SC average length | WVS-AvL | 0.43–0.46 | 0.45 |
| | | Valve: SC average width | WVS-AvW | 0.22–0.24 | 0.23 |
| | Index | Valve: odd PC elongation index | WVPOdd-Elg | 7.36–9.61 | 8.63 |

* Abbreviations: see definitions in Material and methods.

**Paratypes of *Cubitermes congoensis* Emerson, 1928**

DEMOCRATIC REPUBLIC OF THE CONGO • soldier, worker; Banana; 5°58′ S, 12°26′ E; Aug. 1915; Lang-Chapin leg.; study code: DJ 0299; initially *C. congoensis*; AMNH • soldier, worker; Banana; 6°1′ S, 12°25′ E; Aug. 1915; Lang-Chapin leg.; study code: DJ 0484; initially *C. congoensis*; PPRI, ISTM 5690.

Krishna *et al.* (2013: 1918) mention that the holotype is deposited in AMNH, not examined.

**Other material examined**

CAMEROON • soldier, worker; Mbalmayo; 3°31′ N, 11°30′ E; Mar. 1996; P. Eggleton *et al.* leg.; study code: DJ 0648; initially *C. congoensis*; NHMUK 13671845.

**Historical review**

Emerson (1928: 519–520) described this taxon under the name *Mirotermes* (*Cubitermes*) *congoensis*. He provided a description (text, measurements, and figure) of the soldier, mentioning differences with other species.

Snyder (1949: 158) catalogued this taxon under the name *Cubitermes congoensis* in the sub-family Termitinae and reported its known geographical distribution.

Krishna *et al.* (2013: 1918) housed *C. congoensis* in the sub-family Cubitermitinae.

Josens & Deligne (2019: 42–44) placed this taxon in the *finitimus* valve pattern group.

Hellemans *et al.* (2021: 233) placed this taxon in the restored genus *Isognathotermes*. The sample, however, could not be sequenced.

The validity of *Isognathotermes congoensis*, is puzzling: it has been found in two remote places: the type colony (DJ 0299 & DJ 0484) near the mouth of the Congo River, DRC, and another sample near Mbalmayo, Cameroon (DJ 0648). As explained in the chapter *bulbifrons*, four samples from incipient or very young colonies collected by N.M. Collins near Douala, Cameroon, were identified on the basis of their young queens as being *I. bulbifrons*; if the soldiers had been used instead, the resulting identification would have been *I. congoensis*. In the PCA on soldier morphology, those soldiers join the soldiers from *I. congoensis* colonies (ellipse labelled "c+b" in Fig. 22). Therefore, the two samples identified as *I. congoensis* might also be incipient colonies of *I. bulbifrons*. This hypothesis is supported by the absence of imagines. This name might become a synonym if it turns out that it was assigned to an incipient colony of *I. bulbifrons.*

**Redescription**

**Imago**

The imago is unknown.

**Soldier**

Colour. **Head capsule** C4–C5 becoming fader and darker (Cf5–Cf6) in long preserved samples. Gulamentum concolorous with head. Antennae and labrum paler (C3–C4) than head capsule, darker in long preserved samples. Mandibles dark (C7) with an abrupt clearing on their bases (C5–C6) which is same colour as frons. **Thorax**, nota and legs paler than head capsule (C2–C4), darker in long preserved samples. **Abdomen** grey owing to digestive bolus.

Setation. **Head capsule** with few scattered fine setae; on frons a scattered bunch of setae surrounds and overhangs fontanelle (but one sample with very few setae around fontanelle). Antennae with some prominent setae, more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Labrum** always with some large setae on lobes. **Thorax**: pro- and mesonotum with some setae mainly located on margins. **Legs**: fore coxa furnished with only one large seta on carina; fore trochanter generally with five or six aligned setae; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively; all tibiae furnished with a row of 4–6 spines. **Abdomen**: tergites with some large setae, mainly on their posterior margins. Sternites with long setae, erect or slightly directed forward, often coloured, and smaller setae directed backwards.

Structure (measurements in Table 19; Fig. 28). **Size**: the soldiers of *I. congoensis* are, on average, clearly among the smallest of the genus *Isognathotermes*; this is better seen in the soldiers' head lengths (Fig. 29). **Head capsule**: clearly sclerotised and appreciably longer than wide. **Dorsal view**: lateral sides subparallel, slightly convex to narrowed near posterior third or fourth, converging slightly towards anterior until antennal sockets; from antennal sockets sides converge towards bases of mandibles; posterior side rounded. **In profile**: clearly concave; frons with a faint frontal hump overhanging the fontanelle or no hump at all. Gulamentum in ventral view constricted in its posterior half, with sides of anterior part convex; rounded or with a slightly concave, posterior part from side view. Antennae: of 14.5 or 15 articles. **Labrum**: deeply bifurcate, with lyre-shaped sides; lobes angular or subtruncated, with fine, whitish, or translucent tips; anterior margin concave. **Mandibles**: sabre-like; inner edges smooth with one distinct but small marginal tooth, near molar tooth on each mandible; mandibles clearly shorter than head; entire surface of both mandibles smooth and glossy. Right mandible slightly more curved than left. **Thorax**: pronotum sellate, with entire anterior and posterior margins. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: enteric valve seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions showing trilateral symmetry: the odd cushions being somewhat longer and wider than the even cushions; the odd cushions with crests weakly developed; secondary cushions wide at the upstream end narrowing noticeably downstream with a homogeneous spine scattering. **Caecum** best seen in ventral view, near centre of abdomen, with three faint lobes.

**Worker**

The description of the worker is given here for the first time.

Colour. **Head capsule** pale (C2–C3) turning grey in long preserved samples. Antennae: proximal articles pale (C2), distal articles darker (C3). **Thorax**, nota and legs pale (C1–C2). **Abdomen** grey to red-brown owing to digestive bolus.

Setation. **Head capsule** and postclypeus with few, erect scattered setae. Labrum with few, robust scattered setae. Antennae with some prominent setae, some more numerous smaller setae and at distal extremity of distal articles, a bunch of fine, bent setae (visible only at high magnification, 50× or more). **Thorax**: nota with some scattered setae. **Legs**: fore coxa carinated, bearing one fine seta and furnished with 3–5 spines on carina and 0–2 on ventral side; fore trochanter with six spines; fore, mid, and hind tibia bearing 3, 2, 2 apical spurs and 0, 2, 0 subapical spurs respectively and a row of five to six spines. **Abdomen**: tergites with scattered setae. Sternites with long setae, erect or slightly directed forward, often coloured and smaller setae directed backwards.

Structure (measurements in Table 19, Fig. 30). **Size**: the workers of *I. congoensis* are, on average, among the smallest of the genus *Isognathotermes*: Fig. 30. **Head capsule** weakly sclerotised (except mandibles). Antennae 14–14.5 articles. Labrum: cupola shaped, wider than long. **Left mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth three in number, first marginal well developed but with a blunt tip even when fresh, second marginal faint (visible as an undulated edge and disappearing in worn mandibles), third marginal with a blunt tip; premolar tooth with its proximal end generally hidden under molar prominence; molar tooth bearing a rounded molar prominence dorsally and ending posteriorly in a tiny acute apophysis. **Right mandible**: apical tooth well developed with a sharp tip when fresh; marginal teeth two in number; first marginal well developed with a sharp tip when fresh; second marginal smaller and with a blunt tip even when fresh; molar tooth bearing a ventral rounded flange and ending posteriorly in a kind of heel. **Thorax**: pronotum sellate. **Fore coxa** flanged ventrally resulting in a sharp carina. **Gut**: **enteric valve** seating on left side, best seen in ventral view, situated in posterior half of abdomen. Arrangement of enteric valve cushions of the *finitimus* pattern with triradial symmetry: the odd PCs, in their downstream part, are wide and bear at that place a very high density of rather short bristles on a globular bulge; supporting bristles are numerous: 22–33 on each side of the odd PCs; secondary cushions are wide at the upstream end, narrowing noticeably downstream with a homogeneous spine scattering. Caecum rather small, visible in ventral view, near centre of abdomen, shortly lobed (small lobes, sometimes only sketched).

**Chorology-ecology**

The type of this species was collected near the mouth of the Congo River (Fig. 38) and despite several collecting sessions in the Kongo-Central Province by A. Bouillon and his collaborators and by other entomologists, no other samples of this species have been found there.

However, a sample from Cameroon matches *I. congoensis* morphology.

**Molecular data**

No genetic sequence is currently available.

***Isognathotermes*** aff. ***planifrons*** (Sjöstedt, 1924)
Fig. 33

**Diagnosis**

This species has a soldier of *planifrons* morphology; nothing distinguishes it from other *planifrons* but the mitogenome has a dissimilarity >2% with the other samples of *I. planifrons*. It is therefore considered a possible cryptic species. However, there is only one sample that has this genetic signature, so it has not yet been described.

**Material examined**

One sample.

CAMEROON • soldier; Nsimi; 3°10′ N, 11°58′ E; Nov. 1996; M. Harry leg.; study code: DJ P141; GenBank no PQ679213 (mitogenome); MNHN EP9827.

**Historical review**

This putative cryptic species is known from a single nest, sampled in 1996, by one of us (MyH) between Nsimi and Zoétélé, Cameroon.

**Molecular data**

The mitogenome of DJ P141 exhibits up to 2.70% dissimilarity with the other samples of *I. planifrons* (Supp. file 4).

Unknown ***Isognathotermes*** from Malawi
Fig. 33 (as '*I.* sp.')

**Diagnosis**

The worker has a *fungifaber* EVA and is difficult to distinguish from other species.

The soldier' morphology is similar to that of *I. ugandensis malawii* and *I. minitabundus*.

The imago is unknown.

However, this sample (DJ 0937) has a peculiar molecular signature, and as there is only one sample that has this genetic signature, it has therefore not yet been described.

**Material examined**

One sample.

MALAWI • soldier, worker; Nyika N.P.; 10°48.642′ S, 33°35.384′ E; 20 Jun. 2019; P. Stiblik leg.; study code: DJ 0937; GenBank no PV564649 (mitogenome); BE RMCA INS.Iso.059470.

**Historical review**

This unknown species was collected by one of us (PK) in Malawi.

**Molecular data**

This unidentified sample from Malawi was placed as sister to all species of the clade V (containing *similifinitimus* + *phallicaecalis* + *planifrons* + *phalloides* + *finitimus* + *minitabundus* + *ugandensis* + *severus*), and exhibited its highest similarity with *I. minitabundus* (96.5%).

## *Junior synonyms*

***Isognathotermes antennalis*** (Sjöstedt, 1924)
Figs 67–68, distribution map: Fig. 49

Revised herein as junior synonym of *I. ugandensis ugandensis*.

*Cubitermes antennalis* Sjöstedt, 1924c: 493.

*Cubitermes antennalis* – Sjöstedt 1926: 252–253. — Snyder 1949: 156.
*Mirotermes* (*Cubitermes*) *antennalis* – Emerson 1928: 513–515, fig. 57.
*Cubitermes ugandensis* – Williams 1966: 107–108. — Krishna *et al*. 2013: 1943. — Josens & Deligne 2019: 62.
*Isognathotermes ugandensis* – Hellemans *et al.* 2021: 233.

**Etymology**

The name *antennalis* probably refers to the 14-segmented antennae of the soldier (instead of 15 in other species), underlined by Sjöstedt (1924c: 493) in the original description.

**Historical review**

The soldier of *Cubitermes antennalis* was briefly described by Sjöstedt (1924c: 493), mentioning that it is close to C*ubitermes severus* Silvestri, 1914, but with antennae of 14 articles. Two years later he provided more detailed descriptions of all castes (Sjöstedt 1926: 252–253), he included *C. antennalis* in imagines' and soldiers' keys of *Cubitermes* species and inserted it in a "*bulbifrons*-Gruppe" of species with an upwards humped frons (Sjöstedt 1926: 218–226).

Emerson (1928: 513–515) referred to this species under the name *Mirotermes* (*Cubitermes*) *antennalis* and provided further descriptions of all castes on material collected by Lang-Chapin in the Garamba National Park (Haut-Uele province, DRC) but mentioned "antennae with 14 or 15 segments".

Snyder (1949: 156) catalogued *Cubitermes antennalis* in the sub-family Termitinae.

Williams (1966: 107–108) considered that *Cubitermes antennalis* Sjöstedt, 1924 was a synonym of *Cubitermes ugandensis* Fuller, 1923, since the syntype soldiers of the former fell well within the range of variation shown by the very large amount of material of the latter.

Krishna *et al*. (2013: 1943) housed *Cubitermes antennalis* in the sub-family Cubitermitinae, as a junior synonym of *C. ugandensis*. Josens & Deligne (2019: 62) placed this species within the *fungifaber* valve pattern group and echoed the opinion of Williams, considering *C. antennalis* as a junior synonym of *C. ugandensis*. Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

In this study, we relate *I. antennalis* to the subspecies *I. u. ugandensis*.

Two syntype subsamples have been examined (see *I. ugandensis*, DJ 0013 and DJ 0031). Krishna *et al.* (2013: 1943) mention that another subsample is deposited in NHRM (not examined).

### ***Isognathotermes banksi*** (Emerson, 1928)
Figs 43–44; Table 6

Revised herein as junior synonym of *I. fungifaber*.

*Mirotermes* (*Cubitermes*) *banksi* Emerson, 1928: 522–523, fig. 63.

*Cubitermes banksi* – Snyder 1949: 156. – Krishna *et al.* 2013: 1913.
*Cubitermes fungifaber* – Ruelle 1992: 501. — Josens & Deligne 2019: 60.
*Isognathotermes fungifaber* – Hellemans *et al.* 2021: 233.

**Etymology**

In the original description, Emerson (1928: 522–523) stated: "I have named the species in honor of Dr. Nathan Banks, the authority on the termites of the United States and the Neotropical region."

**Historical review**

Emerson (1928) described this species under the name *Mirotermes* (*Cubitermes*) *banksi* in the family Termitidae. He provided a description, biometrical data and figures of imago and soldier, together with a much shorter description of the worker. He noted several morphological differences between imago and soldier of the new species and those already described among which *C. fungifaber.* However, he did not compare with *C. comstocki* or *C. schmidti*.

Snyder (1949: 156) catalogued *Cubitermes banksi* in the sub-family Termitinae.

This is one of the species that Ruelle (1992: 501) called "forgotten species".

Krishna *et al.* (2013: 1913) housed this species in the sub-family Cubitermitinae. According to them, Emerson wrote in his unpublished "card catalog" that *C. banksi* should be considered as a junior synonym of *C. fungifaber*. This latter opinion of Emerson had already been reported by Ruelle (1992: 501). Synonymy of the two species is compatible with their enteric valve morphology, as both species belong to the same *fungifaber* valve pattern group (Josens & Deligne 2019: 39–42). However, *I. banksi*, along with *I. comstocki* and *I. schmidti* are rather small in comparison with most *I. fungifaber* samples (see Table 6). To clarify this possible synonymy, one of us (PA) went and collected new samples at Bipindi, Cameroon (the type locality of *Cubitermes banksi* as well as of *C. comstocki* and *C. schmidti*), and at Mbongé, Cameroon (one of the type localities of *C. fungifaber*). Indeed, some of the samples he collected, especially at Bipindi, were very small and might previously have been identified as *I. banksi*, *I. comstocki*, or *I. schmidti*. Subsequent *COII* and *28S* sequences placed all these samples in one single "*I. fungifaber* clade" (Hellemans *et al.* 2021). Therefore, *I. banksi* (Emerson, 1928) is confirmed as a junior synonym of *I. fungifaber* (Sjöstedt, 1896).

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

Two subsamples have been examined (see *Isognathotermes fungifaber*, DJ 0097 and DJ 0287). Krishna *et al.* (2013: 1943) mention that other subsamples are deposited in UMMZ: holotype (soldier) and morphotype (winged imago), not examined.

### ***Isognathotermes comstocki*** (Emerson, 1928)
Figs 43–44; Table 6

Revised herein as junior synonym of *I. fungifaber*.

*Mirotermes* (*Cubitermes*) *comstocki* Emerson, 1928: 525, fig. 64.

*Cubitermes comstocki* – Snyder 1949: 158. — Krishna *et al.* 2013: 1918.
*Cubitermes fungifaber* – Ruelle 1992: 501.— Josens & Deligne 2019: 60.
*Isognathotermes fungifaber* – Hellemans *et al.* 2021: 233.

**Etymology**

In the original description, Emerson (1928: 525) stated: "I have named the species in honor of Prof. J.H. Comstock, to whom I owe a great deal of my enthusiasm for the study of insects."

**Historical review**

Emerson (1928: 523–525) described this species under the name *Mirotermes* (*Cubitermes*) *comstocki*. He provided a description (with measurements and figures) of queen and soldier, mentioning differences with other species, among which *M.* (*C.*) *fungifaber.*

Snyder (1949: 158) catalogued *C. comstocki* in the sub-family Termitinae and reported its known geographical distribution.

This is one of the species that Ruelle (1992: 501) called "forgotten species".

Krishna *et al.* (2013: 1918) housed *C. comstocki* in the subfamily Cubitermitinae. They reported that Emerson (in his unpublished "card catalog") considered *C. comstocki* as a junior synonym of *C. fungifaber*. This latter opinion of Emerson was also reported by Ruelle (1992: 501).

Synonymy of the two species is compatible with their enteric valve morphology, as both species belong to the same *fungifaber* valve pattern group (Josens & Deligne 2019: 39–42).

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

Three subsamples have been examined (see *Isognathotermes fungifaber*, DJ 0121, DJ 0273, and DJ 0278). Krishna *et al.* (2013: 1943) mention that other subsamples are deposited in UMMZ: holotype (soldier) and morphotype (queen), not examined.

*Isognathotermes comstocki*, along with *I. banksi* and *I. schmidti* are rather small in comparison with *I. fungifaber* (see Table 6). As already explained for *I. banksi*, new material was collected by one of us (PA) and sequenced (Hellemans *et al.* 2021: 233) with the conclusion that the four above species belong to the same clade. Therefore, *I. comstocki* (Emerson, 1928) is confirmed as a junior synonym of *I. fungifaber* (Sjöstedt, 1896).

***Isognathotermes fungifaber*** var. ***elongata*** (Sjöstedt, 1924)
Figs 58–59

Revised herein as junior synonym of *I. planifrons*.

*Cubitermes fungifaber* var. *elongata* Sjöstedt, 1924b: 256.

*Cubitermes fungifaber* var. *elongata* – Sjöstedt 1926: 221–225. — Snyder 1949: 159. — Josens & Deligne 2019: 42–44 (invalid name).
*Cubitermes fungifaber* – Krishna *et al*. 2013: 1923.
*Isognathotermes planifrons* (suspected synonymy) – Hellemans *et al.* 2021: 233.

Junior synonym of *Isognathotermes planifrons* (Sjöstedt, 1924). **Syn. nov.**

**Etymology**

The epithet *elongata* from the Latin *elongatus* (elongated) refers to the soldier's head, longer than in *I. fungifaber*.

**Historical review**

Sjöstedt (1924b: 256) very briefly described the soldier of this taxon under the name *Cubitermes fungifaber* var. *elongata*, mentioning that it had a longer head than the soldier of the main form.

Two years later he included this taxon in his soldier's key of *Cubitermes* species (Sjöstedt 1926: 221–225).

Snyder (1949: 159) catalogued this taxon under the name *Cubitermes fungifaber* var. *elongata* in the sub-family Termitinae and reported its known geographical distribution.

According to Krishna *et al.* (2013: 1923), Emerson wrote in his unpublished "card catalog" that the subspecies *C. fungifaber elongata* was invalid and proposed that this subspecies became a junior synonym of *C. fungifaber*. However, this synonymy can no longer be accepted because the types of both taxa belong to different valve pattern groups, i.e., *finitimus* and *fungifaber* groups respectively (Josens & Deligne 2019: 42–44).

Among the museum material identified as *Cubitermes fungifaber* var. *elongata*, the syntype morphology and EVA agree well with *Cubitermes planifrons* described in the same paper (Sjöstedt 1924b: 255–256). Other samples from the AMNH and bearing the same name are also misidentified and belong to either *I. fungifaber* or *I. severus*. Other samples from the RMCA belong to *I. phalloides* sp. nov.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

One subsample has been examined (see *Isognathotermes fungifaber*, DJ 0270). Krishna *et al.* (2013: 1943) mention that other subsamples are deposited in UMMZ: holotype (soldier) and morphotype (queen), not examined.

Given its EVA and morphology and since it was collected in the same type of ecosystem, *Cubitermes fungifaber* var. *elongata* (Sjöstedt, 1924) is from now on considered a junior synonym of *Isognathotermes planifrons* (Sjöstedt, 1924).

### ***Isognathotermes gaigei*** (Emerson, 1928)
Figs 58–59

Revised herein as junior synonym of *I. planifrons*.

*Mirotermes* (*Cubitermes*) *gaigei* Emerson, 1928: 516–517, fig. 59.

*Cubitermes gaigei* – Snyder 1949: 159. – Ruelle 1992: 501. — Krishna *et al.* 2013: 1923. — Josens & Deligne 2019: 60.
*Isognathotermes gaigei* – Hellemans *et al.* 2021: 233.

Junior synonym of *Isognathotermes planifrons* (Sjöstedt, 1924). **Syn. nov.**

#### Etymology

In the original description, Emerson (1928: 517) stated: "I have named the species in honor of Dr F. M. Gaige, through whose courtesy I was allowed to study the Cameroon collections included in this report."

#### Historical review

Emerson (1928: 516–517) described this species under the name *Mirotermes* (*Cubitermes*) *gaigei*. He provided a description (with measurements and figures) of soldier together with a few measurements of the worker. He considered that the species was very close to *C. loubetsiensis*, and a little larger than *C. fungifaber*; he mentioned some differences with other species.

Snyder (1949: 159) catalogued *C. gaigei* in the sub-family Termitinae.

This is one of the species that Ruelle (1992: 501) called "forgotten species".

Krishna *et al.* (2013: 1923) housed *C. gaigei* in the sub-family Cubitermitinae.

Josens & Deligne (2019: 42–44) placed this species within the *finitimus* valve pattern group.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

Two subsamples have been examined (see *Isognathotermes planifrons*, DJ 0274 and DJ 0288). Krishna *et al.* (2013: 1923) mention that another subsample is deposited in UMMZ: holotype (soldier), not examined.

*Isonathotermes gaigei* has a morphology that matches well that of *I. planifrons* and was collected in the same type of ecosystem; therefore, *I. gaigei* (Emerson, 1928) is from now on considered a junior synonym of *Isognathotermes planifrons* (Sjöstedt, 1924).

### ***Isognathotermes gibbifrons*** (Sjöstedt, 1924)
Figs 35–37

Revised herein as junior synonym of *I. bulbifrons*.

*Cubitermes gibbifrons* Sjöstedt, 1924b: 255.

*Cubitermes gibbifrons* – Sjöstedt 1926: 249–250. — Snyder 1949: 160. — Ruelle 1992: 500. — Bouillon & Vincke 1971: 269. — Krishna *et al.* 2013: 1923. — Josens & Deligne 2019: 60.
*Isognathotermes gibbifrons* – Hellemans *et al.* 2021: 233.

Junior synonym of *Isognathotermes bulbifrons* (Sjöstedt, 1924). **Syn. nov**.

**Etymology**

The epithet *gibbifrons* from the Latin *gibber* (humped) and *frons* (forehead) refers to the upwards humped frons of the soldier.

**Historical review**

Sjöstedt (1924b: 255) briefly described the soldier of this species under the name *Cubitermes gibbifrons*, mentioning that its soldier is close to the soldier of *C. heghi* but smaller.

Two years later Sjöstedt (1926: 249–250) provided a first description of the alate imago and worker together with additional information on soldier. He included (1926: 218–225) *Cubitermes gibbifrons* in the imagines' and soldiers' keys of *Cubitermes* species and inserted it in a "*bulbifrons*-Gruppe" of species with an upwards humped soldier's frons.

Snyder (1949: 160) catalogued this species under the name *Cubitermes gibbifrons* in the sub-family Termitinae and reported its known geographical distribution.

Bouillon & Vincke (1971: 269) described the enteric valve of *C. gibbifrons* as belonging to the first of three types, the "simple type" without any spatula.

This is one of the species that Ruelle (1992: 500) called "forgotten species".

Krishna *et al.* (2013: 1923) housed *Cubitermes gibbifrons* in the sub-family Cubitermitinae.

Josens & Deligne (2019: 42–44) placed this species within the *finitimus* valve pattern group.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

However, sequencing of the mitogenomes, despite the difference in size, confirmed synonymy with *I. bulbifrons*, a synonymy that had been suspected by the fact that samples of *I. bulbifrons* and *I. gibbifrons* had been collected in the same locations.

***Isognathotermes heghi*** (Sjöstedt, 1924)
Figs 36–37

Revised herein as junior synonym of *I. bulbifrons*.

*Cubitermes heghi* Sjöstedt, 1924b: 255.

*Cubitermes heghi* – Sjöstedt 1926: 249, table 9 k1–k3. — Snyder 1949: 160. — Ruelle 1992: 500.
*Mirotermes* (*Cubitermes*) *heghi* – Emerson 1928: 511–513, fig. 56.
*Cubitermes bulbifrons* – Ruelle 1975: 7. — Krishna *et al.* 2013: 1917. — Josens & Deligne 2019: 60.
*Isognathotermes bulbifrons* – Hellemans *et al.* 2021: 233.

Junior synonym of *Isognathotermes bulbifrons* (Sjöstedt, 1924).

**Etymology**

In the original description, Sjöstedt (1924b: 255) stated: "This species is named in honour of Mr E. Hegh, attached to the Belgian Ministry of Colonies and author of the beautiful and well-researched summary work '*Les Termites*'".

**Historical review**

Sjöstedt (1924b: 255) briefly described the soldier of this species under the name *Cubitermes heghi*. Two years later he provided a more detailed description of soldier and a first description of worker (Sjöstedt 1926: 249). He included *Cubitermes heghi* in his soldiers' key of *Cubitermes* species (1926: 221–226) and inserted it in a "*bulbifrons*-Gruppe" of species with an upwards humped soldier's frons.

Emerson (1928: 511–513) referred to this species under the name *Mirotermes* (*Cubitermes*) *heghi* and provided a redescription (with figures) of the soldier; he noted that the soldiers of *M.* (*C.*) *heghi* and of *M* (*C*) *bulbifrons* were similar to each other but that the imagines were very different. However, the imago described by Emerson was misidentified and belonged to *Cubitermes* (now *Polyspathotermes*) *sulcifrons*, characterized by a large fontanelle.

Snyder (1949: 160) catalogued this species under the name *Cubitermes heghi* and housed it in the sub-family Termitinae.

Ruelle (1975: 7) considered *C. bulbifrons* as senior synonym of *C. heghi*; however, later, Ruelle (1992: 500) gave precedence to *C. heghi* over *C. bulbifrons*.

Krishna *et al.* (2013: 1916) housed *C. bulbifrons* in the sub-family Cubitermitinae. Espousing the view of Ruelle 1975 but contesting the reversal of precedence proposed by Ruelle 1992, they considered this species as the senior synonym of *C. heghi*.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

One subsample has been examined (see *Isognathotermes bulbifrons*, DJ 0290). Krishna *et al.* (2013: 1917) mention that other paratype subsamples are deposited in PPRI (not examined) and IEAP; however, the material that was lent by this latter museum did not contain any *Cubitermes heghi* sample.

Synonymy of both species is compatible with their enteric valve morphology, as both species belong to the same *finitimus* valve pattern group (Josens & Deligne 2019: 42–44). Their morphology also supports synonymy. Following Ruelle (1975) and Krishna *et al.* (2013), *I. heghi* is therefore considered a junior synonym of *Isognathotermes bulbifrons* (Sjöstedt, 1924).

***Isognathotermes kemneri*** (Emerson, 1928)
Figs 36–37

Revised herein as junior synonym of *I. bulbifrons*.

*Mirotermes* (*Cubitermes*) *kemneri* Emerson, 1928: 509, fig. 54.

*Cubitermes kemneri* – Snyder 1949: 161.
*Cubitermes zenkeri* – Ruelle 1975: 8; 1992: 501. — Krishna *et al.* 2013: 1945. — Josens & Deligne 2019: 42–44, 60 (incorrect synonym of *C. zenkeri*).
*Isognathotermes kemneri* – Hellemans *et al.* 2021: 233.

Junior synonym of *Isognathotermes bulbifrons* (Sjöstedt, 1924). **Syn. nov.**

**Etymology**

In the original description, Emerson (1928: 509) stated: "I take pleasure in naming this species in honor of Dr. N. Kemner, who has done such valuable work on oriental termites and termitophiles."

**Historical review**

Emerson (1928: 509) described this species under the name *Mirotermes* (*Cubitermes*) *kemneri*. He provided description and measurements of the soldier, noting that it is very close to *Cubitermes heghi.*

Snyder (1949: 161) catalogued this species under the name *C. kemneri* and housed it in the sub-family Termitinae.

Ruelle (1975: 8), on the advice of Emerson (*in litteris*), proposed *C. kemneri* as a junior synonym of *C. zenkeri*. This is one of the species that Ruelle (1992: 501) called "forgotten species".

Krishna *et al.* (2013: 1945) housed *C. kemneri* in the sub-family Cubitermitinae. Espousing the view of Ruelle 1975 they considered this species as a junior synonym of *C. zenkeri*.

However, *C. kemneri* cannot be synonymized with *C. zenkeri* because the types of both species have different EVAs, i.e., of the *finitimus* and *fungifaber* groups respectively (Josens & Deligne 2019: 42–44).

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

One type subsample has been examined (see *Isognathotermes bulbifrons*, DJ 0297). Krishna *et al.* (2013: 1945) mention that other subsamples are deposited in UMMZ: holotype (soldier), and a paratype subsample in PPRI (not examined).

Only two samples in the museum collections bore the name "*C. kemneri*": the type sample and a misidentified sample (presently assigned to *I. fungifaber*). Our morphology study (this article) shows that the type matches well *I. bulbifrons*. Therefore, *I. kemneri* (Emerson, 1928) is from now on considered a junior synonym of *Isognathotermes bulbifrons* (Sjöstedt, 1924).

***Isognathotermes loubetsiensis*** (Sjöstedt, 1924)
Fig. 58

Revised herein as junior synonym of *I. planifrons*.

*Cubitermes loubetsiensis* Sjöstedt, 1924c: 493.

*Cubitermes loubetsiensis* – Sjöstedt 1926: 246–247. — Snyder 1949: 161. — Krishna *et al.* 2013: 1926.
*Mirotermes* (*Cubitermes*) *loubetsiensis* – Emerson 1928: 515–516, text-fig. 58, pl. XXX.
*Cubitermes finitimus* – Josens & Deligne 2019: 60.
*Isognathotermes finitimus* – Hellemans *et al.* 2021: 233.

Junior synonym of *Isognathotermes planifrons* (Sjöstedt, 1924). **Syn. nov.**

**Etymology**

The epithet *loubetsiensis* (from Loubetsi and Latin suffix *-ensis*, from) refers to the type locality (Loubetsi, Republic of Congo).

**Historical review**

Sjöstedt (1924c: 493) briefly described the soldier of this species under the name *Cubitermes loubetsiensis*, mentioning that it is close to the soldier of *C. subarquatus*.

Two years later, he provided a first description and some measurements of imago and worker (Sjöstedt 1926: 246–247). He included (1926: 218–226) this species in imagines' and soldiers' keys of *Cubitermes* species and inserted it in a "*fungifaber*-Gruppe" of species with a not humped soldier's frons.

Emerson (1928: 515–516) re-described the species under the name *Mirotermes* (*Cubitermes*) *loubetsiensis* based on specimens collected at Medje (DRC, Haut-Uele Province). He provided a redescription of queen and soldier together with some measurements of worker. However, these specimens were misidentified (Krishna *et al.* 2013: 1926); they are presently assigned to *I. finitimus*.

Snyder (1949: 161) catalogued this species under the name *Cubitermes loubetsiensis* and housed it in the sub-family Termitinae.

Krishna *et al.* (2013: 1926) housed *Cubitermes loubetsiensis* in the sub-family Cubitermitinae. They reported that Emerson (in his unpublished "card catalog") considered *C. loubetsiensis* as a junior synonym of *C. finitimus*. Synonymy of the two species is compatible with their EVAs, as Josens & Deligne (2019: 42–44) placed this species within the *finitimus* valve pattern group. Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

Two type subsamples have been examined, both limited to the soldier caste (see *Isognathotermes planifrons*, DJ 0281 and DJ 0611). Only four samples in the museum collections bore the name "*C. loubetsiensis*": the type samples and two misidentified samples (presently assigned to *I. finitimus*). Our morphology study (this article) shows that the type matches well *I. planifrons*. Therefore, *I. loubetsiensis* (Sjöstedt, 1924) is from now on considered a junior synonym of *Isognathotermes planifrons* (Sjöstedt, 1924).

***Isognathotermes modestior*** (Silvestri, 1914)
Figs 28, 30–31, 61–63, distribution map: Fig. 45

Revised herein as junior synonym of *I. severus*.

*Cubitermes severus* var. *modestior* Silvestri, 1914: 93–94, fig. LV.

*Cubitermes modestior* – Sjöstedt 1926: 238–239. — Snyder 1949: 161. — Krishna *et al.* 2013: 1927. — Josens & Deligne 2019: 60.
*Isognathotermes modestior* – Hellemans *et al.* 2021: 233.

Junior synonym of *Isognathotermes severus* (Silvestri, 1914). **Syn. nov.**

**Etymology**

The epithet *modestior* means 'smaller' in Latin. It referred to the smaller size of the variety *C. severus modestior* when compared to the main form, as underlined by Silvestri in the original description.

**Historical review**

Silvestri (1914: 93–94) described this taxon under the name *Cubitermes severus* var. *modestior*; it is known from a single nest. He provided a short description of imago, soldier, and worker together with measurements and figures, mentioning that the imagines are like the typical form (= *Cubitermes severus*), and indeed they are among the smallest individuals of the other *I. severus* imagines but also that the soldiers and workers are smaller than the main form.

Sjöstedt (1926: 238–239) considered that this taxon deserved to be elevated to the species level. He referred to it under the name *Cubitermes modestior*, housed it in the sub-family Termitinae, and included it in the "*glebae*-Gruppe" of small *Cubitermes* species.

Snyder (1949: 161) catalogued this species under the name *C. modestior* and housed it in the sub-family Termitinae.

Krishna *et al.* (2013: 1927) referred to this species under the name *C. modestior* and housed it in the sub-family Cubitermitinae.

Josens & Deligne (2019: 39–42) placed this species within the *fungifaber* valve pattern group.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

Two type subsamples have been examined (see *Isognathotermes severus*, DJ 0294 and DJ 0341).

Krishna *et al.* (2013: 1927) mention that another subsample is deposited in PPRI (not examined).

Since the type material of *I. modestior* (Silvestri, 1914) comes from a single nest and is included in the smaller specimens of *I. severus* (from other regions), it is from now on considered a junior synonym of *Isognathotermes severus* (Silvestri, 1914).

***Isognathotermes schmidti*** (Emerson, 1928)
Figs 43–44; Table 6

Revised herein as junior synonym of *I. fungifaber*.

*Cubitermes* (*Mirotermes*) *schmidti* Emerson, 1928: 520–521, fig. 62.

*Cubitermes schmidti* – Snyder 1949: 163. — Krishna *et al.* 2013: 1935.
*Cubitermes fungifaber* – Ruelle 1992: 501. — Josens & Deligne 2019: 61.
*Isognathotermes fungifaber* – Hellemans *et al.* 2021: 233.

Junior synonym of *Isognathotermes fungifaber* (Sjöstedt, 1896).

**Etymology**

In the original description, Emerson (1928: 521) stated: "I have named the species in honor of Mr. Karl P. Schmidt, to whom I owe my first introduction to termites."

**Historical review**

Emerson (1928: 520–521) described this species under the name *Cubitermes* (*Mirotermes*) *schmidti* in the family Termitidae. He provided a description, biometrical data and a figure of imago and soldier, together with a few measurements of worker.

Snyder (1949: 163) catalogued *C. schmidti* in the sub-family Termitinae.

This is one of the species that Ruelle (1992: 501) called "forgotten species".

Krishna *et al.* (2013: 1935) referred to this species under the name *C. schmidti* and housed it in the sub-family Cubitermitinae. They reported that Emerson (in his unpublished "card catalog") considered *C. schmidti* a junior synonym of *C. fungifaber*. This latter opinion of Emerson is also reported by Ruelle (1992: 501). Synonymy of the two species is compatible with their enteric valve morphology, as Josens & Deligne (2019: 39–42) placed *C. schmidti* within the *fungifaber* valve pattern group.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

Two type samples have been examined (see *Isognathotermes fungifaber*, DJ 0124 and DJ 0275).

*Isognathotermes schmidti*, along with *I. banksi* and *I. comstocki* are rather small in comparison with *I. fungifaber* (see Table 6). As already explained for *I. banksi*, new material was collected by one of us (PA) and sequenced (Hellemans *et al.* 2021) with the conclusion that the four above species belong to the same clade. Therefore, *I. schmidti* (Emerson, 1928) is confirmed as a junior synonym of *I. fungifaber* (Sjöstedt, 1896).

### ***Isognathotermes silvestrii*** (Sjöstedt, 1925)
Figs 62–63

Revised herein as junior synonym of *I. severus*.

*Cubitermes Silvestrii* Sjöstedt, 1925: 54.

*Cubitermes silvestrii* – Sjöstedt 1926: 251, table 10 a1–a2. — Snyder 1949: 164. — Ruelle 1992: 500. — Krishna *et al.* 2013: 1937. — Josens & Deligne 2019: 61.
*Isognathotermes silvestrii* – Hellemans *et al.* 2021: 233.

Junior synonym of *Isognathotermes severus* (Silvestri, 1914). **Syn. nov.**

**Etymology**

The species was named in honour of F. Silvestri who collected the type material.

**Historical review**

Sjöstedt (1925: 54) briefly described the soldier of this species under the name *Cubitermes Silvestrii*. One year later Sjöstedt (1926: 251) provided more detailed descriptions together with figures of the soldier, specifying that they were based on specimens from Kakoulima (Guinea) first identified as *Cubitermes severus* by Silvestri. He housed the species in the sub-family Termitinae, included it (1926: 218–226) in a soldier's key of *Cubitermes* species and inserted it in a "*bulbifrons*-Gruppe" of species with an upwards humped frons.

Snyder (1949: 164) catalogued *Cubitermes silvestrii* in the sub-family Termitinae.

This is one of the species that Ruelle (1992: 500) called "forgotten species".

Krishna *et al.* (2013: 1937) housed *C. silvestrii* in the sub-family Cubitermitinae.

Josens & Deligne (2019: 39–42) placed this species within the *fungifaber* valve pattern group.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

One type sample has been examined (see *Isognathotermes severus*, DJ 0302). Krishna *et al.* (2013: 1937) mention that another subsample is deposited in NHRM (not examined).

The type of *Cubitermes silvestrii* came from the same locality as one of the syntypes of *Cubitermes severus* and our morphology study shows that it matches well *I. severus*.

Therefore, *Cubitermes silvestrii* (Sjöstedt, 1925) is from now on considered a junior synonym of *Isognathotermes severus* (Silvestri, 1914).

***Isognathotermes speciosus*** (Sjöstedt, 1924)
Figs 39–41

Revised herein as junior synonym of *I. finitimus*.

*Cubitermes speciosus* Sjöstedt, 1924b: 256.

*Cubitermes speciosus* – Sjöstedt 1926: 242–243, table 10 m. — Snyder 1949: 164. — Bouillon & Vincke 1971: 269. — Krishna *et al.* 2013: 1937. — Williams 1966: 102–104, figs 13, 29, 45, 61, 79. — Josens & Deligne 2019: 61.
*Isognathotermes speciosus* – Hellemans *et al.* 2021: 233.

Junior synonym of *Isognathotermes finitimus* (Schmitz, 1916). **Syn. nov.**

**Etymology**

The epithet *speciosus* means 'beautiful, superb' in Latin.

**Historical review**

Sjöstedt (1924b: 256) briefly described the soldier of this species under the name *Cubitermes speciosus*, mentioning that it is close to the soldier of *C. fungifaber* but larger.

Two years later Sjöstedt (1926: 242–243) provided a first description of alate imago and worker together with additional information on soldier. He included (1926: 218–225) *C. speciosus* in imagines' and soldiers' keys of *Cubitermes* species and inserted it in a "*fungifaber*-Gruppe" of species with a not protruding soldier's frons.

Snyder (1949: 164) catalogued *C. speciosus* in the sub-family Termitinae.

Williams (1966: 102–104) provided a detailed redescription of imago and soldier along with measurements and numerous figures.

Bouillon & Vincke (1971: 269) described the enteric valve of *C. speciosus* as belonging to the "simple type" without any spatula.

Krishna *et al.* (2013: 1937) housed *C. speciosus* in the sub-family Cubitermitinae.

Josens & Deligne (2019: 42–44) placed this species within the *finitimus* valve pattern group.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*.

One type sample has been examined (see *Isognathotermes finitimus*, DJ 0061). Krishna *et al.* (2013: 1937) mention that other syntype samples are deposited in AMNH and PPRI (not examined). As the type material of *Isognathotermes speciosus* (Sjöstedt, 1924) matches well *Isognathotermes finitimus* (Schmitz, 1916) and come from the same forested environment, they are from now on considered as synonyms.

### ***Isognathotermes subarquatus*** (Sjöstedt, 1926)
Figs 39–41

Revised herein as junior synonym of *I. finitimus*.

*Cubitermes subarquatus* Sjöstedt, 1926: 244–245, table 9 g1–g2.

*Mirotermes* (*Cubitermes*) *subarquatus* – Emerson 1928: 510–511, text-fig. 55, pl. XXIX. — Snyder 1949: 164. — Krishna *et al.* 2013: 1938.
*Cubitermes finitimus* – Josens & Deligne 2019: 61.
*Isognathotermes finitimus* – Hellemans *et al.* 2021: 233.

Junior synonym of *Isognathotermes finitimus* (Schmitz, 1916).

*Isognathotermes* aff. *subarquatus* "spA" junior synonym of *Isognathotermes fungifaber.*
*Isognathotermes* aff. *subarquatus* "spB" junior synonym of *Isognathotermes planifrons.*
*Isognathotermes* aff. *subarquatus* "spC" junior synonym of *Isognathotermes bulbifrons*. **Syn. nov.**
*Isognathotermes* aff. *subarquatus* "spD" junior synonym of *Isognathotermes fungifaber.*

**Etymology**

The epithet *subarquatus* from the Latin *sub-* (to a lesser degree) and *arquatus* (yellowish) can refer to the red-yellowish colour of the soldier's head mentioned in the original description, but *arcuatus* (or *arquatus*) also means 'curved, in the shape of a bow'.

**Historical review**

Sjöstedt (1926: 244–245) described alate imago, soldier, and worker, along with a few measurements and provided figures of the soldier's head. He included (1926: 218–226) *Cubitermes subarquatus* in

imagines' and soldiers' keys of *Cubitermes* species and inserted it in a "*fungifaber*-Gruppe" of species with a not protruding soldier's frons.

Emerson (1928: 510–511) referred to this species under the name *Mirotermes* (*Cubitermes*) *subarquatus*. He provided further descriptions (with measurements and figures) of imago and soldier together with photographs of the nest.

Snyder (1949: 164) catalogued *C. subarquatus* in the sub-family Termitinae.

Krishna *et al.* (2013: 1938) housed *C. subarquatus* in the sub-family Cubitermitinae. They reported that Emerson (in his unpublished "card catalog") considered *C. subarquatus* a junior synonym of *C. finitimus*. Synonymy of the two species is compatible with their EVAs, as Josens & Deligne (2019: 42–44) placed this species within the *finitimus* valve pattern group.

Hellemans *et al.* (2021: 233) placed this species in the restored genus *Isognathotermes*; and *COII* and *28S* sequences placed it in the "*I. finitimus* clade". Our morphology study (this article) also shows that the type matches well *I. finitimus*.

Roy *et al.* (2006) pointed to the possible existence of cryptic species on base of nuclear and mitochondrial markers. Among the four cryptic species, two of them ("spA" and "spD") had *fungifaber*-EVAs and their DNA sequences also classified them in *I. fungifaber* (Hellemans *et al.* 2021). The two other cryptic species ("spB" and "spC") had *finitimus*-EVAs: "spB" was recognized as *I. planifrons* and "spC" as *I. bulbifrons*.

## Discussion

### Validity of the genus *Isognathotermes*

Our study evidenced a great variability in both the enteric valves and caeca among species of the genus *Isognathotermes*, with either: (i) a *fungifaber* EVA (crested PCs) and a small caecum (*I. fungifaber*, *I. minitabundus*, *I. severus*, *I. ugandensis*, *I. zenkeri*, and possibly *I. bredoi* and the unknown species from Malawi); (ii) a *finitimus* EVA (swollen PCs) and a small caecum (*I. bulbifrons*, *I. finitimus*, *I. magniplanifrons* sp. nov., *I. modicus* sp. nov., *I. planifrons*, *I. rectimalatus* sp. nov., *I. similifinitimus* sp. nov., and possibly *I. congoensis* and *I.* aff. *planifrons*); (iii) a *finitimus* EVA (swollen PCs) and an elongated, phalloid caecum (*I. phallicaecalis* sp. nov. and *I. phalloides* sp. nov.); or (iv) a *bilobatodes* EVA (uncrested PCs) and a small caecum (*I. acristatus* sp. nov.). With such a variability among species, it is questionable whether the genus *Isognathotermes* should be split into two or more subgenera. However, our phylogenetic analyses did not evidence the monophyly of species with *fungifaber*-type EVAs from those with *finitimus*-type EVAs; nor species with a small, multilobed caecum from those with a phalloid caecum. Therefore, this plasticity of trait states did not warrant the erection of sub-genera.

Our phylogenetic analyses evidenced that the studied species are monophyletic with the exception of *I. similifinitimus* sp. nov. and *I. phallicaecalis* sp. nov., which appear to be intricate (paraphyletic). They exhibit less than 1.5% dissimilarity, but are well separated by the morphology of their caeca. This indicates that the mitogenome alone is not sufficient for species delimitation, and highlights the importance of using an integrative approach. We posit that these respective paraphylies may either stem from incomplete lineage sorting, or mitogenome introgression following hybridization. Future analyses leveraging nuclear loci will be crucial to shed further light on their relationships.

**The integrative species delimitation of *Isognathotermes* species**

"A universal species delineation criterion probably does not exist" (Galtier 2019). To delimit a species within the framework of integrative taxonomy (Padial *et al.* 2010), we adopted a set of five rules using anatomy, morphology, chorology, ecology, and molecular data.

(i) The samples must share certain **anatomical criteria** (difficultly quantifiable) such as the valve and caecum types. This criterion was met for all species but *I. acristatus* sp. nov. due to its peculiar valve. (ii) The samples must share **morphological criteria** (more easily quantified) and form recognisable groups in an analysis such as a PCA which detect size as the first factor and other parameters (variable according to the caste considered) as the second factor. In all cases, these first two factors account for just over 50% of the total variability of the system. However, a large number of samples (around 29%) occur at the limit between two species (i.e., in superimposed PCAs ellipses), and the identification therefore remains probabilistic. (iii) Samples must share **chorological and ecological features**: they must come from a region without a hiatus. This requires samples from a sufficiently large number of sampling sites (at least 20); we have complied with this criterion for seven species, and in one case (*I. fungifaber*), we had to discard six samples coming from regions (and ecoregions) far to the east of the main area (Fig. 45) and to classify them as dubious, possibly cryptic *I. fungifaber* (these samples could not be sequenced). (iv) Conversely, two species with similar anatomical and morphological characteristics should **not be sympatric** except at the limits of their respective areas (Hardin 1960). (v) Finally, a "softer" molecular criterion was applied. We considered that samples showing over **2% dissimilarity in their mitogenomes** belong to different species. However, samples with less than 2% dissimilarity could be considered as distinct species on a case-by-case basis provided sufficient anatomical, morphological, or chorological differences are present. In the case of subspecies of *I. ugandensis* the 2% threshold obviously does not have to be reached. The 2%-limit was chosen in order not to complicate the taxonomy of *Isognathotermes*: if a 1%-limit had been chosen, at least eight cryptic species (each represented by a single sample, which means no data on intraspecific variability) would have had to be erected. Mitogenome sequencing is obviously of the highest value, and is, in some cases, the only decisive factor. Unfortunately, it was not possible to apply this criterion to many samples due to the poor state of conservation of their DNA: only 101 samples (out of 210 trials) were successfully sequenced. The oldest successful samples were collected in 1957 (three samples).

Without access to sequencing, species-level identification of *Isognathotermes* remains arduous. Like Williams, in his 1966 revision of the East African *Cubitermes* (sensu Wasmann), we were faced with the great intraspecific variability that complicates species delimitation, although partially facilitated by anatomical features (enteric valve and caecum: Bouillon & Vincke 1971; Johnson 1979). As in Williams' revision, soldiers (and workers) were found to exhibit a greater variability than the imagines (but in *I. ugandensis*) as mentioned in the remarks of the chapter *I. fungifaber*. And despite this, soldiers generally provide the best morphological distinction between species. The plethora of intermediate morphologies between species is further confirmed by the absence of discontinuity in the measurements of morphological characters (e.g., Fig. 71). Additionally, this is highlighted by significant overlap on the PCAs (Figs 20–22).

As most species have a rather limited geographical distribution (with *I. severus* as an exception), their chorology was of great help in identification and has therefore been included in the identification key. However, our study relies on samples' collection labels which are not all reliable:

Some samples of *I. banksi*, *I. bulbifrons*, *I. comstocki*, *I. gaigei*, *I. heghi*, *I. kemneri*, *I. planifrons*, *I. schmidti*, and *I. zenkeri* all bear the same label: "Bipindi, Cameroon, G. Zenker, 1920". This is most likely a simplification of reality. In fact, Georg August Zenker lived in Bipindi from 1896 to 1922 (Wikipedia 2024a, German version) and collected in several regions of Cameroon.

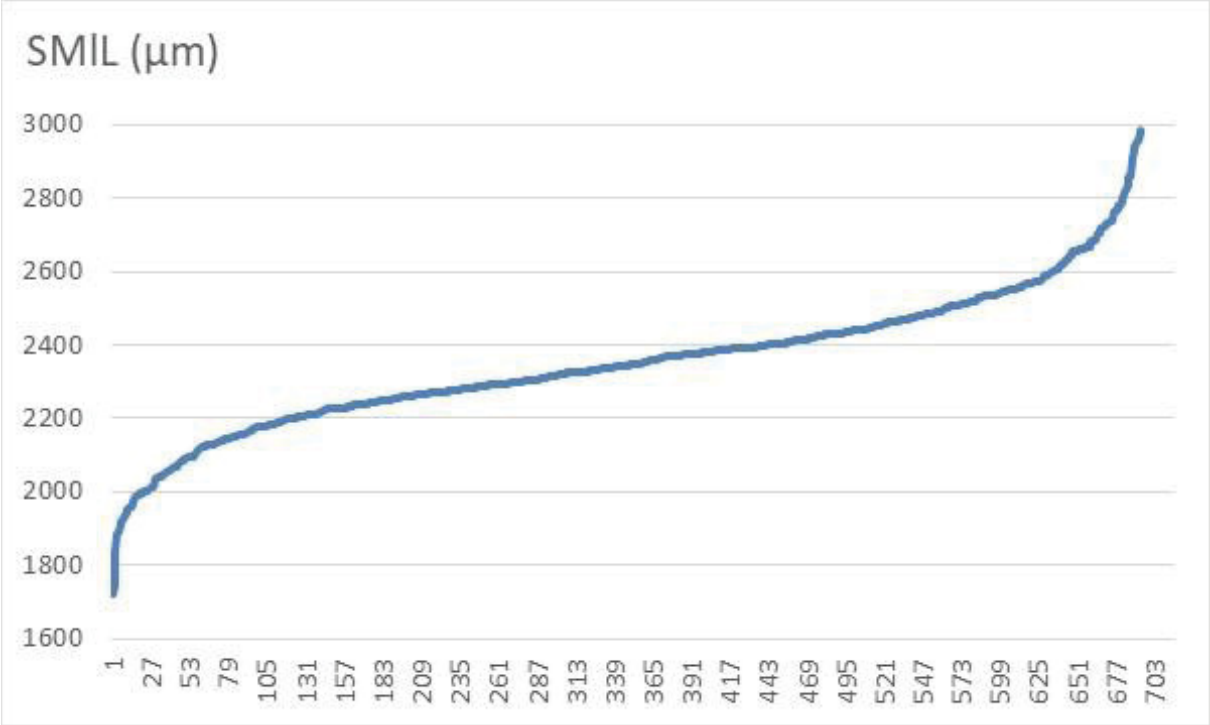


**Fig. 71.** Distribution of soldiers' left mandible length (all species of *Isognathotermes* Sjöstedt, 1926, individuals sorted in ascending order): all the intermediaries exist between the smallest and the largest individuals.

The same applies to the types of five *Isognathotermes* taxa (*I. bulbifrons*, *I. heghi*, *I. fungifaber* var. *elongata*, *I. gibbifrons*, and *I. planifrons*). These samples were labelled as collected in "Mukimbungu, in 1904" by the Swedish missionary and ethnographer Karl Edvard Laman, who stayed in the region between 1890 and 1919 (Wikipedia 2024b) but prospected a wide area around its base.

**Competitive exclusion between species with similar niches**

The distinction between EVAs is a very useful criterion for identification. However, the distinction between *fungifaber*- and *finitimus*-type valves is not always clear: some specimens attributed to species with a *fungifaber* EVA, (particularly *I. severus* and *I. ugandensis*) show intermediate types. Furthermore, shifts among these two main EVA types occur along the evolution of *Isognathotermes* species, which suggests it bears an adaptive ecological value. It is likely that the types of valves (and possibly also the types of caeca) are linked to the food niche (Bouillon & Vincke 1971). Competitive exclusion (Hardin 1960) in termites is still poorly documented and mainly concerns wood-feeding species (Wood & Lee 1971; Perdereau *et al.* 2011); competitive exclusion in soil-feeding termites has not been clearly established but a differentiation of their food niches has been demonstrated (Williams 1966; Florencio *et al*. 2013; Josens & Makatia Wango 2019; Hellemans *et al.* 2019).

As reported herein (Fig. 32), species with *finitimus* and *fungifaber* EVAs are distributed between ecosystems: *finitimus* EVAs mostly in evergreen forests from Cameroon to east DRC, and *fungifaber* EVAs in several other environments from Gambia to Malawi but also in evergreen and humid forests from West Africa to Cameroon. If the valve and caecum types are food niche markers, two species with the same EVA and caecum should not usually share the same biotopes, while species with different EVAs or caeca might coexist. Indeed, observations in the Cubitermitinae subfamily point in this direction:

- At Upemba National Park (Haut-Katanga, DRC), *Nitiditermes sankurensis* (*sankurensis* EVA) frequently coexist with *I. ugandensis* (*fungifaber* EVA) (as "*Cubitermes antennalis*" in Harris 1958).
- At Bondoé (CAR), *N. sankurensis* and *I. severus* (*fungifaber* EVA) (as *C. ugandensis* in Wango & Josens 2011) coexist with high densities.
- In East Africa, *Nitiditermes testaceus* (*sankurensis* EVA) and *I. ugandensis* (*fungifaber* EVA) were frequently found together to the extent that "this particular association could be found at virtually any grassland swamp margin … so that it seems clear that in such areas an equilibrium is set up between the two species" (Williams 1966).
- Near Kinshasa (DRC), the populations of *Ternicubitermes weissi* (*bilobatodes* EVA) and *N. sankurensis* are clearly intermingled (Bouillon & Vincke 1973).
- At Luki (Kongo-Central, DRC), *I. bulbifrons* and *I. phalloides* coexist: both exhibiting a *finitimus* EVA but with different caeca (reported herein).
- Similarly, *I. planifrons* and *I. phallicaecalis* coexist in two locations of northern Congo: they have the same *finitimus* EVA with distinct caeca (reported herein).

There are, however, also some exceptions, with species exhibiting similar EVAs coexisting together. As such, *I. bulbifrons* and *I. planifrons* have been collected together in three sites at La Lopé National Park (Gabon) (Roy *et al.* 2006).

**Ambiguities remain for the distinction of several species**

Firstly, the delimitation between *I. bulbifrons* and *I. finitimus*, (both with the same EVA and caecum types) is ambiguous when mitogenomes are not available: the soldiers of *I. finitimus* occupy a central position in the PCA of species with a *finitimus*-type EVA (Fig. 22), thereby rendering this species the most difficult to delimit without the help of geographical distributions. However, this geography criterion loses its effectiveness where two species meet. For example, two samples from Central Africa (DJ 0679 and DJ 0680) were collected at the distribution limits of *I. finitimus* and *I. bulbifrons*, and they exhibit intermediate soldier morphology according to the PCA (Fig. 72).

Second, the distinction between *I. fungifaber* and *I. severus* remains difficult using morphology and anatomy alone. Our survey indicates that *I. fungifaber* and *I. severus* (both with the same EVA and caecum types) appear mutually exclusive in western and western-central Africa. While *I. fungifaber* seems restricted to evergreen forests, *I. severus* is common in the savannah landscapes of West Africa, and north of the Congolese forests (from Gambia to CAR) but also in orchards, woodlands, and secondary forests. However, *I. severus* is also present in the evergreen forests of western RCI (region of Man-Zéalé-Taï, near the border with Liberia) and in the Lobaye province (southwest CAR), but only in places devoid of *I. fungifaber*. In these evergreen forests, the overall morphology of *I. severus* (identity ascertained by mitogenome) appears smaller and resembling that of *I. fungifaber*. In the absence of its competitor, the morphology of *I. severus* seems to converge with that of *I. fungifaber*.

Finally, several ambiguities remain between *I. severus*, *I. ugandensis* and *I. minitabundus*. Our survey suggests that in East Africa *I. severus*, *I. ugandensis* and *I. minitabundus* form a morphological continuum (see Lowry & Gould 2016) when considering soldiers or workers. The distinction among these three species is best achieved from the comparison of imagines, with the exception of *I. severus* with *I. ugandensis ugandensis* (Fig. 65). However, imagines are missing in many samples, and the delimitation of *I. ugandensis* subspecies is (provisionally) mostly relying on their geographical range. Similarly, *I. ugandensis* is composed of four subspecies occurring in allopatry (Fig. 49), and mostly recognizable from their imagines (Fig. 65). It is remarkable that the imagines of *I. ugandensis kenyae* and *I. u. malawii* have very similar morphologies even though their geographical ranges are more than 1000 km apart. It is not impossible that this convergence is the result of adaptations to altitude.

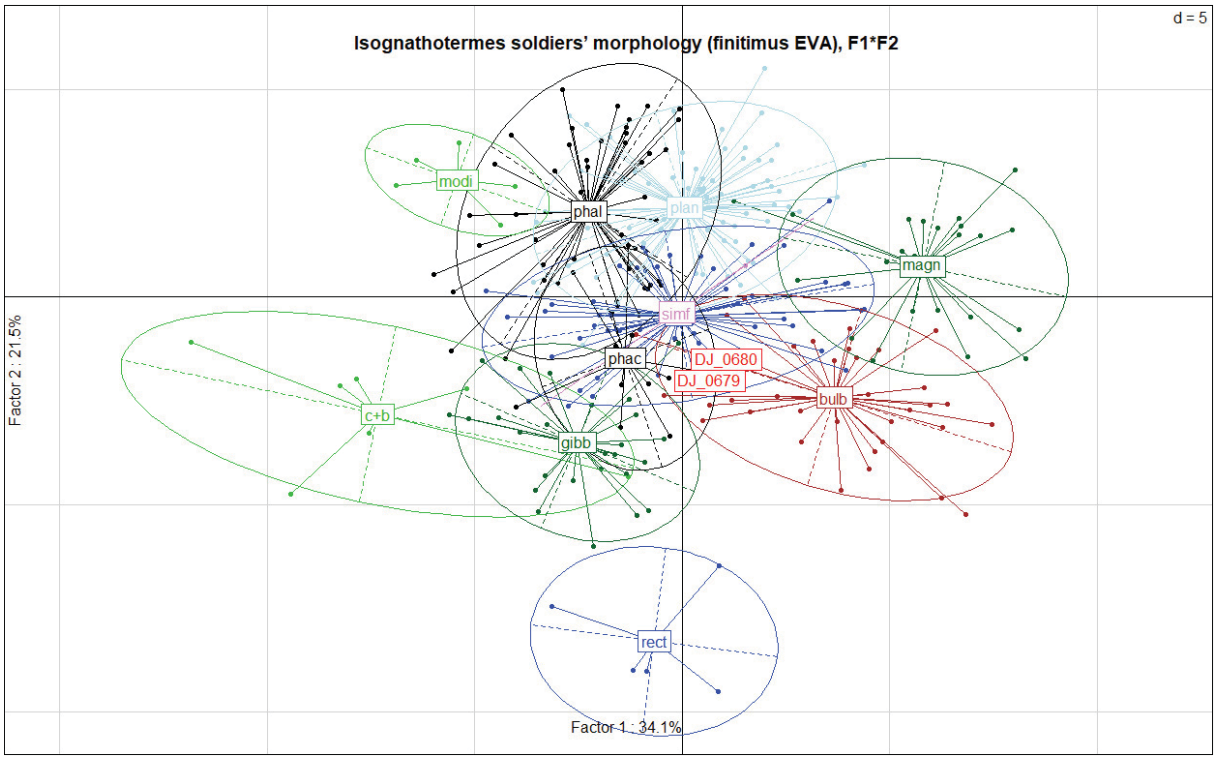


**Fig. 72.** PCA on soldier's morphology involving only the species of *Isognathotermes* Sjöstedt, 1926 with a *finitimus*-type EVA (same symbols as in Fig. 22). Examples of indeterminacy: DJ 0679 and DJ 0680 are projected at the morphological boundary between *I. finitimus* (Schmitz, 1916) (blue ellipse) and *I. bulbifrons* (Sjöstedt, 1924) (brown ellipse) and originate from the boundary between the geographical distributions of these species. In this figure the two forms of *I. bulbifrons* are figured separately: "bulb" for the large form and "gibb" (as *gibbifrons*) for the medium sized form.

Unfortunately, little molecular data could be obtained, as most of the material used in this study was collected over 50 years ago. The available molecular data clearly separate *I. severus* and *I. ugandensis*, but the *I. minitabundus* samples are in an uncertain sister-relationship with *I. ugandensis* (Fig. 33), with whom they exhibit less than 2% dissimilarity (Supp. file 4). The boundaries between species proposed in this study will therefore have to be confirmed or adapted by future surveys.

Unlike the species that are difficult to distinguish, *I. bulbifrons* has two different morphologies with the same mitogenome. The two forms differ essentially in size: the medium-sized form corresponds to what Sjöstedt called *Cubitermes gibbifrons* while the large one corresponds to *C. bulbifrons*. This size difference is evident in all castes and is so clear that there is no overlap of ellipses in a PCA (Fig. 72). Remarkably the two forms have sometimes been found in the same localities (e.g., Luali, Sona Pangu, and Mukimbungu (Congo Central, DRC) and Mbalmayo (Cameroon)), with the provision that 'the same locality' does not necessarily mean the same biotope (on this subject, see the discussion above on chorology).

## Nomenclatural changes made in this work

Holotypes selected of seven species and four subspecies: *I. acristatus* sp. nov., *I. magniplanifrons* sp. nov., *I. modicus* sp. nov., *I. phallicaecalis* sp. nov., *I. phalloides* sp. nov., *I. rectimalatus* sp. nov., *I. similifinitimus* sp. nov., *I. ugandensis ugandensis* subsp. nov., *I. ugandensis burundii* subsp. nov., *I. ugandensis kenyae* subsp. nov., and *I. ugandensis malawii* subsp. nov.

**New synonymies**

*Cubitermes fungifaber* var. *elongata* Sjöstedt, 1924 → *I. planifrons* (Sjöstedt, 1924)
*Cubitermes gibbifrons* Sjöstedt, 1924 → *I. bulbifrons* (Sjöstedt, 1924)
*Cubitermes loubetsiensis* Sjöstedt, 1924 → *I. planifrons* (Sjöstedt, 1924)
*Cubitermes silvestrii* Sjöstedt, 1925 → *I. severus* (Silvestri, 1914)
*Cubitermes speciosus* Sjöstedt, 1924 → *I. finitimus* (Schmitz, 1916)
*Cubitermes subarquatus* Sjöstedt, 1926 → *I. finitimus* (Schmitz, 1916)
*Cubitermes modestior* Silvestri, 1914 → *I. severus* (Silvestri, 1914)
*Cubitermes* sp. affinis *subarquatus* "spC" (Roy *et al.* 2006) → *I. bulbifrons* (Sjöstedt, 1924)
*Mirotermes* (*Cubitermes*) *banksi* Emerson, 1928 → *I. fungifaber* (Sjöstedt, 1896)
*Mirotermes* (*Cubitermes*) *comstocki* Emerson, 1928 → *I. fungifaber* (Sjöstedt, 1896)
*Mirotermes* (*Cubitermes*) *gaigei* Emerson, 1928 → *I. planifrons* (Sjöstedt, 1924)
*Mirotermes* (*Cubitermes*) *kemneri* Emerson, 1928 → *I. bulbifrons* (Sjöstedt, 1924)
*Mirotermes* (*Cubitermes*) *schmidti* Emerson, 1928 → *I. fungifaber* (Sjöstedt, 1896)

## Acknowledgements

We are particularly indebted to David Grimaldi for welcoming GJ in the AMNH and to Jessica Ware for following and encouraging the progress of this study; and to George Beccaloni for welcoming GJ in the NHMUK. Some valuable samples were taken during the Boyekoli-Ebale-Congo Expedition in May–June 2010 organised by the Royal Museum for Central Africa (Tervuren, Belgium), the University of Kisangani (DR Congo), the Royal Belgian Institute of Natural Sciences and the National Botanical Garden of Belgium (expedition supported by the Belgian Development Cooperation, BELSPO). We also thank Mrs Geo Trembleau, Mr Benoît Host, and Sébastien Lenz who provided us with valuable samples. Many thanks to the reviewers and in particular F. Legendre for their constructive comments and suggestions.

The morphological part of this work was carried out by two retired termitologists who would like to thank the Tervuren Africa Museum (and especially Didier Van den Spiegel, Head of the "Biological collections and data management" unit) and the Université Libre de Bruxelles (and especially Pierre Meerts, Head of the "Ecologie végétale et biogéochimie" unit) for hosting them and encouraging the progress of this study. We thank the Sequencing Section (SQC) and the Scientific Computation & Data Analysis Section (SCDA) of OIST for assistance with sequencing and providing access to the OIST computing cluster, respectively. This work was supported by subsidiary funding to OIST.

## Data availability statement

The newly-generated data that support the findings of this study are deposited in GenBank (mitogenomes and mitochondrial *COII* gene) under accessions: see Supp. file 3 for details).

## Authors' contributions

JD sorted and carried out preliminary identifications of the large Tervuren collection, particularly Bouillon's collection; GJ and JD conducted the anatomical and morphological studies and wrote the manuscript draft; the photos, drawings, maps, and data analyses on morphology were produced by GJ. YR checked conformity to the ICZN.

SH and EK performed library preparation for Illumina sequencing; MyH and VR carried out Sanger sequencing of the *COII* gene for some samples. SH performed the phylogenetic analyses.

Most authors (ABN, BLR, CK, GG, GJ, JD, JŠ, KD, LEYL, MyH, MiH, MV, NCS, PA, PK, PS, SL, ST, SW, TC, and YR) collected fresh samples.

All authors read and approved the final manuscript.

## Conflict of interest declaration

The authors declare they have no competing interests.

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## Supplementary material

**Supp. file 1.** Figure SF1. Phylogenetic relationships between species of *Isognathotermes* Sjöstedt, 1926 reconstructed from complete mitogenomes with 41 partitions in IQ-TREE (see methods). Node support values are Shimodaira–Hasegawa approximate likelihood-ratio/Ultrafast bootstrap (SH-aLRT/UFB). Intra-specific support values on short edges were omitted for clarity. Numbers after the slash in the study code indicate the type of enteric valve: /11 = *bilobatus* pattern, /12 = *muneris* pattern, /13 = *oculatus* pattern, /14 = *bilobatodes* pattern, /15 = *fungifaber* pattern, /15 = *finitimus* pattern, /22 = *sankurensis* pattern, /23 = *oblectatus* pattern, /26 = *sulcifrons* pattern. The mention "type" in the label indicates specimens sequenced from the type series. Red edges and labels indicate the intricate paraphylies of *I. similifinitimus* Josens & Deligne sp. nov. and *I. phallicaecalis* Josens & Deligne sp. nov.
https://doi.org/10.5852/ejt.2025.1024.3099.13819

**Supp. file 2.** Figure SF2. Phylogenetic relationships between species of *Isognathotermes* Sjöstedt, 1926 reconstructed from the mitochondrial *COII* gene in IQ-TREE. Node support values are Shimodaira–Hasegawa approximate likelihood-ratio/Ultrafast bootstrap (SH-aLRT/UFB). Intra-specific support values on short edges were omitted for clarity. Numbers after the slash in the study code indicate the type of enteric valve: /11 = *bilobatus* pattern, /12 = *muneris* pattern, /13 = *oculatus* pattern, /14 = *bilobatodes* pattern, /15 = *fungifaber* pattern, /16 = *finitimus* pattern, /22 = *sankurensis* pattern, /23 = *oblectatus* pattern, /26 = *sulcifrons* pattern. The mention "type" in the label indicates specimens sequenced from the type series. Red edges and labels indicate non-monophyletic taxon (*I. similifinitimus* Josens & Deligne sp. nov.) or taxa rendering other species non-monophyletic (*I.* aff *planifrons*, *I. phalloides* Josens & Deligne sp. nov., *I. ugandensis kenyae* subsp. nov.). https://doi.org/10.5852/ejt.2025.1024.3099.13821

**Supp. file 3.** GenBank accessions of mitogenomes and mitochondrial *COII* gene used in this study, together with samples' collection details and mitogenome sizes as indicators of completeness. https://doi.org/10.5852/ejt.2025.1024.3099.13823

**Supp. file 4.** Pairwise mitogenome similarities between samples of *Isognathotermes*. Similarities were obtained with megaBLASTn. https://doi.org/10.5852/ejt.2025.1024.3099.13825