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REVISED TAXONOMY AND ILLUSTRATED KEY FOR *Bulbitermes* OF SABAH: INTEGRATING MORPHOLOGY AND CLUSTER ANALYSIS

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ABSTRACT

This study presents a taxonomic assessment of *Bulbitermes* Emerson (Termitidae: Nasutitermitinae) in Sabah, Malaysian Borneo. These arboreal, wood-feeding termites are important decomposers in tropical forests and are typically associated with undisturbed habitats, inhabiting various forms of decaying wood. However, species-level identification within Bulbitermes remains challenging due to high morphological similarity among taxa. This study aimed to refine morphological taxonomy, update the species checklist, and develop an illustrated identification key for *Bulbitermes* in Sabah. Fresh specimens were collected from 11 localities using a standardised belt transect method and supplementary sampling, and additional material from the BORNEENSIS collection at the Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, was examined. A total of 15 termite taxa initially assigned to *Bulbitermes*, comprising six described species and nine provisional taxa, were evaluated based on soldier and worker caste morphology. Of these, 13 taxa were confirmed as *Bulbitermes*, while two were reassigned to the genera *Ceylonitermes* and *Lacessititermes*. Four provisional taxa (sp. A–D) were resolved and assigned to described species based on consistent diagnostic morphological characters and overlapping morphometric variation. Two taxa are retained as provisionally identified forms, *Bulbitermes* cf. *germanus* and *Bulbitermes* cf. *prabhae*, while one taxon (*Bulbitermes* sp. E) remains unresolved due to insufficient material. Observations from 425 colonies, supported by phenetic cluster analysis using the MultiVariate Statistical Package (MVSP), corroborated species groupings and taxonomic decisions. The results were used to develop an illustrated identification key and provide an updated checklist of Bulbitermes in Sabah. This study provides a foundation for future integrative taxonomic research incorporating molecular data to further resolve species boundaries within the genus.

Keywords: Nasutitermitinae; species identification; morphometrics; phenetic analysis; Sabah

ABSTRAK

Kajian ini memfokuskan kepada semakan taksonomi *Bulbitermes* Emerson (Termitidae: Nasutitermitinae) di Sabah, Malaysia Borneo. Anai-anai pemakan kayu ini merupakan pengurai penting dalam ekosistem hutan tropika dan lazimnya ditemui di habitat tidak terganggu, mendiami pelbagai jenis kayu reput. Walau bagaimanapun, pengecaman spesies dalam *Bulbitermes* adalah mencabar disebabkan persamaan morfologi yang tinggi antara taksa. Kajian ini bertujuan memperhalusi taksonomi morfologi, mengemaskini senarai spesies, dan membangunkan kekunci pengenalan berilustrasi bagi *Bulbitermes* di Sabah. Spesimen yang terkumpul dari 11 lokaliti menggunakan kaedah transek piawai dan pensampelan rawak, dan spesimen daripada koleksi BORNEENSIS di Institut Biologi Tropika dan Pemuliharaan, Universiti Malaysia Sabah turut diperiksa. Sebanyak 15 taksa anai-anai yang pada awalnya dikenalpasti sebagai spesies atau morfospesies *Bulbitermes* telah dianalisis berdasarkan ciri morfologi kasta askar dan pekerja. Daripada jumlah ini, 13 taksa disahkan sebagai *Bulbitermes*, manakala dua lagi kenalpasti sebagai genera *Ceylonitermes* dan *Lacessititermes*. Empat taksa (sp. A–D) dikenalpasti sepadan dengan spesies yang telah dideskripsikan sebelum ini. Dua taksa dikekalkan sebagai *Bulbitermes* cf. *germanus* dan *Bulbitermes* cf. *prabhae*, manakala satu takson (*Bulbitermes* sp. E) dikekalkan kerana kekurangan spesimen yang lengkap. Pemerhatian terhadap 425 koloni, disokong oleh analisis kelompok menggunakan Perisian Statistik Multivariat (MVSP), menyokong pengelompokan spesies berdasarkan ciri-ciri morfologi. Hasil kajian ini digunakan untuk membangunkan kekunci pengenalan berilustrasi serta menyediakan senarai terkini *Bulbitermes* di Sabah. Kajian ini menyediakan senarai terkini spesies *Bulbitermes* dan mewujudkan platform untuk kajian filogeni molekul, variasi genetik serta perbezaan spesies dalam genus ini.

Kata Kunci: Nasutitermitinae; pengenalpastian spesies; morfometri; analisis fenetik; Sabah

INTRODUCTION

Termites were traditionally classified under the order Isoptera however, advances in molecular phylogenetics have demonstrated that termites evolved from within the cockroach lineage and are most closely related to the wood-feeding cockroach genus *Cryptocercus* (Bourguignon et al. 2015; Hellemans et al. 2024). Consequently, termites are now placed within the clade Termitoidea under the order Blattodea (Bourguignon et al. 2015; Inward et al. 2007). This reclassification reflects a major shift in the understanding of termite evolution and highlights their eusocial origin within cockroaches (Arab et al. 2021; Aguilera-Olivares et al. 2023). Globally, more than 3,000 living and fossil termite species have been described, exhibiting remarkable diversity in morphology, behaviour, feeding strategies, and nesting habits (Constantino 2021; Krishna et al. 2013).

Southeast Asia represents one of the global centres of termite diversity, with particularly high species richness in lowland and montane tropical forests. The family Termitidae, commonly known as higher termites, dominates the regional fauna and accounts for approximately 75% - 80% of all described termite species worldwide (Krishna et al. 2013; Tho 1992). This family is subdivided into several subfamilies, among which Nasutitermitinae Hare is especially distinctive. Members of this subfamily are characterized by the presence of nasus in the soldier caste, which is used to eject defensive chemical secretions, accompanied by reduced or vestigial mandibles (Arumugam et al. 2018; Bourguignon et al. 2015; Deligne et al. 1981).

Within Nasutitermitinae, the genus *Bulbitermes* was established by Emerson (1949), to delimit a group of strictly Indo-Malayan nasute species characterised by constricted head capsules, and it currently comprises more than 30 described species distributed mainly throughout the Indo-Malayan region and Oriental (Krishna et al. 2013). Species of *Bulbitermes* are primarily arboreal or wood-dwelling termites, inhabiting dead branches, fallen logs, standing dead wood, and carton nests attached to trees. Although they are not considered structural pests, *Bulbitermes* species play an important ecological role as early-stage wood decomposers, contributing to nutrient recycling in forest ecosystems (Chey 2012; Liu et al. 2025; Rahman et al. 2017).

In Malaysian Borneo, particularly in the state of Sabah, *Bulbitermes* species are commonly encountered in both lowland dipterocarp forests and montane forest habitats (Nivaarani & Homathevi 2015). Despite their abundance, reliable species-level identification remains challenging. The most comprehensive taxonomic treatment and identification key for Sabah termites was published more than four decades ago (Thapa 1981), prior to more extensive sampling efforts across multiple habitats, and no comprehensive revision of *Bulbitermes* has been undertaken since then. Identification is further complicated by strong morphological similarity among species, particularly in the soldier caste, which is the primary caste used in termite taxonomy. This morphological similarity limits the effectiveness of existing identification frameworks and contributes to difficulties in distinguishing closely related taxa. Similar taxonomic difficulties have also been reported across other genera within Nasutitermitinae and Termitinae, where morphological convergence and cryptic species complexes are common (Boulogne et al. 2017; Eggleton 2011; Hellemans et al. 2017).

Subsequent ecological studies, which involved broader geographic sampling and examination of larger numbers of specimens across multiple sites, revealed substantial morphological variation that exceeded the range described in existing species descriptions and identification keys. As a result, many studies conducted in Sabah have relied on provisional morphospecies designations such as *Bulbitermes* sp. A, sp. B, or sp. C (Eggleton et al. 1997; Homathevi et al. 2002; Jones et al. 1998). While these designations reflect observable variation, they lack clearly defined diagnostic criteria and consistent application, leading to persistent uncertainty in species identity and limiting the accuracy of assessments of species composition, distribution, community structure, and ecological function.

Given these limitations, the present study conducts a comprehensive taxonomic revision of *Bulbitermes* in Sabah by examining and documenting morphological variation in the soldier and worker castes using both field-collected and museum specimens, revising and updating the checklist of *Bulbitermes* species occurring in Sabah, and developing an illustrated identification guide to facilitate accurate species-level identification for taxonomists, ecologists, and conservation practitioners. In addition, this study explicitly tests the taxonomic status of previously designated morphospecies to determine whether they correspond to described species, represent intraspecific variation, or constitute distinct but currently unresolved taxa pending further evidence based on consistent morphological characters and phenetic clustering. These outputs are expected to improve the reliability of termite biodiversity studies in Borneo and provide a critical foundation for future integrative taxonomic research incorporating molecular and ecological data.

This study presents a taxonomic reassessment of *Bulbitermes* in Sabah through detailed examination of soldier and worker morphology, an updated regional species checklist, and the development of an illustrated identification guide. Importantly, this study clarifies the status of

previously designated morphospecies by linking them to described species or retaining them as provisionally identified or unresolved taxa where definitive assignment is not supported by the available morphological evidence. The results provide essential baseline data for future comparative, biogeographical, and conservation-oriented studies and establish a framework for integrative taxonomic approaches combining morphological and molecular evidence (Bourguignon et al. 2013).

MATERIALS AND METHODS

Study Sites

This study examined *Bulbitermes* specimens collected from multiple forested sites across Sabah, Malaysian Borneo, encompassing a wide range of lowland, hill and montane forest ecosystems. Sampling localities included Danum Valley Conservation Area (N 04°57'55.6" E 117°48'02.6"), Imbak Canyon Conservation Area (N 05006'00" E 117002'00"), Inobong Sub-station Crocker Range Park (N 05°51'20.6" E 116°08'14.2"), Mahua Sub-station Crocker Range Park (N 05°47'51.5" E 116°24'23.3"), Poring sub-station Kinabalu Park (N 06°2'38" E 116°42'14"), Sayap sub-station Kinabalu Park (N 06°09'54.9" E 116°33'57.0"), Tawau Hills Park (N 04023'55.1" E 117053'20.1"), Kabili–Sepilok Forest Reserve (N 05°51'47.1" E 117°56'54.2"), Kalabakan Forest (N 04040'00" E 117034'00"), Gaya Island (N 06°00'43.9" E 116°00'37.2"), and Maliau Basin Conservation Area (N 04044'49.5" E 116058'05.9") (Figure 1). These sites represent both primary and secondary forests and span an altitudinal gradient from approximately 20 m to over 1,100 m above sea level, providing broad ecological coverage of *Bulbitermes* habitats in Sabah. Coordinates represent central reference points for each study site and were recorded using the WGS84 datum.

In addition, *Bulbitermes* specimens from institutional collections were examined. These included specimens housed at BORNEENSIS, Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, as well as comparative material from the Forest Research Centre (Sepilok, Sabah) and the Forest Research Institute Malaysia (FRIM), Selangor.

Data Collection

Field sampling and specimen collection

Fresh specimens were collected using standardized belt transects (100 m × 2 m; equivalent to 200 m² per transect) following Eggleton et al. (1997) and Homathevi et al. (2002). Two transects were established per site, resulting in a total sampling area of 400 m² per site with standardized sampling effort. Each transect was subdivided into 20 contiguous sections, with a standardised sampling effort of one person-hour per section. Additional opportunistic sampling was conducted to maximize the detection of *Bulbitermes* colonies.

Termites were collected manually using forceps from all potential microhabitats, including dead wood at various stages of decay, leaf litter to a depth of approximately 5 cm, soil surface, tree buttresses, root systems, arboreal runways, and carton nests (Arumugam et al. 2020). When arboreal nests of *Bulbitermes* were located, entire colonies were collected to assess intraspecific variation. Prior to removal, nest dimensions, height above ground and geographic coordinates were recorded. Environmental parameters, including canopy cover and altitude, were measured using a spherical densiometer and a handheld GPS unit, respectively. All specimens were preserved in 80% ethanol and labeled with locality, date and collector information before being transported to the laboratory for further examination.

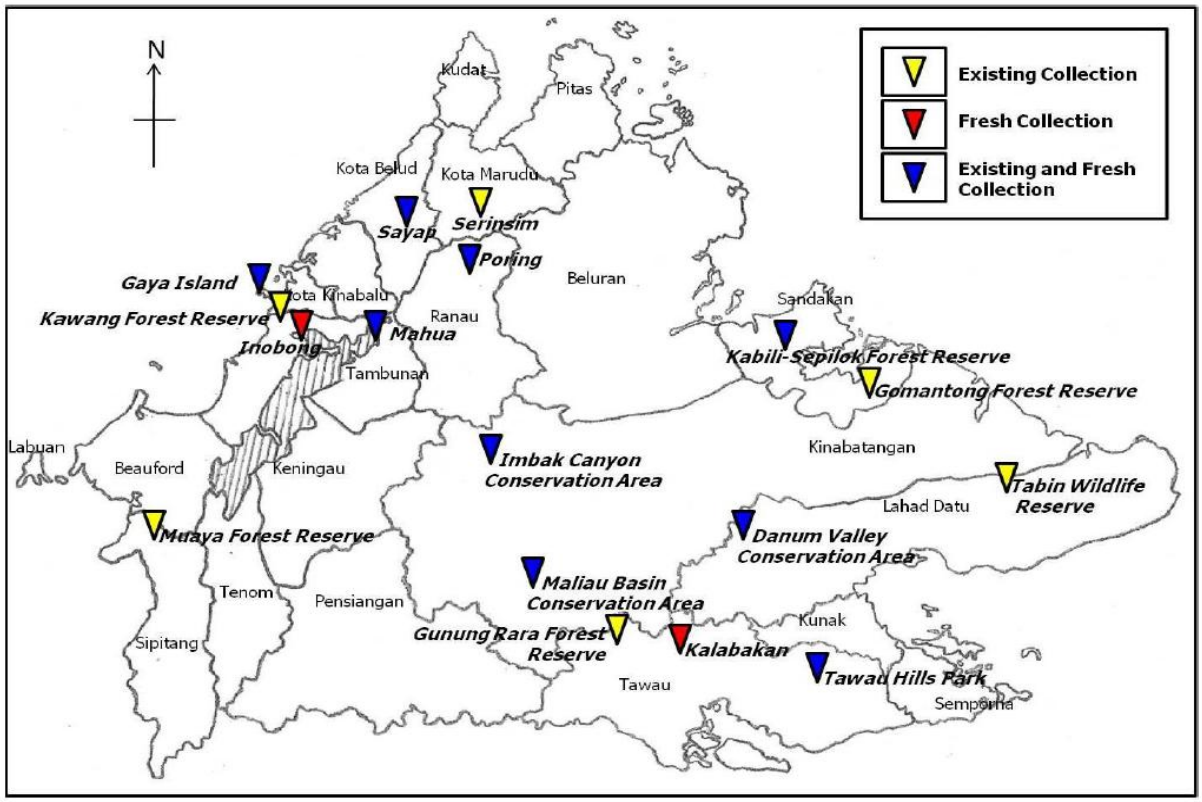


Figure 1. Sampling site locations for *Bulbitermes* in Sabah, Malaysian Borneo, indicating sites with existing collections, fresh field collections and combined specimen sources

Morphological examination and taxonomic assessment

Morphological analyses were conducted on both soldier and worker castes using a stereomicroscope (Olympus SZX12). A total of 15 termite taxa assigned to *Bulbitermes* were examined, comprising six described species and nine provisional taxa (corresponding broadly to previously recognised morphospecies, *Bulbitermes* sp. A–E and sp. 1–2). Species delimitation was based primarily on soldier caste morphology, which provides the most reliable diagnostic characters in Nasutitermitinae. Diagnostic characters of the soldier caste were emphasised, including head capsule shape, rostrum morphology, antennal segmentation, pronotum structure, and leg proportions, following the taxonomic framework of Thapa (1981). Standardised measurements were taken following established taxonomic conventions, and all measurements were recorded in millimetres.

Worker caste morphology was examined primarily to support genus-level placement, with particular focus on mandibular dentition, including the configuration of marginal teeth and molar structures. Morphological terminology and character definitions followed established taxonomic treatments, and taxonomic assessment was based mainly on soldier caste characters through comparison with published descriptions, identification keys, and reference material from institutional collections (Thapa 1981; Tho 1992).

This study focused on the taxonomic reassessment and species delimitation of *Bulbitermes* species in Sabah rather than providing formal redescriptions of previously described species. In particular, the study aimed to evaluate whether previously recognised morphospecies correspond to described species or represent distinct morphological entities.

Species delimitation was based on consistent combinations of diagnostic morphological characters rather than single traits. Taxa were considered distinct when they exhibited differences in at least three independent morphological characters, consistent expression of these differences across multiple individuals and colonies, and non-overlapping or clearly separable ranges in key morphological features.

Given the high morphological similarity within *Bulbitermes*, some taxa could not be confidently assigned to described species but exhibited consistent and repeatable differences. These were treated as provisional, diagnosable taxa pending further taxonomic evaluation. Where possible, affinities with described species were indicated using standard taxonomic notation (e.g., aff., cf.), replacing informal morphospecies designations used in earlier studies. This approach provides a consistent framework for species delimitation while allowing provisional recognition of unresolved taxa.

Data Analysis and Phenetic Clustering

A phenetic approach was used to evaluate overall morphological similarity among *Bulbitermes* taxa based on characters from both soldier and worker castes. A total of 171 morphological characters were defined and coded into a binary data matrix, with character states scored as present (1) or absent (0). These characters included features of the head capsule, rostrum, antennae, pronotum, abdominal tergites, legs, and worker mandibles, following established termite taxonomic frameworks (Thapa 1981; Tho 1992).

Phenetic analyses were conducted using the MultiVariate Statistical Package (MVSP). The Gower similarity coefficient was selected due to its suitability for analysing datasets comprising mixed morphological character types. Patterns of morphological similarity among taxa were visualised using dendrograms based on overall morphological resemblance. Similarity matrices were generated and used to construct dendrograms based on both nearest-neighbour (single linkage) and farthest-neighbour clustering methods, following principles of numerical taxonomy (Oti & Olusola 2024; Sneath & Sokal 1973).

Phenetic clustering was used as a supporting analytical tool to assess patterns of morphological similarity among taxa. Species delimitation was based primarily on diagnostic morphological characters, with clustering results providing supplementary evidence for evaluating morphological consistency among taxa.

Construction of the Identification Key

An illustrated identification key to the soldier caste of *Bulbitermes* taxa in Sabah was developed based primarily on the results of morphological analyses. Diagnostic characters were selected from the morphological data matrix, prioritising stable, clearly defined, and easily observable traits traditionally used in termite taxonomy (Thapa 1981; Tho 1992). Illustrations depicting character states were prepared from microscope images to enhance clarity and usability. The key was constructed to facilitate consistent and reproducible taxon recognition and to support both taxonomic and ecological studies, while avoiding the use of informal or non-diagnosable morphospecies.

RESULTS AND DISCUSSION

Taxonomic Status

Of the 15 taxa examined, 13 were confirmed as belonging to the genus *Bulbitermes*, comprising six described species and seven taxa previously treated as morphospecies (Table 1). The six

described species retained their original identifications following detailed morphological re-examination, whereas two taxa were reassigned to the genera *Ceylonitermes* Holmgren and *Lacessititermes* Holmgren, representing a new generic record (*Ceylonitermes*) for Sabah.

Table 1. Revised status of *Bulbitermes* species and previously recognised taxa before and after revision based on morphological examination of soldier and worker castes

Before Revision	**After Revision**
Bulbitermes borneensis (Haviland)	*Bulbitermes borneensis* (Haviland)
Bulbitermes constrictiformis (Holmgren)	*Bulbitermes constrictiformis* (Holmgren)
Bulbitermes constrictus (Haviland)	*Bulbitermes constrictus* (Haviland)
Bulbitermes flavicans (Holmgren)	*Bulbitermes flavicans* (Holmgren)
Bulbitermes sarawakensis (Haviland)	*Bulbitermes sarawakensis* (Haviland)
Bulbitermes umasumasensis Thapa	*Bulbitermes umasumasensis* Thapa
Bulbitermes sp. A	*Bulbitermes constrictus*
Bulbitermes sp. B	*Bulbitermes constrictus*
Bulbitermes sp. C	*Bulbitermes sarawakensis*
Bulbitermes sp. D	*Bulbitermes borneensis*
Bulbitermes sp. E	*Bulbitermes* sp. E
Bulbitermes sp. F	*Ceylonitermes* sp.
Bulbitermes sp. G	*Lacessititermes* sp.
Bulbitermes sp. 1	*Bulbitermes* cf. *germanus*
Bulbitermes sp. 2	*Bulbitermes* cf. *prabhae*

Note: cf. indicates tentative identification based on morphological similarity; synonymy is not formally proposed pending examination of type material and molecular data.

Previously recognised informal morphospecies (*Bulbitermes* sp. A–E) were reassessed using detailed morphological descriptions. Based on consistent diagnostic morphological characters, these taxa are assigned to described species. Specifically, *Bulbitermes* sp. A and sp. B are assigned to *B. constrictus*, while sp. C and sp. D are assigned to *B. sarawakensis* and *B. borneensis*, respectively. These assignments are supported by agreement in head capsule morphology, rostrum proportions, antennal segmentation, and quantitative morphometric measurements. One taxon (*Bulbitermes* sp. E) remains unresolved due to limited material and is retained as an unidentified *Bulbitermes* species.

In addition, two taxa (*Bulbitermes* sp. 1 and sp. 2) exhibit closest morphological similarity to *B. germanus* and *B. prabhae*, respectively; however, consistent differences in diagnostic characters, including antennal segmentation, mandible structure, and head proportions, preclude definitive assignment to these species. These taxa are therefore treated as provisionally identified forms within *Bulbitermes* pending further integrative taxonomic evaluation. Diagnostic justification for species assignments is presented here to ensure clarity, with the identification key serving as a practical application tool.

Morphological Delimitation of *Bulbitermes* Species

Species delimitation within *Bulbitermes* in this study was based primarily on morphological characters of the soldier caste, with supplementary observations from the worker caste. Soldier

morphology provides the most reliable diagnostic characters, whereas worker morphology is comparatively conserved and offers limited resolution at the species level. Key characters used to delimit species include head capsule shape (in dorsal and lateral views), degree of constriction behind the base of the antennae, rostrum shape and proportional length, antennal segmentation and proportions of individual antennal articles, and quantitative head measurements. These characters were evaluated in combination, allowing consistent and reliable discrimination of species across multiple colonies and localities.

The degree of constriction behind the antennae is particularly informative for distinguishing species groups within *Bulbitermes*. Species such as *B. constrictus* and *B. constrictiformis* exhibit strong constriction, whereas *B. flavicans* shows only weak constriction, thereby providing a clear diagnostic distinction between these taxa, with similar patterns observed across other examined species. Rostrum shape also varies consistently among species, ranging from slender and elongate to comparatively stout, with thickening most accurately described as occurring at the middle rather than at the base. This character is most reliable when interpreted in combination with other morphological features.

Antennal segmentation ranges from 12 to 16 segments, with variation observed both among and within species. However, consistent differences in segment number and the relative proportions of the second, third, and fourth antennal articles are used to distinguish morphologically similar species. Quantitative measurements obtained from multiple soldiers per species expand the ranges reported in earlier studies and facilitate clearer separation of intraspecific variation from interspecific differences, with overlapping ranges interpreted as intraspecific variation rather than evidence of distinct taxa. Morphometric variation among populations has also been documented in other Malaysian termites (Mee et al. 2025), highlighting the importance of considering such variation in morphological assessment.

Worker characters, including mandibular dentition and antennal structure, are largely conserved across species and therefore play a secondary role in species delimitation. Accordingly, worker morphology is used primarily to support genus-level placement rather than species-level identification. Overall, the integration of qualitative and quantitative soldier characters provides a robust and reproducible framework for delimiting *Bulbitermes* species in Sabah. These characters form the basis for consistent species recognition and provide diagnostic support for the species assignments presented in this study.

In addition, three taxa (*Bulbitermes* sp. E, *Bulbitermes* sp. 1, and *Bulbitermes* sp. 2) exhibit distinctive morphological characteristics that require careful taxonomic interpretation. *Bulbitermes* sp. E is characterised by a weakly constricted head capsule with a raised posterior bulge and a comparatively thickened rostrum, although interpretation is limited by the small number of available specimens. *Bulbitermes* sp. 1 exhibits a moderately constricted head capsule, a slight elevation at the base of the rostrum, and 12–13 antennal segments, but differs from *B. germanus* in possessing distinct marginal teeth on the mandibles. *Bulbitermes* sp. 2 is distinguished by weak constriction behind the antennal bases, absence of head bristles, a cylindrical rostrum, and 13–14 antennal segments, and differs from *B. prabhae* in head proportions and rostrum length. Accordingly, *Bulbitermes* sp. 1 and *Bulbitermes* sp. 2 are treated as provisionally identified forms (*Bulbitermes* cf. *germanus* and *Bulbitermes* cf. *prabhae*), while *Bulbitermes* sp. E is retained as an unresolved taxon pending further taxonomic evaluation.

Phenetic Cluster Analysis

Phenetic cluster analysis based on binary morphological characters revealed clear separation among *Bulbitermes*, *Lacessititermes*, and *Ceylonitermes*, supporting the taxonomic reassessments proposed in this study (Figure 2). The nearest-neighbour dendrogram shows that the three genera cluster only at a low similarity value of approximately 0.33 (Gower general similarity coefficient), indicating weak overall phenetic affinity. This separation confirms that the two taxa previously treated as *Bulbitermes* sp. F and sp. G are not conspecific with *Bulbitermes*. Diagnostic characters contributing to this separation include differences in abdominal tergite bristling, antennal proportions, hind femur length relative to the abdomen, and the presence of soldier and worker dimorphism.

In particular, the taxon previously recorded as *Bulbitermes* sp. F exhibits dimorphic soldiers, consistent with the diagnostic features of *Ceylonitermes* as outlined by Gathorne-Hardy (2001), thereby supporting its reassignment to that genus. Similarly, the taxon formerly designated as *Bulbitermes* sp. G displays morphological characters consistent with the generic diagnosis of *Lacessititermes* as defined by Thapa (1981), Tho (1992), and Gathorne-Hardy (2001), supporting its transfer to that genus.

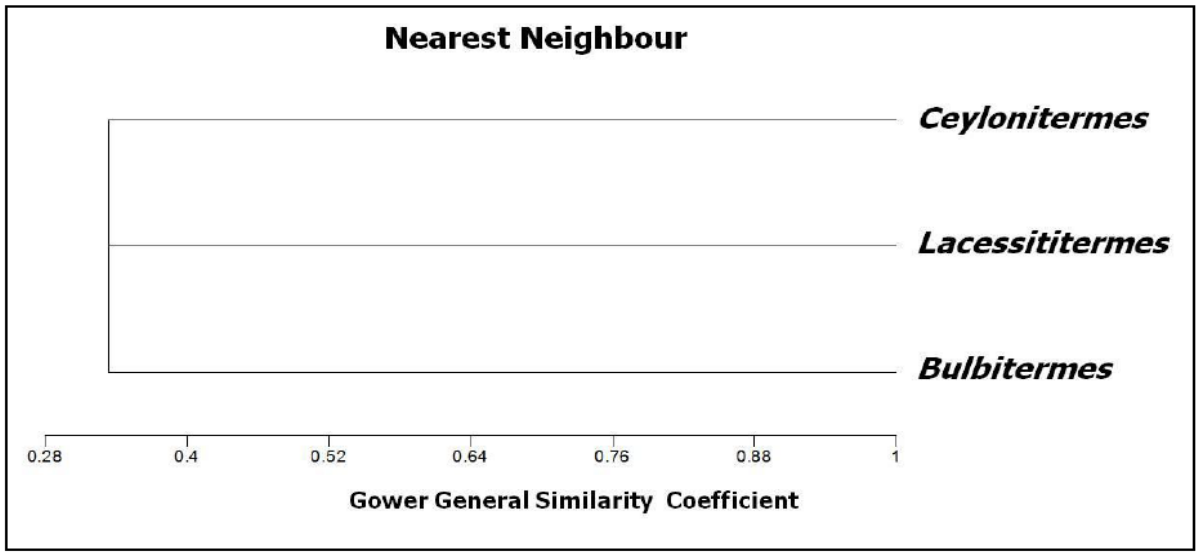


Figure 2. Nearest-neighbour dendrogram showing genus-level separation among *Bulbitermes*, *Lacessititermes* and *Ceylonitermes* based on Gower similarity coefficient

Phenetic analyses were conducted to evaluate overall morphological similarity among *Bulbitermes* taxa based on the binary character matrix described above. Similarity relationships were calculated using the Gower coefficient, which is appropriate for datasets comprising mixed morphological character types. Resulting similarity matrices were used to generate dendrograms based on nearest-neighbour (single linkage) and farthest-neighbour clustering methods, following principles of numerical taxonomy (Figures 3 & 4).

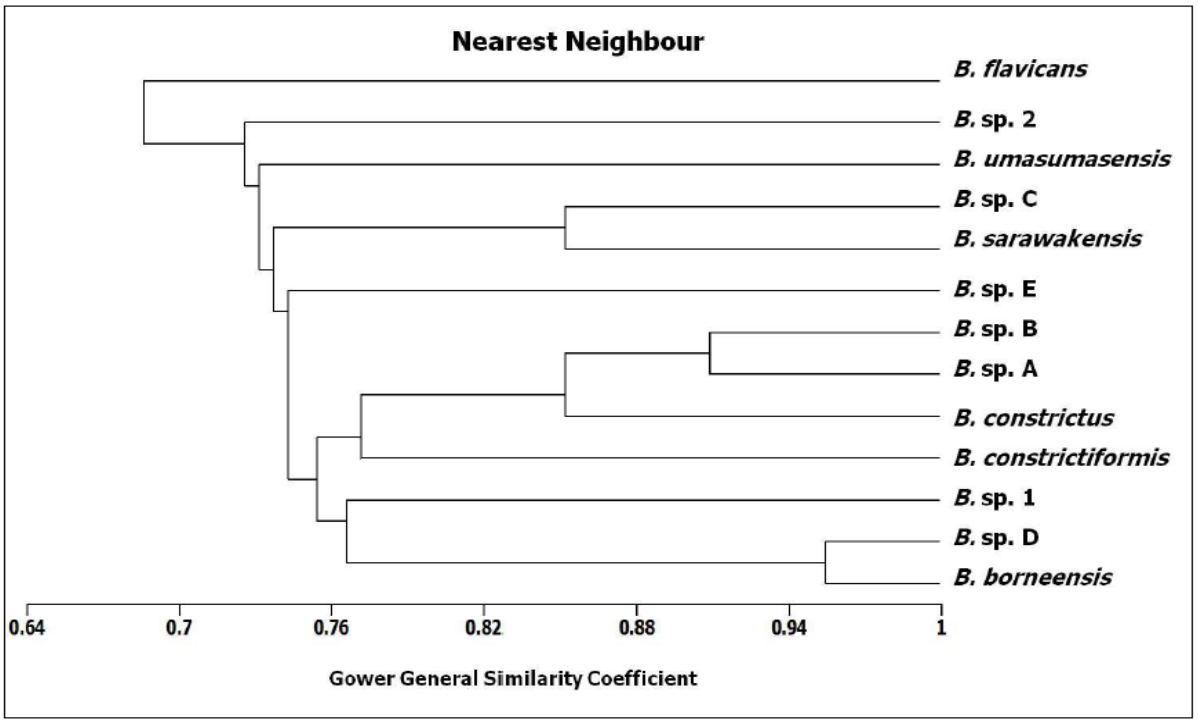


Figure 3. Nearest-neighbour dendrogram of *Bulbitermes* species based on Gower general similarity coefficient

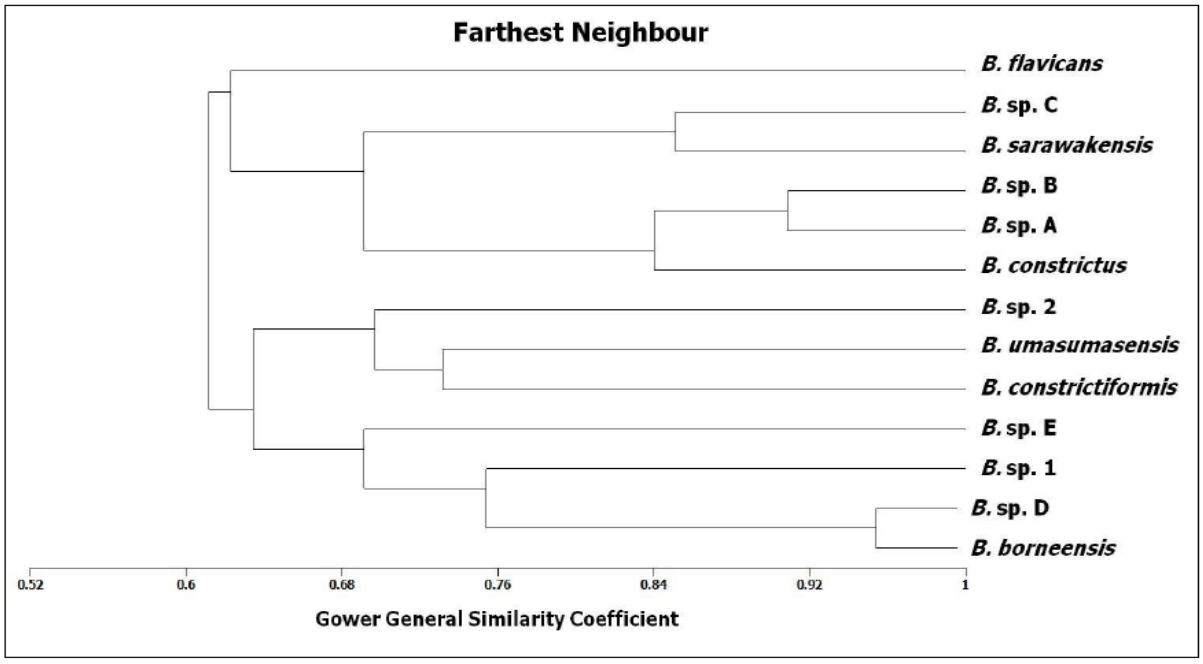


Figure 4. Farthest-neighbour dendrogram of *Bulbitermes* species based on Gower general similarity coefficient

The resulting dendrograms are consistent with species assignments based on diagnostic morphological characters and illustrate patterns of overall morphological similarity among taxa. Clustering patterns were interpreted in conjunction with diagnostic morphological characters to assess the consistency of species assignments. In this context, phenetic clustering

serves as a supplementary analytical tool, providing an overview of morphological resemblance among taxa without implying phylogenetic relationships or independent taxonomic decisions, and is not used as the primary basis for species delimitation, which relies on diagnostic morphological characters.

Patterns observed in the dendrograms are broadly consistent with the morphometric variation illustrated in the bivariate plot of total head length (including rostrum) versus maximum head width (Figure 5). The plot demonstrates partial overlap among morphologically similar taxa, particularly within groups corresponding to *B. constrictus* (including specimens reassigned from *Bulbitermes* sp. A and sp. B) and *B. sarawakensis* (including specimens reassigned from sp. C). A similar pattern is observed for *B. borneensis* and specimens reassigned from sp. D, which occupy overlapping morphometric space. These overlaps indicate that observed variation falls within the range of intraspecific morphological variability.

In contrast, taxa such as *B. flavicans* occupy distinct morphometric space with little or no overlap, supporting their clear separation based on diagnostic characters. Other taxa, including *Bulbitermes* sp. 1 and sp. 2, are positioned outside the main clusters and show limited or no overlap with examined described species. These taxa exhibit closest morphological similarity to *B. germanus* and *B. prabhae*, respectively, based on qualitative comparison with published descriptions (Tho 1992); however, these species were not included in the present analysis.

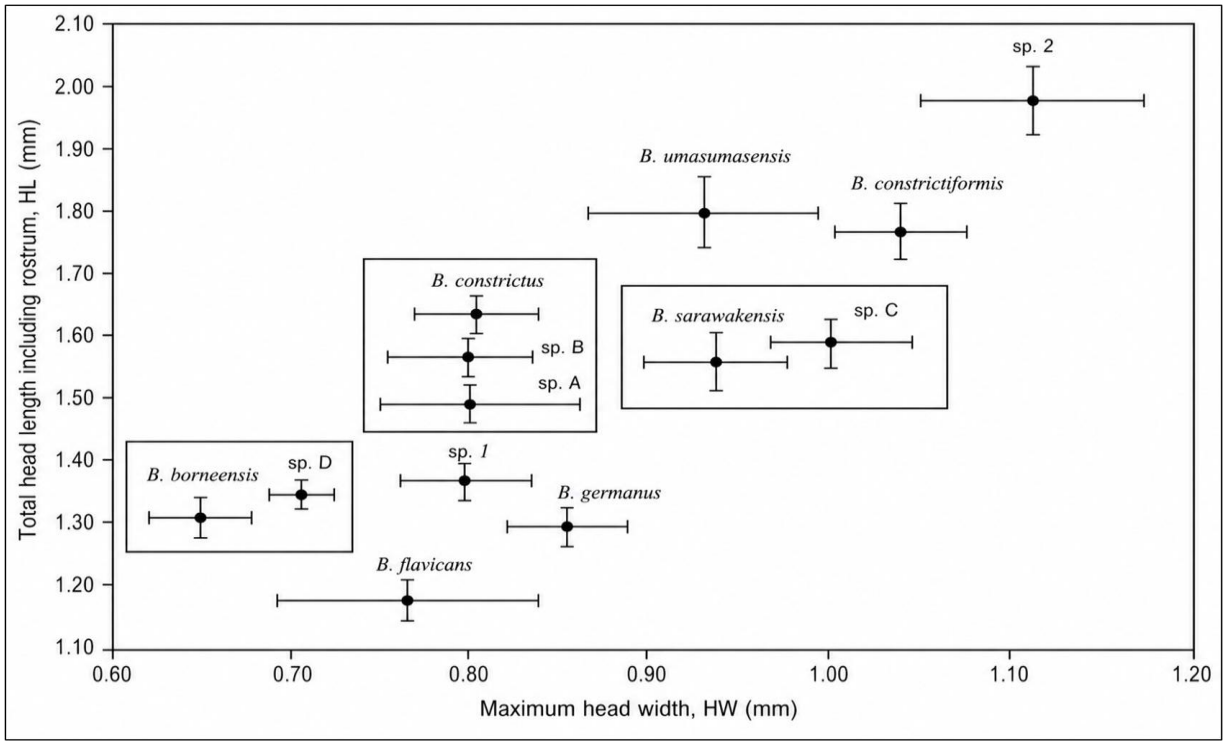


Figure 5. Bivariate plot of head length with rostrum versus maximum head width for *Bulbitermes* taxa. Points show means, error bars show ranges, and boxes indicate overlapping morphometric variation among taxa

Diagnostic Notes on *Bulbitermes* Species

Diagnostic characters of the examined *Bulbitermes* species generally conform to previously

published descriptions. Detailed comparison of specimens, including those previously designated as morphospecies, indicates that observed variation is consistent with intraspecific differences rather than representing distinct species.

Specimens assigned to *B. constrictus*, including those previously identified as *Bulbitermes* sp. A and sp. B, match the diagnostic description of the species in exhibiting a strongly constricted head capsule behind the antennal bases, a moderately elongate rostrum with slight thickening at mid-length, and comparable antennal segmentation (typically 13–15 segments). Quantitative measurements of head length and maximum head width fall within the range reported for *B. constrictus*, and substantial overlap in morphometric values is observed among all examined specimens. Minor differences, including slightly smaller head dimensions and variation in rostral bristle presence, are inconsistent and fall within the expected range of intraspecific variation.

Specimens corresponding to *Bulbitermes* sp. C are consistent with *B. sarawakensis* in overall head capsule shape, degree of constriction behind the antennal bases, and rostrum proportions. Antennal segmentation and morphometric measurements also fall within the range observed for *B. sarawakensis*. Although slight differences in proportional measurements were observed, these do not constitute stable diagnostic characters and are therefore interpreted as intraspecific variation.

Specimens previously designated as *Bulbitermes* sp. D correspond to *B. borneensis* in both qualitative and quantitative characters, including head capsule morphology, weak to moderate constriction behind the antennal bases, and relative head proportions. Morphometric ranges overlap extensively with those recorded for *B. borneensis*, and no consistent distinguishing characters were identified. In contrast, *Bulbitermes* sp. E remains unresolved due to limited material and incomplete character representation, preventing reliable comparison with described species.

Two additional taxa (*Bulbitermes* sp. 1 and sp. 2) exhibit consistent morphological differences from examined species and show closest similarity to *B. germanus* and *B. prabhae*, respectively (Tho 1992). However, differences in head proportions and antennal segmentation preclude confident assignment. These taxa are therefore treated as provisionally identified forms within *Bulbitermes* pending further integrative taxonomic evaluation.

Development of an Illustrated Identification Key

An illustrated identification key was developed to facilitate reliable identification of *Bulbitermes* species and related genera recorded in Sabah. The key was constructed primarily using diagnostic characters of the soldier caste, as this caste provided the most consistent and informative characters for species delimitation. Key characters employed include head capsule shape in dorsal and lateral views, degree of constriction behind the base of the antennae, rostrum shape and proportional length, antennal segmentation and relative head measurements. Characters were selected based on their stability across multiple colonies and their effectiveness in separating closely related taxa.

The key incorporates both genus-level and species-level diagnoses, enabling separation of *Bulbitermes* from *Lacessititermes* and *Ceylonitermes*, followed by identification of *Bulbitermes* species and diagnosable taxa recorded in Sabah. All taxa included in the key are defined by consistent diagnostic characters, ensuring that all terminal units represent clearly identifiable entities. Illustrations were prepared from microscope images to depict critical

diagnostic features and character states, thereby reducing ambiguity associated with textual descriptions alone. Compared with earlier keys, particularly Thapa (1981), the present key incorporates refined character definitions, revised terminology, and additional diagnostic features, improving usability for both taxonomists and non-specialist researchers. This key provides a practical tool for future taxonomic, ecological and biodiversity studies involving subfamily Nasutitermitinae termites in Sabah.

Genus-level Identification Key

A genus-level illustrated identification key (Figure 6) is provided to facilitate the separation of *Bulbitermes*, *Lacessititermes* and *Ceylonitermes* recorded in this study. The key is based primarily on diagnostic morphological characters of the soldier caste, including abdominal tergite bristling, antennal proportions, hind femur length relative to the abdomen, and the presence or absence of soldier and worker dimorphism. These characters were selected for their consistency across examined material and their effectiveness in distinguishing genera that exhibit superficial morphological similarity.

Species-level Identification Key for Bulbitermes

An illustrated species-level identification key (Figure 7) is presented for *Bulbitermes* species and diagnosable taxa recorded in this study. The key is based on soldier morphology and employs diagnostic characters such as head capsule shape in dorsal and lateral views, degree of constriction behind the base of the antennae, rostrum shape and proportional length, antennal segmentation, and relative head measurements. Taxa included in the key are defined by consistent combinations of diagnostic characters and, where applicable, supported by morphometric separation (Figure 5) and phenetic clustering. This key is designed to enable reliable species-level identification and to accommodate intraspecific variation observed across multiple colonies and localities.

Taxonomic Implications and Future Directions

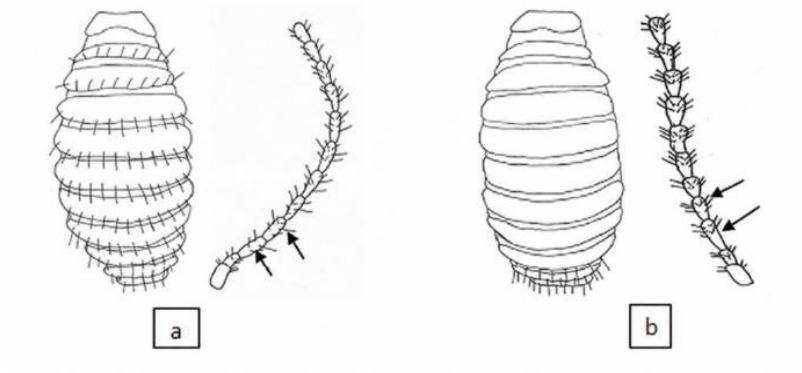
This study provides an updated taxonomic assessment of *Bulbitermes* in Sabah, resulting in improved resolution of species boundaries and clarification of the status of several previously ambiguous taxa. Detailed examination of soldier morphology allowed the recognition of multiple diagnosable taxa allied to described species, highlighting the presence of closely related but distinct forms within the genus.

The reassignment of two taxa formerly treated as *Bulbitermes* to *Lacessititermes* and *Ceylonitermes* refines current understanding of Nasutitermitine diversity in Sabah. The recognition of *Ceylonitermes* as a new genus record for Sabah highlights the substantial termite diversity of the region and reinforces the importance of continued systematic and integrative taxonomic research.

These findings emphasize the importance of detailed soldier caste morphology, particularly head capsule shape, constriction behind the base of the antennae, rostrum proportions, and antennal segmentation, in delimiting species within *Bulbitermes*. The expanded sampling effort and increased number of individuals examined per species further improved character assessment and reduced the potential for misidentification. Integration of molecular data with morphological evidence will be necessary to test species boundaries and confirm proposed affinities. Examination of type material and adoption of an integrative taxonomic framework combining morphological, molecular, and geographic data will be essential to resolve remaining uncertainties and refine species-level taxonomy within the genus.

1 Abdominal tergites with long bristles; third and fourth antennal segments at least twice as long as wide (a) ..... *Lacessititermes*

Long bristles seen at posterior tergites; third and fourth antennal segments not twice as long as wide (b) 2



2 Dimorphic soldier (a); hind femur equal or slightly longer than abdomen (b) ..... *Ceylonitermes*

Monomorphic soldier (c); hind femur shorter (rarely equal in few specimens) than abdomen (d) ..... *Bulbitermes*

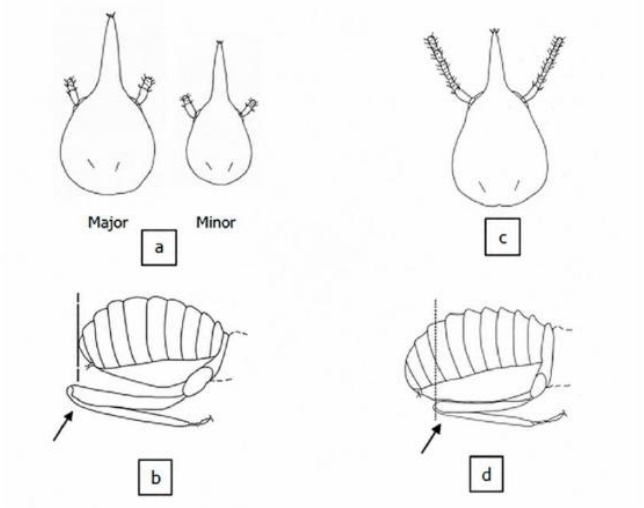
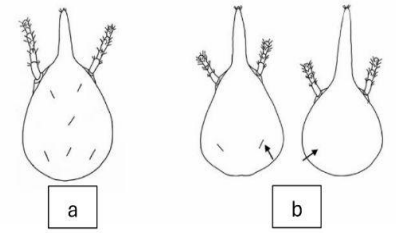
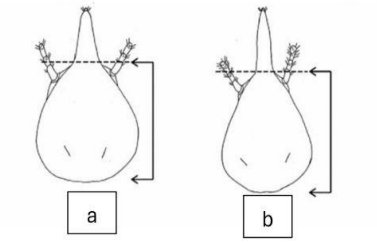


Figure 6. Genus-level identification key for *Bulbitermes*, *Lacessititermes*, and *Ceylonitermes* based on soldier caste morphology

1 Head with 5–7 bristles scattered around head (a) ..... *flavicans*
Head with or without a pair of bristle at posterior bulge (b) 2

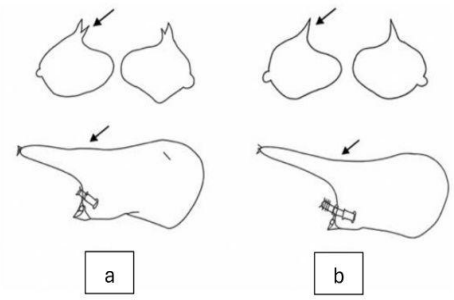


2 Head without rostrum in round-shaped; head dark coloured (a) 3
Head without rostrum in pear-shaped; head bright coloured (b) 5



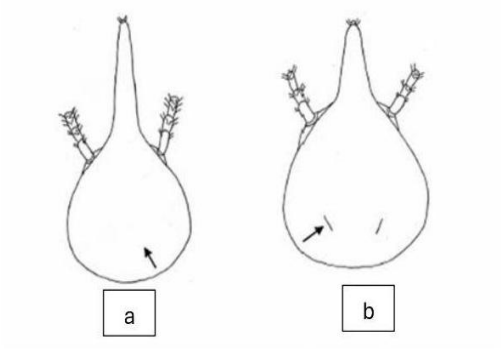
3 Distinct teeth present on both mandibles (soldier); have a slight hump at rostrum base (a) ..... *Bulbitermes* cf. *germanus*

Distinct teeth absent on both mandibles (soldier); slight hump absent at rostrum base (b) 4



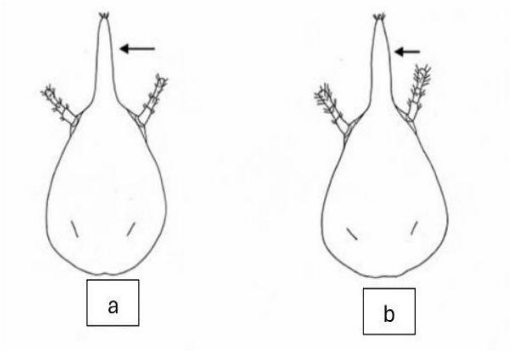
4 Head without bristle at posterior bulge; length of head to tip of rostrum 1.85–2.05 mm (a) ..... *Bulbitermes* cf. *prabhae*

Head with a pair of bristle at posterior bulge; length of head to tip of rostrum 1.44–1.75 mm (b) ..... *sarawakensis*



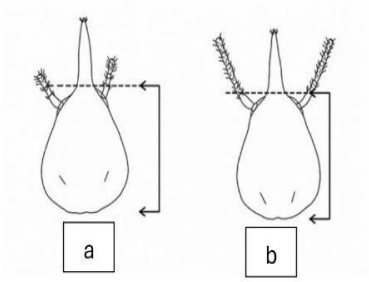
5 Rostrum cylindrical (a) ..... *umasumasensis*

Rostrum thicker at middle (b) 6



6 Smaller species; head length without rostrum is 0.83–0.90 mm (a) …… *borneensis*

Larger species; head length without rostrum is 0.98–1.25 mm (b) …… 7



7 Antennal segment four is longer than antennal segment two (a); length of head to tip of rostrum 1.42–1.65 mm (b); head length without rostrum 0.98–1.08 mm …… *constrictus*

Antennal segment four is subequal with antennal segment two (c); length of head to tip of rostrum 1.67–1.90 mm (d); head length without rostrum 1.13–1.25 mm …… *constrictiformis*

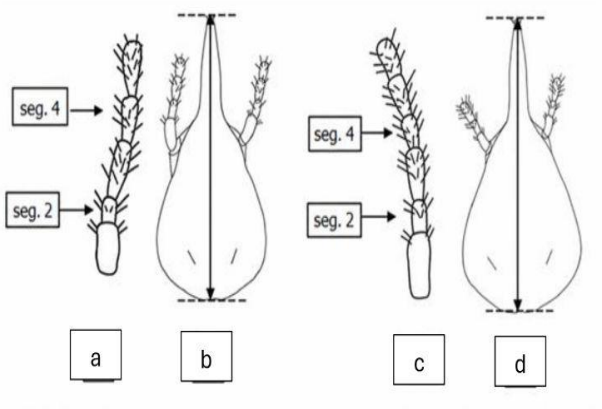


Figure 7. Species-level illustrated identification key to the soldier caste of *Bulbitermes* species and diagnosable taxa recorded from Sabah

CONCLUSION

A total of 15 taxa previously assigned to *Bulbitermes* in Sabah were reassessed using detailed morphological characters of the soldier and worker castes. Thirteen taxa were confirmed as belonging to *Bulbitermes*, while two were reassigned to *Ceylonitermes* and *Lacessititermes*, refining genus-level boundaries within Nasutitermitinae. Among the *Bulbitermes* taxa, six correspond to previously described species. Specimens previously designated as sp. A–D are

reassigned to *B. constrictus*, *B. sarawakensis*, and *B. borneensis* based on consistent agreement in diagnostic morphological characters and overlapping morphometric variation, indicating that the observed differences represent intraspecific variation rather than distinct taxa. Two taxa are retained as provisionally identified forms, *Bulbitermes* cf. *germanus* and *Bulbitermes* cf. *prabhae*, as consistent differences in diagnostic characters preclude formal assignment. One taxon, *Bulbitermes* sp. E, remains unresolved due to insufficient material for confident reassessment. The recognition of *Ceylonitermes* as a new genus record for Sabah and the clarification of species boundaries within *Bulbitermes* highlight the importance of detailed morphological assessment in resolving taxonomic uncertainty. Future integrative studies incorporating molecular data and examination of type material will be essential for resolving remaining uncertainties and establishing a stable taxonomy of *Bulbitermes* in Borneo.

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AUTHORS DECLARATION

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Conflict of Interest

The authors declare that they have no conflicts of interest.

Data Availability Statement

The data supporting this study's findings are available on request from the corresponding author.

Authors' Contributions

Nivaarani Arumugam (NA) contributed to study conceptualization, conducted data collection and analysis, administered the project, and drafted the manuscript. Homathevi Rahman (HR) contributed to study conceptualization, supervised all stages of the research, and reviewed and edited the manuscript

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