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Review of subterranean termites in India: Understanding taxonomy, distribution patterns and ecological functions

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Abstract

A plethora of extensive studies have been conducted to explore the diversity and distribution of termites in India, revealing a rich and diverse fauna across different regions. The field of termite taxonomy in India has been significantly influenced by historical taxonomic studies dating back to the late 18th century. Recent contributions have further expanded the list of known species. This review aims to examine the taxonomy, ecological roles and distribution patterns of subterranean termites in India, focusing on the integration of morphological and molecular methods to improve species identification. However, challenges remain, such as the lack of reliable morphological characteristics and standardised sampling methods. Therefore, further research and a comprehensive national strategy for termite taxonomy in India are required. Key findings highlight the effectiveness of holistic taxonomy in resolving cryptic species, addressing taxonomic ambiguities and developing conservation strategies. Furthermore, the study emphasises the importance of sustainable pest management practices tailored to India's diverse ecosystems. Various environmental factors, including climate, habitat preference and seasonal variation, influence the classification and distribution of termites. Holistic taxonomy has emerged as an important tool for conserving the diverse termite fauna in India by providing better insights into evolutionary relationships, which are crucial for termite management and conservation strategies.

Keywords

holistic taxonomic approaches; morphological characters; termite conservation; termite diversity

Introduction

In most ecosystems across the world, termites play a significant role as major agricultural and structural pests, vital decomposers and part of the food chain in the natural world. Termites, also known as "eusocial roaches", belong to the order Blattodea and have been one of the most prolific insect species on the planet for over 100 million years, colonising almost all regions except Antarctica. They are polymorphic insects living in large colonies in their architecture, the termitarium. A termite colony comprises reproductives (King and Queen), soldiers for defence and workers. Workers are involved in foraging, grooming, nest building and maintenance and feeding the young ones, soldiers and the royal pair (1). Termites, especially workers, appear white due to poor sclerotisation of the abdomen; hence, they are often referred to as white ants. The colony of social insects is not just a group of individuals but a functionally coordinated group with various interactions between their nest mates. Each caste is assigned specific tasks that coordinate the overall function of the colony. Sometimes, when there is a death of primary reproductive, the immature workers may develop into supplementary reproductives. Soldiers are responsible for the protection of nestmates and mounds (2).

Termites are ubiquitous in the tropical and subtropical regions and play a crucial role in the soil ecology. Termites contribute significantly to the maintenance of biodiversity in a range of ecosystems. It has various impacts on edaphic properties, particularly water infiltration, soil porosity, changes in the soil pH, changes in the soil texture and the role of microbial gut biota in organic matter transformation (3). Although termites play a beneficial role in the ecosystem, they are notorious pests that cause significant damage to crops and buildings (4). Despite the important economic and ecological functions served by subterranean termites, their hidden social structure makes it difficult to understand various fundamental biological aspects, including the dynamics of their populations, patterns of foraging behaviour, methods of species identification and distribution, differentiation of castes and their reproductive strategies. Identifying species and characterising colonies based solely on physical traits can be challenging (5). At this point, an integrative taxonomic approach that combines morphological and molecular methods is a viable solution (6, 7).

This review highlights the crucial role of taxonomic studies in India, revealing the complex ecological relationships among termite species and their habitats. These insights not only enhance our knowledge of biodiversity but also provide opportunities to develop effective strategies for minimising termite damage to human settlements and agricultural areas. Embracing holistic taxonomic approaches can pave the way for sustainable coexistence with these ancient and resilient insects.

1. Classification of termites

Termites are classified into various types, such as subterranean termites, dry wood termites, damp wood termites, Formosan termites and conehead termites (8). Taxonomy poses a significant challenge in the study and management of termites due to the vast diversity of species, a considerable number of which remain undescribed or inadequately documented, as well as the limited taxonomic expertise among many researchers. The classification of termites into families and subfamilies, which is widely adopted is as follows (9):

Family I	Mastotermitidae
Family II	Kalotermitidae
Family III	Hodotermitidae
Family IV	Rhinotermitidae
Family V	Serritermitidae
Family VI	Termitidae

A map of the worldwide generic richness of termites was given in a published article (10). The biogeographical region of Ethiopia is the richest in genera, while the Neotropical and Indo-Malayan regions are less rich. Different levels of Quaternary climatic disturbance were responsible for the differences in termite generic richness in the three tropical regions. The Computer-Aided Biological Identification Key (CABIKEY) for termites is a notable acronym for a series of CD-ROMs produced by CABI (Centre for Agriculture and Biosciences International) (11). Termites have been present for over 100 million years from the Mesozoic or late Palaeozoic period. *Uralotermes permianum*, from the Ural Mountains, was the oldest known evidence of the fossil termite (1). The molecular and genetic evidence from the recent phylogenetic studies indicated that the termites are descended from the cockroach lineage cladistically. Termites are considered the sister group of the genus *Cryptocercus*, a wood-eating cockroach (12).

2. Diversity and distribution in India

Globally, approximately 3,107 termite species have been identified, with 80 of these species recognised as serious pests belonging to the families Rhinotermitidae, Termitidae, Kalotermitidae, Hodotermitidae and Mastotermitidae (13). In India, the diversity of termite fauna is relatively limited, comprising 337 species and subspecies across 59 genera within seven families (14). Among these, ninety-two species are wood destroyers, with 35 reported as agricultural crop pests. The largest family of wood-destroying termites is Termitidae (41%), followed by Kalotermitidae (33%), Rhinotermitidae (18%), Stylotermitidae (7%) and Termopsidae (1%) . Notably, the genera *Odontotermes* includes 18 species, representing the largest share, followed by the genera *Neotermes* and *Microcerotermes* (15).

Koenig's pioneering 18th-century work provided the first scientific description of termite mounds in Southern India, probably from *Odontotermes redemanni*. He documented the presence of fungus combs in the nests and speculated that the fungi served as food for newly hatched termites. His findings laid the foundation for termite-fungi symbiosis and termite taxonomy in India (16). Later, a comprehensive overview of the largest termite family, Termitidae, which includes 239 species was published by (17). Subsequently, the imago, soldier and pseudoworker castes of a newly identified species, *Procryptotermes valeriae*, from Tamil Nadu, India, were detailed (18). In another study, a taxonomic examination was conducted on 95 species across five families: Kalotermitidae, Hodotermitidae, Rhinotermitidae, Stylotermitidae and Termitidae (19). In addition, the detailed keys and descriptions of 98 species from the families Hodotermitidae, Termopsidae, Stylotermitidae, Rhinotermitidae, Kalotermitidae and Indotermitidae in India have been published (20).

Eighteen termite species belonging to the two families Rhinotermitidae and Termitidae were identified in Kerala (21). In the Kasargod district of Kerala, *Heterotermes indicola* (Wasmann) was damaging old papers for the first time in Southern India (22). Additionally, *Coptotermes beckeri* Mathur and Chhotani, a subterranean termite species belonging to the

Rhinotermitidae family, was recorded for the first time in Kerala (23). Ten species from two families, Termitidae and Rhinotermitidae, spanning eight different genera were identified. *Hypotermes obscuriceps* was the most abundant species, followed by *Macrotermes convulsionarius*, while *Odontotermes feae* was the rarest species (24). In Southern Tamil Nadu, twenty-one termite species from twelve genera and five families were documented (25). Ten species were recorded from Gandhigramam, including *Cryptotermes tropicalis* Gay and Watson, *Cr. brevis* (Walker), *Cr. cynocephalus* Light, *Coptotermes formosanus* Shiraki, *Incisitermes minor* (Hagen), *I. immigrans* (Snyder), *Schaedorhinotermes actuosus*, *S. reticulatus* (Forgatt), *Zootermopsis angusticollis* (Hagen) and *R. flavipes* (Kollar) (26). Ten species of Termitidae and Rhinotermitidae were reported from the Coimbatore districts of Tamil Nadu (27).

A thorough taxonomic analysis of 35 termite species from Central India, divided into 14 genera and three families, of which only one was from Kalotermitidae under the genus *Cryptotermes* and two from Rhinotermitidae under the genus *Coptotermes*. Thirty species were described under Termitidae under four subfamilies, *viz.,* Macrotermitinae, Termitinae, Nasutitermitinae and Amitermitinae. The highest number of 15 species were described under *Odontotermes* and *Microtermes* of the subfamily Macrotermitinae. The study also included eight species from the state of Chhattisgarh (28). In another study, eight subterranean species of the termite genus *Odontotermes* were identified in Chhattisgarh, six of which were reported from the state for the first time (29).

Fifty species of termites have been identified in the state of Haryana, which fall under three families (Kalotermitidae, Rhinotermitidae and Termitidae), six subfamilies (Amitermitinae, Termitinae, Macrotermitinae, Apicotermitinae, Coptotermitinae and Heterotermitinae) and 12 genera (*Amitermes, Odontotermes, Microtermes, Microcerotermes, Heterotermes, Trinervitermes, Coptotermes, Eremotermes, Bifiditermes, Angulitermes, Speculitermes and Neotermes*) (30). Eight species, *viz., O. obesus* (Rambur), *O. redemanni*, *O. feae* (Wasmann), *M. obesi* (Holm.), *M. mycophagus* (Desneux), *T. biformis* (Wasmann), *H. indicola* (Wasmann) and *Co. hemi* (Wasmann), were collected from the samples from Rajasthan, Haryana and Uttar Pradesh (31). From Delhi region, *Bifiditermes beesoni* (Gardner), *Co. heimi* (Wasmann), *Amitermes belli* (Desneux), *Eremotermes paradoxalis* Holmgren, *Microcerototermes beesoni* Snyder, *Mi. tenuignathus* Holmgren, *Mi. mycophagus* (Desneux), *Mi. obesi* Holmgren, *O. bhagwatii* Chatterjee and Thakur, *O. dehraduni Snyder*, *O. giriensis* Roonwall and Chhottani, *O. obesus* (Rambur), *O. wallonensis* (Wasmann) and *Trinervitermes biformis* (Wasmann) were recorded (32). A taxonomic study on Gujarat's termite fauna recognised four families comprising sixty species and sixteen genera (33).

The Northeastern region comprises eight states of India, significantly known for its richness in flora and fauna and also harbours several termite faunas that are rich in composition in comparison to the other regions of India. Northeastern India harbours around 77 species and subspecies under 27 genera and five families (14). These families include Termitidae, Kalotermitidae, Rhinotermitidae, Stylotermitidae and Indotermitidae, representing about 3.5% of the global termite fauna and 25% of the termite species found in the Indian subcontinent (34). Arunachal Pradesh harbours the highest number of termites among all the states, with 44 species, followed by Meghalaya with 33 species, Assam and Tripura with 25 species each, Manipur with 12 species, Nagaland with 11 species and Mizoram with five species (14). The majority of *Reticulitermes* species in the Indian subcontinent are found in northeastern India and Bhutan. The Indian species *R. assamensis* (Gardner), distributed in Sikkim, Assam, Meghalaya and Arunachal Pradesh (35), *R. tirapi* (Chhotani and Das) in Arunachal Pradesh (34) and *R. saraswati* (Roonwal & Chhotani) in Meghalaya are endemic to the subcontinent (35). Additionally, *R. chinensis* (Snyder), distributed in Arunachal Pradesh and Assam, has been distinguished from *R. assamensis* (Gardner), highlighting its distinctiveness (19, 36). Thirteen species from the families Kalotermitidae, Rhinotermitidae and Termitidae have been recorded in northeastern India, including a new Kalotermitid species, *G. tikaderi* (Chhotani and Bose), which is distributed in Arunachal Pradesh (34).

Nineteen termite species were identified in the Andaman and Nicobar Islands (37). *Nasutitermes triloki* Bose, a member of the Nausitermitidae family, was discovered for the first time on Havelock Island in South Andaman (37). Additionally, that recorded the first instance of *Neotermes andamanensis* Snyder (Kalotermitidae family) in the Andaman and Nicobar Islands. The adult and soldier of two newly discovered species of termites, *Glyptotermes krishnai* and *G. nicobarensis,* were found in the great Nicobar Island in the Indian Ocean (38).

3.Host range and distribution of agriculturally important termites in India

Termites, being among the most polyphagous pests, are destructive to all cultivated crop plants . Approximately 35 species are known to contribute to such damage (39, 40). Infestations can lead to extensive damage to major crops, including rice, wheat, barley, maize, millets, sorghum, pulses, oilseeds, vegetables and various fruits such as guava, citrus, banana, mango, papaya and grapes, as well as sugarcane and cotton. It is crucial to implement effective measures to mitigate risks and protect crops from harm (33). In the drier regions of India, termite infestations have been recorded in maize, pearl millet, pulses, sugarcane, cotton, rice, peanuts, citrus fruits, vegetables, spices and other fruit crops (41). Additionally, termites pose a significant threat to forest ecosystems in India, where various species damage timber and wood products . Notably, species such as *Trinervitermes biformis, Odontotermes redemanni and O. bellahunisensis* have been identified as particularly destructive to eucalyptus plantations and silver oak and casuarina (15, 42). The distribution of termite species infesting various agro-ecosystems is summarised in Table 1.

Table 1. Host range and distribution of subterranean termites in India

S. No.	Termite species	Distribution	Host	Reference
1.	*Anacanthotermes viarum* (Konig)	Rajasthan, Drier parts of South India	Paddy, Millets and Grasses	(36)
2.	*Coptotermes ceylonicus* Holm.	Tamil Nadu Andhra Pradesh and Kerala	Tea, *Acacia sp., Albizia chinensis, Alerites moluccanus, Camellia sinensis*	(43)
3.	*Coptotermes heimi* (Wasmann)	U.P, Bihar and Gujarat	Sugarcane, Wheat, Apple, Mango, Coconut	(33)
		Gujarat	Palm, ficus	(44)
4.	*Eremotermes paradoxi* Holm.	Rajasthan	Sugarcane	(45)
5.	*Eurytermes topslipensis* (Chatterjee and Thapa)	Kerala	Eucalyptus	(46)
6.	*Microcerotermes beesoni* Sydner	Haryana	*Dalbergia sissoo*	(47)
7.	*Microcerotermes heimi* Wasmann	Kerala	Dried roots of bamboo	(46)
8.	*Microcerotermes pakistanicus* Akhtar	Kerala	Cashew, tea	(46)
9.	*Microtermes mycophagus* Desneux	Gujarat	Groundnut, Wheat, Barley, Bajra, Sugarcane	(44)
10.	*Microtermes obesi* Holmgren	Rajasthan, Haryana and Gujarat	Groundnut, Wheat, Barley, Oats, Maize, Bajra, Jowar, Sugarcane, Tea	(47, 48)
11.	*Microtermes tenuignathus* (Holm.)	Arid Zone of Rajasthan	Wheat	(49)
12.	*Nasutitermes* sp.	Tamil Nadu, Karnataka, Kerala, Meghalaya, Uttar Pradesh, Nicobar Islands, Tripura, Orissa, Assam, West Bengal, Arunachal Pradesh and Andaman Islands.	Wheat	(50)
13.	*Odontotermes assmuthi* Holm	Gujarat	Sugarcane	(44)
14.	*Odontotermes bangalorensis* (Holm. and Holm.)	UP, Maharastra, AP and Tamil Nadu	Wheat, Sugarcane	(44)
15.	*Odontotermes bellahunisensis* Holmgren and Holmgren	North West Zone	Sugarcane, *Cocos nucifera, Eucalyptus sp. and Tectona grandis*	(47)
16.	*Odontotermes bruneus* (Hagen)	Haryana	*Pterocarpus marsupium, Tectona grandis,Santalum album* and *Dalbergia sissoo*	(47)
17.	*Odontotermes ceylonicus* (Wasmann)	Kerala	Ficus	(46)
18.	*Odontotermes distans* Holmgren and Holmgren	Haryana	Mango, *Shorea robusta, Pinus roxburghii, Engelhardtia spicata, Syzygium nudiflora, Shorea robusta*	(47)
19.	*Odontotermes escherichi* (Holmgren)	Kerala	Millets	(46)
20.	*Odontotermes feae* (Wasmann)	Kerala	Mango, *Butea monosperma, Eucalyptus sp., Dalbergia latifolia, Dipterocarpus indicus, Tectona grandis, Gmelina arborea, Madhuca longifolia, Terminalia crenulata, Pterocarpus marsupium, Syzygium cumini* and *Garuga pinnata*	(53)
21.	*Odontotermes giriensis* Roonwal and Chhotani	Haryana	*Celtis australis* and *Dalbergia sissoo*	(47)
22.	*Odontotermes guptai* Roonwal and Bose	Rajasthan	Bajra	(51)
23.	*Odontotermes gurdaspurensis* (Holmgren and Holmgren)	Rajasthan Haryana	Wheat,Barley, Maize, *Pinusroxburghii, Pinuswallichiana* and *Eucalyptus sp.*	(47, 51)
24.	*Odontotermes horni* (Wasmann)	North west Zone of India	Sugarcane, Cashew, Tamarind, *Eucalyptus sp.* and *Hevea brasiliensis*	(44)
25.	*Odontotermes latigula* Snyder	Haryana	Barley	(40)
26.	*Odontotermes latiguloides* (Roonwal and Verma)	Haryana	Barley, *Acacia tortilis*	(40)
27.	*Odontotermes obesus* (Rambur)	Rajasthan Kerala Haryana	Groundnut, Wheat,Barley, Maize, Tea, Bajra, Jowar, Sugarcane, Cotton, Chillies, Tea, Mango, Citrus, Grapevine, Peach, Japanese Mint, *Abies pindrow, Eucalyptus sp., Bamboo sp., Cassia fistula, Ficus benghalensis, Calophyllum sp., Shorea robusta, Pinus wallichiana* and *Garuga pinnata*	(47, 51, 40)
		Gujarat North west Zone	Sugarcane	(44)
		Rajasthan	Bajra	(51)
		Andhra Pradesh, Tamil Nadu, Kerala	Wheat, Barley, Maize	(52, 41)
28.	*Odontotermes redemanni* (Wasmann)	Kerala, Tamil Nadu	Coconut, *Acacia sp., Mangifera indica, Shorea robusta, Cassia siamea, Artocarpus hirsutus, Pterocarpus marsupium, Dalbergia latifolia* and *Terminalia coriacea*	(41)
		Haryana	Eucalyptus	(47)
		Gujarat	Sugarcane, wheat	(44)
29.	*Odontotermes taprobanes* (Walker)	Southern India	Sugarcane	(44)

30.	*Odontotermes taprobanes* (Walker)	Southern India	Sugarcane	(44)
31.	*Odontotermes vaishno* Bose	North West Zone	Sugarcane	(44)
32.	*Odontotermes wallonensis* (Wasmann)	Karnataka	Groundnut, Maize, Coconut, Mango, Jackfruit, Cashew, *Tectona grandis, Boswellia serrata, Eucalyptus sp., Pterocarpus santalinus, Pterocarpus marsupium, Cassia siamea, Syzygium cumini* and *Dalbergia latifolia*	(53)
33.	*Trinervitermes biformis* (Wasmann)	Himalayan Region	Groundnut, Sugarcane, Vegetables	(54)

4. Taxonomic identity

4.1 Morphological characteristics of subterraneantermites in India : In order to categorise Indian termites accurately, it is important to have a deep understanding of their physical characteristics. This section provides a comprehensive overview, including identification keys and discusses the finer points of physical features used in taxonomy. Indian termites have a range of physical adaptations that correspond to their various ecological roles. For a general introduction to morphological features such as body segmentation, antennal structure and reproductive caste characteristics. The identification of termite species is based on the mentioned features and the observations of the worker and soldier caste. When it comes to termite taxonomy, identification keys are important resources for scientists and entomologists. Termite identification keys for India have been published earlier (20). These keys help the user in distinguishing closely related species by providing a systematic procedure and a set of morphological characters. The incorporation of advanced imaging technologies has increased the accuracy and user-friendliness of these identification keys. The morphology of the soldier caste is often a key factor in the classification of termites (56). In a species-rich ecosystem, identification of termites may be possible based on important key features (Fig. 1), namely: number of antennal segments, length of antenna, length and width of labrum, head length with mandibles, head length to base of mandibles, maximum width of head, length of mandibles, distance of teeth from tip, maximum length and width of pronotum, length of thorax and maximum length and width of postmentum (27). The morphological key characters of subterranean termite genera and species in India are summarised in Table 2.

***4.2 Molecular insights into termite taxonomy*:** Molecular genetic methods have revolutionised our understanding of subterranean termites. These tools provided new insight into fundamental processes such as development and caste differentiation. Molecular techniques helped to comprehend the reproductive structures and colony and population dynamics of termites that were previously difficult to understand due to their secretive nesting and feeding habits (57). Since termites scavenge and damage wood outside of their nests, their taxonomy depends mainly on the soldier and worker caste (58). Identifying termite species through their morphological characteristics can be challenging since there are limited diagnostic markers, which are usually restricted to the soldier or alate castes. In such cases, DNA barcoding or sequencing of gene fragments has become a significant molecular technique, extensively used to determine the evolutionary relationships among different taxa and to categorise species. A certain level of skill is required in utilising taxonomic keys to prevent errors in similarities that are difficult to distinguish (59). DNA analysis is a promising method for species identification due to the stability and longevity of DNA (60). Furthermore, it has the ability to resolve issues related to morphological identification in specimens that are damaged (61). Mitochondrial genome sequences, including the cytochrome oxidase genes, 16S rDNA and AT-rich region, are effective substitutes for identifying species and performing phylogenetic analyses (62, 63). A comprehensive analysis of contemporary termite phylogenetics, focusing on tree topologies as phylogenetic hypotheses, provides crucial insights into both the systematic placement of termites within the Dictyoptera and the evolutionary relationships between termite families (64). Recent studies have focused on the position of Isoptera within Dictyoptera and the

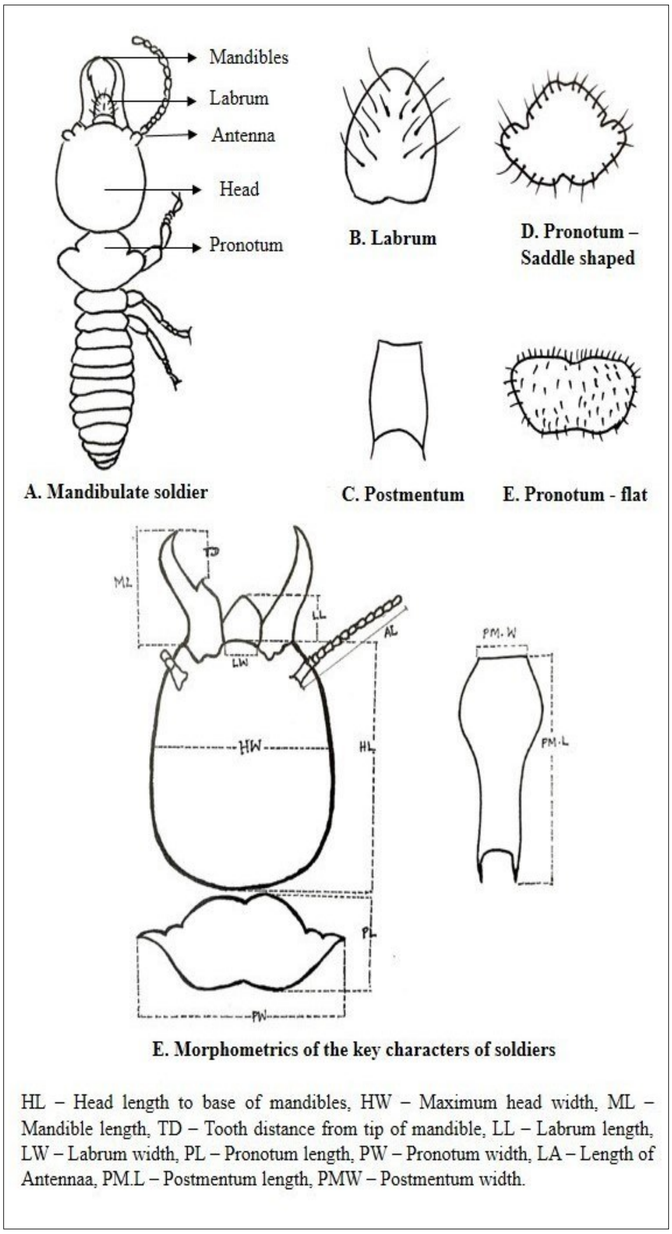

Fig. 1. Schematic representation of morphological characters used for identification of mandibulate soldiers.

Table 2. Morphological key characters

Sl. No.	Name of the Family/ Genus/ species	Morphological Characters	Reference
	FAMILY: RHINOTERMITIDAE Froggatt	Pronotum flat.	(19)
	Genus: Coptotermes Wasmann	Head capsule oval-shaped; fontanel large, circular and lying medially on the inner margin	(19, 31)
1.	*Coptotermes ceylonicus* Holm.	Postmentum somewhat narrower and gradually narrowing at the waist; head capsule slender, length to the base of the mandible 1.30-1.40 m	(19)
2.	*Coptotermes heimi* (Wasmann)	Larger species; the waist of the postmentum lies in the middle of the line connecting the level of maximum width and the posterior margin; the postmentum has a minimum width of 0.25-0.34 mm; head: length 1.2–1.4, width 1.0–1.35 mm; soldier population maximum in a colony.	(19, 31)
	Family: TERMITIDAE Westwood	The pronotum appears saddle-shaped.	(19, 31)
	Genus: Eurytermes Wasmann	Mandibles not very broad at the base, each with a small tooth	(19)
3.	*Eurytermes topslipensis* (Chatterjee and Thapa)	Head with almost parallel sides; mandibles weakly incurved apically; tooth on left mandible obtuse and short	(19)
	Genus: Eremotermes Silvestri	Head with frontal projection; mandible long, slender, slightly to noticeably curved approximately in the centre at the outer edge and slightly curved apically	(19)
4.	*Eremotermes paradoxi* Holm.	Head width 0.68–0.75 mm; pronotum width 0.40–0.45 mm; frontal projection weak to well developed; mandible generally shorter than the bulge; smaller species	(19)
	Genus: Microcerotermes Silvestri	Mandibles fine, without any crenulations; left mandible devoid of tooth	(19, 31)
5.	*Microcerotermes beesoni* Sydner	Mandibles shorter (0.80–0.92 mm long). Pronotum weakly notched at the postor	(17)
6.	*Microcerotermes heimi* Wasmann	Head generally larger, length 1.20–1.25, mandibles weakly curved at the tips. Max. Width of postmentum approximately in the centre	(17)
7.	*Microcerotermes pakistanicus* Akhtar	Index mandible-length/head-length 0.46–0.56 indicates that the mandible is significantly shorter than the head.	(17)
8.	*Microtermes mycophagus* Desneux	Antennae with 15 segments	(19, 31)
9.	*Microtermes obesi* Holmgren	The second segment of the antennae is as long as the third and fourth segments combined, with a moderately hairy head capsule.	(19, 31)
10.	*Microtermes tenuignathus* (Holm.)	Head: 1.0–1.27 mm in length, usually smaller. Mandibles with a more curved tip. Maximum width of the postmentum on the anterior side	(17)
11.	*Genus: Nasutitermes* Dudley *Nasutitermes* sp.	Head pear-shaped or round; antenna 12–13 segmented; mandible with or without spine-like process	(19)
	Genus: Trinervitermes Holmgren	Head formed into nasute; mandibles degenerated	(19, 31)
12.	*Trinervitermes biformis* (Wasmann)	Antennae with 12–14 segments; pronotum with a weak anterior notch; in the fourteen-segmented state, the third segment is marginally longer than the second.	(19, 31)
	Genus: Odontotermes Holmgren	Left mandible with a prominent tooth on the inner edge	(19, 31)
13.	*Odontotermes assmuthi* Holm.	Mandibles generally shorter and thicker, with a base length that is slightly longer than half the length of the head (index mandible-length / head-length 0.51–0.57). The tooth situated in the distal third of the mandible is approximately the left mandible (tooth index 0.33–0.37).	(17)
14.	*Odontotermes bellahunisensis* Holmgren and Holmgren	Mandibles are relatively longer in smaller species, with head index of 0.52–0.57 mm; head length to base of mandibles 1.20–1.25 mm, head width 1.08–1.10 mm	(19)
15.	*Odontotermes bruneus* (Hagen)	Head length to mandibular base: 1.75–2.03 mm; larger species	(19)
16.	*Odontotermes ceylonicus* (Wasmann)	Left mandibular tooth situated in the center; head subrectangular, sides sub straight	(19)
17.	*Odontotermes distans* Holmgren and Holmgren	Tooth of the left mandible tiny and located in the basal third of the mandible	(17)
18.	*Odontotermes escherichi* (Holmgren)	Pronotum very slightly notched at anterior and posterior margins. Postmentum a little longer than broad	(17)
19.	*Odontotermes feae* (Wasmann)	The mandible's tooth index is 0.50–0.54 mm and the posterior third of the mandible has the widest head capsule. The tooth on the left mandible lies close to the center.	(31)
20.	*Odontotermes giriensis* Roonwal and Chhotani	Sabre-shaped, thin mandibles with a weaker distal curvature. The left mandible's tooth is positioned more anteriorly (index tooth length/ apex = 0.21-0.27). The postmentum's sides abruptly narrowed in front.	(17)

21.	*Odontotermes guptai* Roonwal and Bose	More hair on the head and body. 15-16 segment antennae. Stronger and shorter mandibles. The anterior margin of the labrum is widely rounded. Convex sides of postmentum	(17)
22.	*Odontotermes gurdaspurensis* (Holmgren and Holmgren)	Head length to base of mandibles 1.42-1.63, max. head width 1.20–1.40 mm. Head rectangular oval, sides straighter. Mandibles longer	(19)
23.	*Odontotermes horni* (Wasmann)	Sides of head straighter, slightly converging in front; left mandibular tooth slightly below the centre	(19)
24.	*Odontotermes latigula* Snyder	The head's convergence index (0.60-0.68) indicates that it is less convergent in front and widest in the middle. The left lower jaw tooth is positioned backward.	(17)
25.	*Odontotermes latiguloides* (Roonwal and Verma)	smaller species Head width: 1.0-1.21 mm, head length to base of mandibles: 1.0-1.26 mm. Labrum: broadly rounded, tongue-shaped anterior	(17)
26.	*Odontotermes obesus* (Rambur)	Mandibles thicker and stouter; larger species; head length 1.15-1.48, head-width 0.98-1.18	(19)
27.	*Odontotermes obesus* (Wasmann)	Mandibles thicker and stronger; larger species; head length 1.15-1.48, head width 0.98-1.18	(19)
28.	*Odontotermes redemanni* (Wasmann)	Mandible longer, outer margin shortly bent near the basal third; mandibular index length/head length 0.69–0.79 mm	(19, 31)
29.	*Odontotermes vaishno* Bose	Labrum rounded at anterior margin, wider than or as wide as length. Antennas made up of sixteen segments. Mandibles with greater distal curvature and the left mandible's tooth in the distal third	(17)
30.	*Odontotermes wallonensis* (Wasmann)	Head length to the base of the mandibles 1.53-------1.68 mm; smaller species	(19)
	Family: HODOTERMITIDAE Desneux	Ocelli absent, antennae long, with 22-23 segments	(19)
31.	*Anacanthotermes viarum* (Konig)	Frons rugose, with several transverse ridges in the middle. Mandibles larger and apically less curved (Index Left mandlble-length/ Head length to mandible-base 0.66-0.76)	(56)

relationships among Isoptera families. It is now widely accepted that the Mastotermitidae is the most primitive family of termites (64).

The taxonomical identification of termites is primarily based on soldier characteristics, particularly the mandibles. Damage to the mandibles during collection and preservation, as well as crisscrossing or interlocking of the mandibles, makes it difficult to confirm the genus or species level using soldier mandible characteristics. Alates, the reproductive forms of termites, are typically found before dawn but are rarely encountered alongside soldiers and workers. As a result, matching the alate form with other castes of the same termite species can be challenging, especially in areas with high termite diversity. In such cases, molecular tools provide the best solution for species identification and confirmation. Additionally, these tools offer researchers an extra method for examining the relationships between species and evaluating the accuracy of classification schemes (58). Mitochondrial DNA is predominantly used for confirming insect species at the molecular level using universal mitochondrial cytochrome oxidase primers, due to its ease of isolation, even from poorly preserved samples. The 16S rRNA gene is significant in phylogenetic research across a broad range of insects because of its moderate size and the variation in evolutionary rates among sequences (65). The first molecular analysis of the relationships between the five families, considering ten genera, using 16S rRNA (66). Universal termite oligonucleotide primers 16S 104F (5'-CCTCYCATCRCCCCAACRAA-3') and 16S 368R (5'-TTGAAGGGCCGCGGTATYTT-3') were designed using composite termite sequences. These primers amplify the 16S rRNA region of the mitochondrial gene at 262 bp, whereas the DNA product amplified using the Formosan-specific primers FST-F (5'-TAAAACAAACAAACAACAAACAAAC-3') formed an additional band at 221 bp. This helps to differentiate Formosan termites from other termite species in the study (67).

5. Ecological factors influencing termite taxonomy

The major ecological factors influencing the spread of termites in India include monsoon rainfall, air temperature and humidity, vegetation, altitude, soil type, natural enemies and other associated organisms (68).

5.1 Climate and seasonality on termite taxonomy: The temperature and humidity levels in the environment are crucial factors that greatly affect termites. Individual species of termites are influenced by temperature and they are highly sensitive to changes in air temperature. Both of these factors play a significant role in determining the distribution of termites. In hot and arid regions, many species retreat deep into the ground during the midday heat, with early morning being the most active period for foraging (68). *Archotermopsis wroughtoni*, the primitive termite, can withstand a broad range of temperature fluctuations. In the regions that *A. wroughtoni* visits, summer temperatures frequently reach 37.7 °C in June and drop almost to freezing in December and February. Throughout all of these months, the termites continue to be active (68, 69). It is unclear how *Archotermopsis wroughtoni* insulates its nest against temperature fluctuations, as it does not build termitaria. Although external temperatures vary considerably more, the interior of the mounds of *Odontotermes obesus* varies slightly with the seasons (68).

Indian termites have been studied extensively for their tolerance to moisture and water stress. While little is known about their temperature tolerance, most species prefer high humidity levels close to the saturation point. However, species belonging to other families do not have the same tolerance for low humidity levels as those in the Kalotermitidae, which can survive for longer periods in low-humidity conditions. *Neotermes*, one of the Kalotermitidae, can withstand a relative humidity of up to 98%, while *Bifiditermes beesoni* and *Cryptotermes bengalensis* can cope better with 92% RH (68, 71). Rapid mortality of termites at a relative humidity of 98%, possibly due to water intoxication (72).

The termite from northern India that builds carton nests, *Microcerotermes beesoni*, has been shown to exhibit seasonal variations in its nesting population (71). On average, a larger percentage of wooden stakes were infested in summer than in winter (73). In the study, higher termite diversity was observed in the summer months (July, August and September), when air and soil temperatures are favourable for termite activity in the summer (74). According to findings, the Western subterranean termite, *Reticulitermes hesperus* Banks, prefers temperatures between 29 and 32 °C, with workers favouring 14 and 19 °C (75).

5.2 Habitat preferences and distribution: Termites are important lignocellulose-digesting insects that consume wood. They also have a variety of symbiotic microorganisms in their guts (76). A study conducted in South India observed that topography, soil type and cropping patterns all had an impact on the diversity and abundance of subterranean termites (77). In the Bhadrachalam forest region of Andhra Pradesh, 11 out of 13 species were plant pests (78), of which *O. obesus* (24%) was the most dominant. Other significant plant pests included *O. brunneus* (16%), *O. redemanni* (13%), *O. wallonensis* (12%), *Heterotermis indicola* (6%), *Microcerototermes beesoni* (6%), *O. guptai* (5%), *Coptotermes hemi* (4%), *Microtermes obesi* (3%), *O. feae* (2%) and *O. indicus* (1%). In tropical lowland ecosystems, termites are the primary decomposers, making up to 95% of the biomass of soil insects. The diversity of termite species is the highest in tropical closed-canopy rainforests, where over 90% of species are members of the Termitidae family (64, 79). In addition to being the largest family, the Termitidae also show the highest level of behavioural and ecological diversity. Moisture is an important and most essential factor for the subterranean termites. Hence, they live in or near the soil surface and connect with their food resources through mud galleries, sheets, or small connecting mounds. These connecting shelter tubes are made of chewed cellulosic materials with saliva, excreta and soil (80). Some termites, such as *Microcerotermes* and *Nasutitermes*, are typical of forest vegetation, while others, such as *Trinervitermes* and *Anacanthotermes,* are limited to the grasslands. A forest seems to be a useful barrier against *Trinervitermes*, even though most humid rainforests harbour a comparatively higher number of termite genera. It can be claimed that *Eurytermes* is only found in deciduous forests of the central and peninsular areas of India, including Ceylon (81). Habitat preferences of some subterranean termites have been mentioned in Fig. 2.

To enhance termite management and conservation strategies, it is essential to understand factors like moisture levels, soil types and vegetation, which significantly influence termite populations (82, 83). Effective practices should aim to deter pest species while supporting beneficial termites, particularly in biodiverse ecosystems such as tropical rainforests, where they contribute to decomposition and nutrient cycling (83). Incorporating indigenous ecological knowledge can improve termite control, especially in regions where communities utilise traditional practices. For instance, in India, indigenous methods often involve using natural barriers and specific planting techniques to minimise termite infestations (85). The proper tillage and mulching can effectively manage termite activity and increase yields under conservation agriculture, indicating the importance of integrated agricultural practices (84). By combining traditional knowledge with modern methods, we can create effective pest management strategies that promote sustainable agricultural productivity and conservation (85).

6. Holistic taxonomy for termite conservation

Holistic taxonomy is an approach that utilises quantitative methods to identify species across various datasets, aiming to extend beyond qualitative comparisons. It has developed to include multiple datasets for species delimitation, achieved either through congruence or accumulation (84, 86). The Holistic taxonomic approach operates on the principle of combining as much evidence as possible to define species boundaries (87, 88), incorporating genetic (both mtDNA and nuclear), morphological, distributional and ecological data (89). The effectiveness of Holistic taxonomy in delimiting species within cryptic species complexes of conservation concern (87). This approach, by integrating multiple data sources, is essential for accurate species identification and classification, which is particularly important for termite conservation. The importance of accurate termite taxonomy

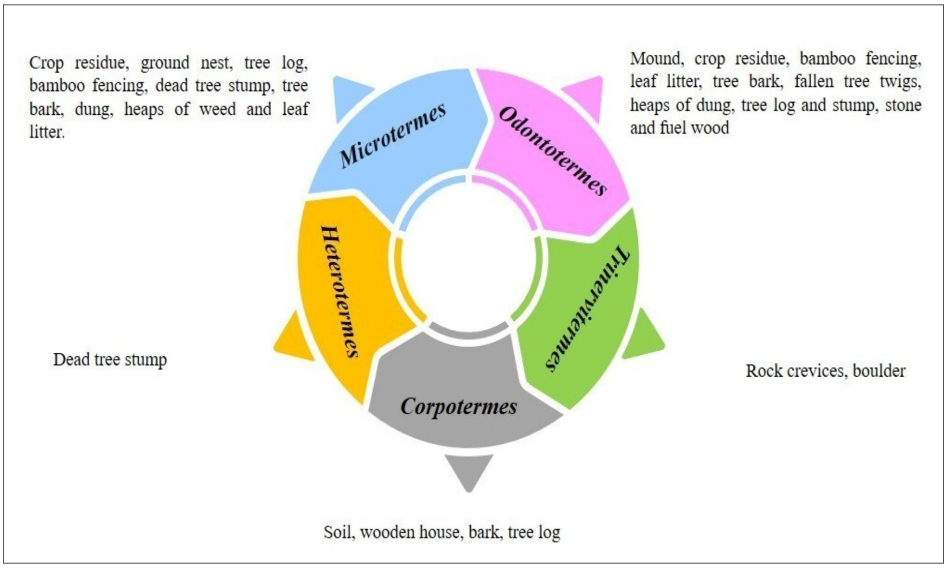

Fig. 2. Habitat preferences of some subterranean termites.

for conservation management is crucial, as it can help to identify and prioritise species of conservation concern (58, 88). There is a need for molecular markers and barcoding techniques to overcome the taxonomic challenges of termites (91). However, a coordinated national strategy for taxonomy and systematic research is essential in India (86), which could further advance the use of integrative taxonomy in termite conservation. The imperative for sustainable termite management can be enhanced through the application of eDNA approaches (91). The potential of eDNA in monitoring biodiversity and reconstructing paleoenvironments highlights its relevance in understanding termite diversity and evolution (92).

7. Challenges and limitations in holistic termite taxonomy

Termites are vital as ecosystem engineers, yet their identification is often complicated due to the scarcity of consistent morphological features specific to many species, which impedes ecological research (90). The taxonomy of termite pests in tropical regions, where diversity is extensive, poses numerous challenges. Taxonomists work with the available tools, specimens and data, continually refining our knowledge of termites (58). The field of integrative termite taxonomy faces significant challenges, including the difficulty of identifying species due to the lack of reliable morphological characters (90). This is compounded by the need for standardised sampling methods, which vary across habitats and biogeographical regions (93). Despite these challenges, there is potential for the integration of indigenous knowledge, such as farmers' knowledge of termite diversity and damage in agroforestry (94). In addition, the use of biological control methods, such as entomopathogenic nematodes and fungal pathogens, can be a valuable tool in integrated termite management (94). Although it has been determined that there is only one main pest species in the majority of Southeast Asia, the puzzle of subterranean termites invading buildings in the region has not been fully solved. Observation of several pest species of *Coptotermes* in neighbouring areas bears a strong resemblance to Asian subterranean termites, potentially representing the same species under different names. This complex of species, found from India in the west to the Philippines in the east, includes taxa like *C. heimi*, *C. ceylonicus* and *C. vastator*, which show significant morphological overlap with *C. gestroi*, differing only slightly (95). To resolve the ambiguities associated with this species complex, it is crucial to examine a comprehensive set of samples from various populations within these regions. Until such detailed investigations are undertaken, it is advisable to consider these taxa as separate species (58).

The challenges and limitations that affect the taxonomy and classification of termite species are due to several factors. Early descriptions of termite species were often inadequate because the diversity and variation of termites were not properly understood. Consequently, several species were either grouped under one name or given different names in different regions. Despite advances in biological species systems, the taxonomy of many termite groups has stalled due to a lack of taxonomic expertise and difficulty in accessing specimens. The International Code of Zoological Nomenclature provides guidelines for the naming and classification of zoological organisms, relying on type specimens as the basis for species descriptions. However, many early descriptions lack the specificity required for accurate identification by modern standards, which complicates taxonomic endeavours. Access to and study of type specimens held in various museums around the world presents a logistical challenge, exacerbated in particular by political barriers in certain countries such as China (58, 95). Political instability and unrest in certain regions have hindered the collection of specimens for taxonomic research, which has led to gaps in the understanding of geographic variation within termite populations (96). Overall, these factors contribute to the complexity and difficulty of the taxonomy and classification of termite species.

Conclusion

The taxonomy of Indian termites, particularly subterranean species, reveals a rich and complex biodiversity. Despite their ecological significance and economic impact, many aspects of termite biology and taxonomy remain elusive due to their cryptic lifestyles. Traditional morphological methods, while foundational, often fall short in accurately identifying and classifying termite species, necessitating the adoption of molecular techniques. DNA barcoding and sequencing of mitochondrial and nuclear genes have proven instrumental in resolving taxonomic ambiguities and uncovering phylogenetic relationships that are otherwise difficult to discern through morphology alone. The diversity of termites in India spans various families, with the Termitidae family being the most dominant. The distribution and abundance of termites are influenced by several ecological factors, including climate, vegetation and soil type. This ecological diversity underscores the importance of region-specific studies to fully comprehend the termite fauna across different habitats. The review also highlights the agricultural and economic significance of termites, identifying numerous species that pose serious threats to crops and forest ecosystems. Holistic taxonomic approaches combining both morphological and molecular data offer a comprehensive understanding of termite biodiversity. These methods not only enhance species identification accuracy but also provide insights into the evolutionary relationships and ecological adaptations of termites. This integrated framework is crucial for developing effective pest management strategies and for the conservation of termite diversity in India's varied ecosystems. Embracing such approaches will pave the way for a more sustainable coexistence with these ecologically vital yet economically impactful insects.

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Authors' contributions

KP and DG conceptualized the review and led the writing process. KP and DG conducted an extensive literature search and provided critical input on relevant studies. MM contributed to structuring the manuscript and conducted a thorough review of the final draft. PSS and SH assisted in the critical evaluation of the selected literature and offered significant revisions to enhance the manuscript's clarity. DU and MM supervised the project, providing guidance and feedback throughout and reviewed and approved the final manuscript to ensure compliance with journal guidelines and standards. All authors contributed equally to the writing, revision and approval of the manuscript.

Compliance with ethical standards

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