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Comparative Study on Nest Density, Nesting Site, and Nest Architecture of *Tetragonula* nr. *pagdeni* Schwarz and *Tetragonula* nr. *shubhami* Viraktamath in the Lateritic Zone of Eastern India

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Abstract

This study documented the nest density, nesting site, and nest architecture of two poorly studied stingless bee species, *Tetragonula* nr. *pagdeni* Schwarz and *Tetragonula* nr. *shubhami* Viraktamath, from the lateritic zone of eastern India. Three 100×100 m plots were sampled from each surveyed village to determine the nest density. The external architecture of 57 nests was described, and 12 nests were dissected to observe their internal structure. The average nest density of *T. pagdeni* (0.88±0.75 nests/ha) was three times higher than *T. shubhami* (0.29 ± 0.57 nests/ha). *T. pagdeni* showed the highest nest density in Bankura (1.30 ± 0.75 nests/ha), a district with greater forest cover, while *T. shubhami* reached higher values in Birbhum (0.52 ± 0.67 nests/ha), an industrialized district with less forest cover. Both species showed a higher frequency (~65%) of nests in man-made structures than trees (~35%) and exhibited a tendency of building south-facing nests (~37–42%). There was no significant variation in the nest's external architectural features between them. The nest height indicated a high degree of overlap between the two species, although *T. shubhami* reached greater heights (237.00 ± 95.64 cm). Both utilize cavities of similar size ($p > 0.05$), but *T. shubhami* built significantly ($p < 0.05$) larger brood cells and food storage pots. Number of guard bees was related ($r = 0.87$; $p < 0.001$) to nest's entrance size, expressing an adjustment to maintain effective colony defense. Despite their fLexibility in using cavities, both *Tetragonula* species nest in tree hollows in regional forests. So their long-term persistence depends on the preservation of their habitats and the conservation of native trees.

Introduction

Stingless bees (Apidae: Meliponini) are highly diverse eusocial insects with complex colony structure and high ecological values. Worldwide, there are more than 600 described species of stingless bees belonging to over 60 genera (Wille, 1983; Michener, 2000; Rasmussen & Cameron, 2010; Engel et al., 2023). As the largest and most diverse group of corbiculate bees, stingless bees exhibit an astonishing array of life histories, morphologies, and behaviours (Shanahan & Spivak, 2021). The practice of stingless beekeeping, or meliponiculture, has brought stingless bees and humans into a close relation for millennia (Cortopassi-Laurino et al., 2006; Suryanarayanan & Beilin, 2020). Different species of stingless bees have significant ecological and economic value, particularly in pollination and meliponiculture (Slaa et al., 2006; Chidi & Odo, 2017). Usually, this group of insects is widely distributed in the tropical and subtropical regions of the world and provides highly valued pollination service to a vast array of wild and domestic flora (Heard, 1999; Slaa et al., 2006). As a part of tropical to subtropical world, India is home to approximately 28 species of stingless bees, predominantly under three genera, *i.e*., *Tetragonula* Moure, *Lisotrigona* Moure, and *Lepidotrigona* Schwarz, with *Tetragonula* being the most common and ubiquitous (Sakagami, 1978; Rasmussen, 2013; Vijayakumar & Jyaraaj, 2014; Viraktamath & Jose, 2017; Shanas & Faseeh, 2019; Chauhan & Singh, 2020; Vijayakumar & Jyaraaj, 2020; Viraktamath & Thangjam, 2021; Viraktamath & Roy, 2022; Viraktamath & Thangjam, 2022; Viraktamath et al., 2023; Hadimani & Dey, 2024; Layek et al., 2025).

For stingless bees, the presence of suitable nesting sites and ample food resources greatly influences their survival, maintenance, and reproduction (Batista et al., 2003; Kleinert et al., 2012). Usually, stingless bees exhibit wide variation in habitat preferences and nesting requirements and are considered generalist feeders based on their visits to flowers (Roubik, 2006, 2023; Kleinert et al., 2012). Depending on the species of stingless bee, nesting can take place in a variety of sites, including tree cavities, human constructions, rocks, active ant or termite nests, or they can even build subterranean nests approximately three meters below the ground level (Roubik, 2006; Shanahan & Spivak, 2021; Hadimani et al., 2024; Manzanares-Villasana et al., 2025). The availability and types of nesting sites influence the distribution of stingless bee species and are crucial for their effective conservation (Brown & Albrecht, 2001; Chakuya et al., 2022).

When it comes to their defense techniques, the lack of functional stingers causes this group of bees to develop alternative defense mechanisms, specifically through their nests. These miniature architects of nature built their nests in such a majestic way that the nest structure itself can supplement the active defense mechanism (Roubik, 2021; Shanahan & Spivak, 2021). Such nest designs have been tested by a variety of enemies, including vertebrates, insects, bee parasites, competitors, and disease-causing microbes (Roubik, 2021). They build very elaborate nests out of cerumen (wax and plant resins) (Rasmussen et al., 2024) that are incredibly diverse and highly species-specific (Roubik, 2006). Actually, the nest entrance, brood cell construction, and site preference are indicators of interspecific variability and ecological adaptation. Usually, the internal structure of the nest remains largely hidden, and when cut open, it appears to consist of distinct components, much like a building's furnishings (Roubik, 2021). A stingless bee nest can consist of hundreds or thousands of individuals and various structures, including entrance tubes, brood combs, food storage pots (pollen and honey pots), an involucrum, and protective outer layers (Michener, 2007; Shanahan & Spivak, 2021). All these components are fully functional and arranged in orderliness (Roubik, 2021). Such structural defenses provide solutions for survival in a wide variety of environmental conditions (Kajobe, 2007; Njoya et al., 2019; Engel et al., 2023) and are tested by a variety of enemies against which their nest acts as a defensive shield (Roubik, 2021). Therefore, a comprehensive understanding of nesting sites and nest architectures of stingless bees plays a fundamental role in understanding their taxonomy, ecology, and conservation.

Till date, detailed information on the nesting biology and distribution of most Indian stingless bee species is limited. Furthermore, although about 28 stingless bee species have been recorded from India, most studies have focused on *Tetragonula iridipennis* Smith and *T. ruficornis* (Smith) (Choudhary et al., 2021; Sabatina et al., 2024; Saranya et al., 2024; Hadimani et al., 2024). Therefore, this study was conducted to examine and compare the nesting sites, nest architecture, and nest density of two less-studied stingless bee species, *i.e*., *Tetragonula* nr. *pagdeni* Schwarz and *Tetragonula* nr. *shubhami* Viraktamath, from the Lateritic zone in Eastern India. For instance, *T. shubhami* was first reported from India just three years back (Viraktamath & Roy, 2022), and this is the first account on its nesting habits and nest architecture. Such a comparison will provide insights into the differential distribution pattern of these two species across different anthropogenic habitats and will offer potential diagnostic traits to distinguish the nesting habits between different *Tetragonula* species.

Materials and Methods

Study Area

The study was conducted in various villages in the Lateritic zone of West Bengal, Eastern India. The villages come under six districts of West Bengal, namely Bankura, Birbhum, Jhargram, Paschim Medinipur, Paschim Bardhaman, and Purulia (Fig 1). Actually, this lateritic zone is the eastern extension of the Chota Nagpur plateau and has undulating topography, red lateritic soils, and a tropical monsoon climate. In summer (April – June months), the temperatures can exceed 40°C, while in winter (December – February months), the temperature can drop to nearly 7°C. The region has an annual average rainfall of 1100 – 1400 mm, mainly due to the southwest monsoon during July – September. The landscape of this zone includes agricultural lands, scrub forests, isolated plantations, and small human settlements, providing diverse nesting sites for stingless bees.

Survey and Species Identification

A systematic field survey was conducted across several villages in these six districts from June 2021 to May 2024 to search for stingless bee colonies. The nesting sites were

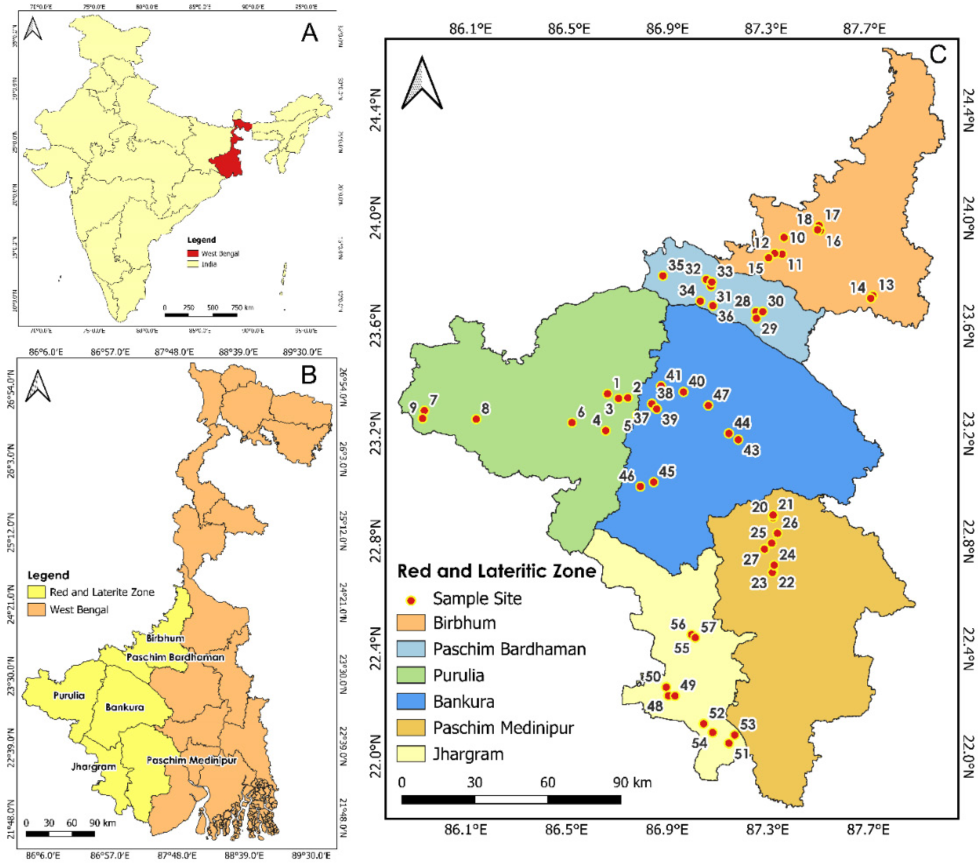

Fig 1. Map of the study area. (A) Location of West Bengal in India; (B) Districts under the lateritic zone of West Bengal; (C) Location of the sampling sites or stingless bee nests.

identified through visual searches and by contacting local villagers and traditional honey collectors. From each identified nest, a few workers and drones were captured, placed in glass vials, and returned to the laboratory for species identification. In the laboratory, the specimens were dried, pinned, and observed under an Olympus SZX7 stereo-zoom microscope to ensure proper identification using established taxonomic keys (Rasmussen, 2013; Viraktamath & Roy, 2022). Further, the specimens were sent to the eminent taxonomists at the University of Agricultural Sciences, Bengaluru, India, for confirmation of their identities.

Nest Density Estimation

After a systematic field survey on 57 potential villages, three random 100×100 m (*i.e.*, 10,000 m^2 or 1 hectare) plots were selected from each village to determine nesting density using the random quadrat sampling method. In each plot, the total number of nests for each stingless bee species was identified, and the density data were expressed as the number of active nests per hectare.

Nesting Site and Nest Architecture Examination

A total of 57 nests (including 43 nests of *T. pagdeni* and 14 nests of *T. shubhami*) were sampled, and different substrates utilized by both bee species were classified as human constructions and trees.

The nest's external architecture was characterized as follows: facing direction/orientation of the entrance, height of the entrance above the ground, length of the entrance tube, shapes and dimensions of the entrance opening, occurrence of multiple nest entrances, and number of guard bees at the entrance. Basic equipment (hand tally meter, vernier caliper, and magnetic compass) was used for observation/measurement of nest features. The number of guard bees was estimated by counting stationary individuals at the nest entrance under undisturbed conditions (in more aggressive colonies, a 5-minute rest period was allowed before counts were taken). Length of the entrance tube was determined as the distance between the base of the substrate and the furthest edge of the tube. The dimensions of the entrance opening were recorded as maximum length and width. The shape of entrance openings was distinguished according to Layek and Karmakar (2018). All of these architectural features were grouped in different categories (Table 1).

Among the observed nests, 12 were dissected to examine their internal structure. Physical features of the cavity, inner tunnel, brood cells, and honey and pollen pots were used to characterize the internal architecture.

Table 1. Categories used to describe the external architecture of stingless bee nests.

	Orientation	Entrance height (cm)	Entrance tube length (mm)	Multiple nest entrances	Shape of entrance opening	No. of guard bees
Categories	East	<100	Absent	Present	Round	<5
	West	100–200	1–25	Absent	Slit-like	5–10
	North	201–300	26–50	—	Oval	>10
	South	>300	> 51	—	Irregular	—
	—	—	—	—	Semi-oval	—

Statistical Analysis and Data Visualization

Arithmetic mean, standard deviation (SD), median, mode, and data range were estimated using the nest architectural measures. These data were further analysed using one-way ANOVA to assess variation in nest architectural measures among stingless bee species and nesting substrates, and were represented using box plots. Pearson's correlation was used to evaluate how nest density in both species correlated and how the number of guard bees correlated with nest entrance size. All these statistical analyses were performed using RStudio®, v4.4.1 (R Core Team, 2024). Nest density (nests/ha) was calculated for each sampling location, and density maps for both stingless bee species were constructed using QGIS software, v3.38 (QGIS Development Team, 2024). As the nest density data violates the assumptions of normality (performed using the Shapiro-Wilk test) and homogeneity of variance (performed using the Bartlett test), the variation in nest density of each species across the districts was explored by means of a non-parametric Kruskal-Wallis test followed by pairwise comparisons between the districts using RStudio®, v4.4.1 (R Core Team, 2024).

Results

Spatial Nest Density and Distribution Patterns

The average nest density in the lateritic zone of West Bengal in Eastern India, considering both species together, was 1.19 ± 0.72 nests/ha, with the nest density in the Bankura district (1.70 ± 0.91 nests/ha) being relatively higher than that of other districts. Among the stingless bee species, *T. pagdeni* had a mean density of 0.88 ± 0.75 nests/ha, which was far greater than that of *T. shubhami* (0.29 ± 0.57 nests/ha) (Table 2). The Kruskal-Wallis test reveals that differences in nest density of *T. pagdeni* were significant ($p < 0.001$) across districts, whereas those for *T. shubhami* were not ($p = 0.386$). Moreover, the spatial nest density of both species exhibited a significant negative correlation ($r = -0.43$, $p < 0.001$), with the highest nest density of *T. pagdeni* in the Bankura district (1.30 ± 0.75 nests/ha) and the lowest in the Birbhum district (0.44 ± 0.67 nests/ha). In contrast, *T. shubhami* had maximum density in the Birbhum district (0.52 ± 0.67 nests/ha) and minimum in the Paschim Medinipur district (0.15 ± 0.44 nests/ha). A map of the spatial nest density of both bee species is presented in Fig 2.

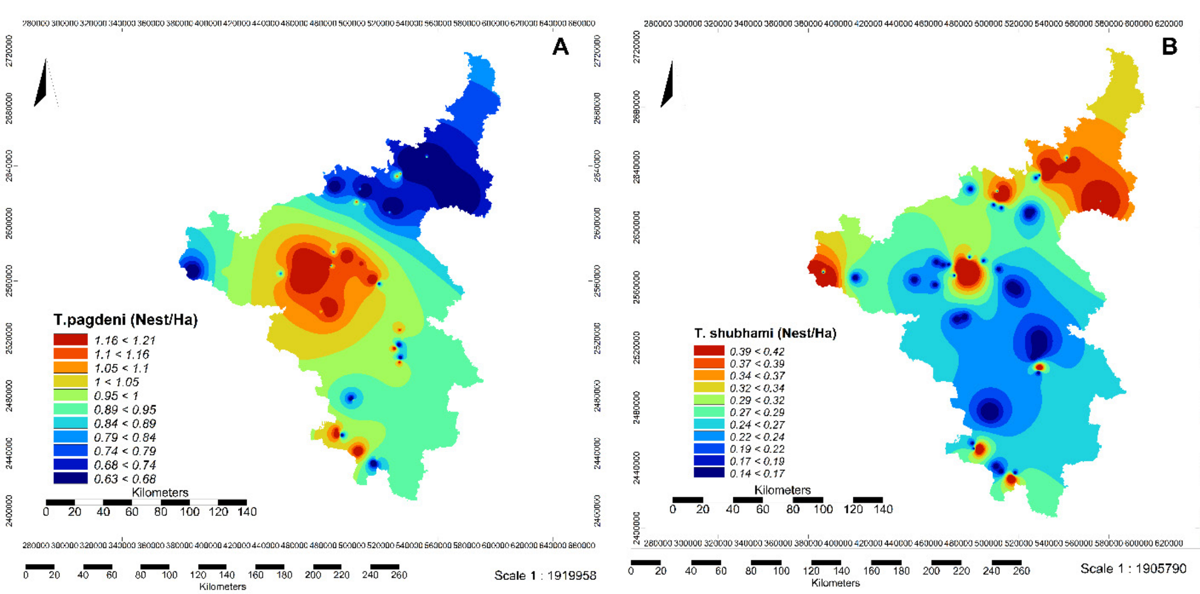

Fig 2. Spatial nest density (no. of nests/ha) of both *Tetragonula* species in the lateritic zone of West Bengal. (A) *T. pagdeni.* (B) *T. shubhami.*

Table 2. Assessment of district-wise variation in nest density (nests/ha) of *T. pagdeni* and *T. shubhami* using non-parametric Kruskal-Wallis test followed by pairwise comparisons.

Districts	T. pagdeni (mean ± SD)	T. shubhami (mean ± SD)	District-wise cumulative mean (mean ± SD)
Bankura	1.30 ± 0.75	0.39 ± 0.71	1.70 ± 0.91
Purulia	1.19 ± 0.69	0.19 ± 0.56	1.37 ± 0.54
Jhargram	0.93 ± 0.89	0.23 ± 0.50	1.17 ± 0.74
Paschim Medinipur	0.93 ± 0.60	0.15 ± 0.44	1.07 ± 0.49
Birbhum	0.44 ± 0.67	0.52 ± 0.67	0.96 ± 0.61
Paschim Bardhaman	0.48 ± 0.58	0.26 ± 0.57	0.74 ± 0.62
Species-wise mean	0.88 ± 0.75	0.29 ± 0.57	1.19 ± 0.72

Kruskal-Wallis test

	T. pagdeni	*T. shubhami*
N	171	171
df	5	5
chi-squared	21.819	5.251
p-value	<0.001	0.386

Pairwise comparison (in case of *T. pagdeni*)

	Purulia	Jhargram	Paschim Medinipur	Birbhum	Paschim Bardhaman
Bankura	1.000	0.531	0.008	0.002	0.008
Purulia		1.000	0.182	0.072	0.182
Jhargram			1.000	0.505	1.000
Paschim Medinipur				1.000	1.000
Birbhum					1.000

Note: In case of *T. shubhami*, pairwise comparisons haven't been performed because of no significant variation in nest density across the districts.

Nesting Sites and Habitat Utilization

T. pagdeni and *T. shubhami* showed a great ecological range of nesting habitats using a large variety of nesting sites, including human constructions and living trees (Fig 3). Considering habitat use, both species showed a higher occurrence in anthropogenic sites, with 65.12% and 64.29% preference for human constructions in *T. pagdeni* and *T. shubhami*, respectively. Such human constructions include cement-brick or mud walls, window frames, and an abundance of water pumps. The frequency of nests in trees was 34.88% and 35.71% in *T. pagdeni* and *T. shubhami*, respectively, with no evidence of multiple stingless bee nests in the same tree. However, a large variation was observed in the number of tree species used for nesting between the two bee species. *T. pagdeni* nests were recorded from a total of nine plant species, with most of them (5 nests) recovered from Sal (*Shorea robusta*). Whereas, *T. shubhami* nests were found in four plant species, each with one nest. Only two plant species, *i.e.*, Sal (*Shorea robusta*) and Arjun (*Terminalia arjuna*), were found to be utilized by both bee species as nesting sites (Table 3).

Examination of External Nest Characteristics

Our study revealed no significant variation ($p > 0.05$) in external nest architectural characteristics between the two species (Fig 4). Both *T. pagdeni* and *T. shubhami* built their nests facing in any direction. However, south-facing nest entrances were more common in both species (37.21% and 42.86% for *T. pagdeni* and *T. shubhami*, respectively). The average height of the nest entrance relative to the ground was relatively greater in *T. shubhami* (237.00 ± 95.64 cm) than in *T. pagdeni* (189.70 ± 110.24 cm). However, there was significant overlap in nest heights between the two species. Comparison between the type of nesting substrates also revealed no significant ($p = 0.531$) variation in the nest height between man-made structures (194.65 ± 106.40 cm) and trees (213.65 ± 112.56 cm). Entrance tubes were observed in 81.40% and 92.86% of nests of *T. pagdeni* and *T. shubhami*, respectively, and most of them had a length range of 50 mm in both species. In *T. pagdeni*, four nests were recorded to have more than one entrance, while this character was absent in *T. shubhami* (Table 3).

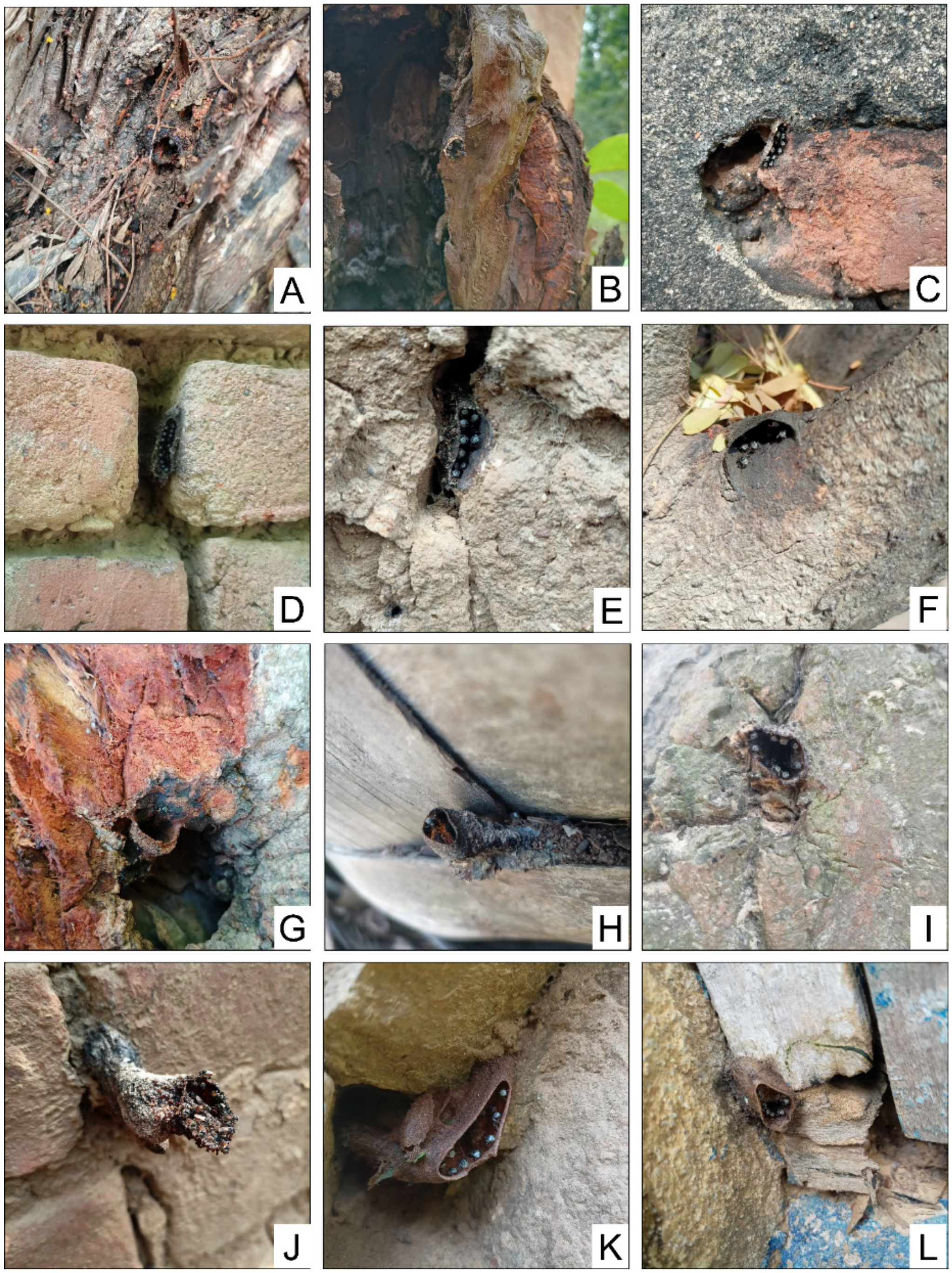

Fig 3. Types of nesting sites utilized by both stingless bees. (A–E) *T. shubhami* [(A) *Acacia auriculiformis*, (B) *Eucalyptus globulus,* (C) Bricks with cement wall, (D) Bricks with mud wall; (E) Mud wall], (F–L) *T. pagdeni,* [(F) *Tamarindus indica*, (G) *Madhuca longifolia*, (H) *Borassus flabellifer*, (I) *Shorea robusta*, (J) Bricks with mud wall, (K) Stone wall, (L) Window rim].

A variety of nest entrance shapes were observed, including rounded, slit-shaped, oval, irregular, and semi-oval openings (Fig 5). Irregular-shaped entrances were the most frequent in both species (30.23% and 35.71% for *T. pagdeni* and *T. shubhami*, respectively), while slit-like was the least frequent. The dimensions of the entrance openings were quite similar between the two species, with widths of 8.51 ± 3.07 mm and 9.57 ± 3.06 mm and lengths of 14.93 ± 5.64 mm and 14.57 ± 3.98 mm for *T. pagdeni* and *T. shubhami*, respectively. The number of guard bees counted at the nest entrances ranged from 4 to 16 in both species, with similar averages (8.95 ± 3.32 individuals in *T. pagdeni* and 8.36 ± 4.05 individuals in *T. shubhami*) (Table 3). Furthermore, the number of guard bees showed a significant positive correlation ($r = 0.87$; $p < 0.001$) with nest entrance size. Detailed measurements of the external structures of the nests are presented in the supplementary Tables 1 and 2.

Table 3. Comparative account on nesting site and external nesting architecture of *T. pagdeni* and *T. shubhami*.

Nesting site and architecture			Percentage utilization	
			***T. pagdeni* (N = 43)**	***T. shubhami* (N = 14)**
Nesting sites	Human constructions		28 (65.12%)	9 (64.29%)
	Type of constructions	Cement with bricks wall	9 (20.93%)	3 (21.43%)
		Mud wall	7 (16.28%)	2 (14.29%)
		Mud with bricks wall	10 (23.26%)	3 (21.43%)
		Window rim	1 (2.33%)	1 (7.14%)
		Abandoned water pump	1 (2.33%)	–
	Trees		15 (34.88%)	5 (35.71%)
	Tree species	*Acacia auriculiformis* A.Cunn. ex Benth	2 (4.65%)	–
		Borassus flabellifer L.	1 (2.33%)	–
		Butea monosperma (Lam.) Taub.	1 (2.33%)	–
		Cocos nucifera L.	–	1 (7.14%)
		Eucalyptus globulus Labill.	2 (4.65%)	–
		Madhuca longifolia (J. Konig) J.F. Macbr.	–	1 (7.14%)
		Mangifera indica L.	1 (2.33%)	–
		Phoenix dactylifera L.	1 (2.33%)	–
		Shorea robusta Roth	5 (11.63%)	1 (7.14%)
		Tamarindus indica L.	1 (2.33%)	–
		Terminalia arjuna (Roxb.) Wight & Arn.	1 (2.33) %	1 (7.14%)
		Terminalia chebula Retz.	–	1 (7.14%)
Orientation	East		13 (30.23%)	4 (28.57%)
	West		9 (20.93%)	1 (7.14%)
	North		5 (11.63%)	3 (21.43%)
	South		16 (37.21%)	6 (42.86%)
Entrance height above ground (cm) (mean ± SD) [Range]			189.70 ± 110.24 [36–472]	237.00 ± 95.64 [90–412]
	Categories	<100 cm	9 (20.93%)	1 (7.14%)
		100–200 cm	21 (48.84%)	4 (28.57%)
		201–300 cm	5 (11.63%)	5 (35.71%)
		>300 cm	8 (18.60%)	4 (28.57%)
Entrance tube length (mm) (mean ± SD) [Range]			30.14 ± 21.41 [5–95]	33.54 ± 22.50 [5–82]
	Categories	Absent	8 (18.60%)	1 (7.14%)
		1–25 mm	18 (41.86%)	6 (42.86%)
		26–50 mm	12 (27.91%)	4 (28.57%)
		> 51 mm	5 (11.63%)	3 (21.43%)
Multiple nest entrances	Present		4 (9.30%)	–
	Absent		39 (90.70%)	14 (100%)
Shape of entrance opening	Round		9 (20.93%)	3 (21.43%)
	Slit-like		6 (13.95%)	1 (7.14%)
	Oval		8 (18.60%)	2 (14.29%)
	Irregular		13 (30.23%)	5 (35.71%)
	Semi-oval		7 (16.28%)	3 (21.43%)
Width of entrance mouth (mm) (mean ± SD) [Range]			8.51 ± 3.07 [5–16]	9.57 ± 3.06 [4–14]
Length of entrance mouth (mm) (mean ± SD) [Range]			14.93 ± 5.64 [6–29]	14.57 ± 3.98 [7–20]
No. guard bees at entrance (mean ± SD) [Range]			8.95 ± 3.32 [4–16]	8.36 ± 4.05 [4–16]
	Categories	<5	3 (6.98%)	2 (14.29%)
		5–10	25 (58.14%)	7 (50.00%)
		>10	15 (34.88%)	5 (35.71%)

Note: N = Number of colonies observed for that particular species.

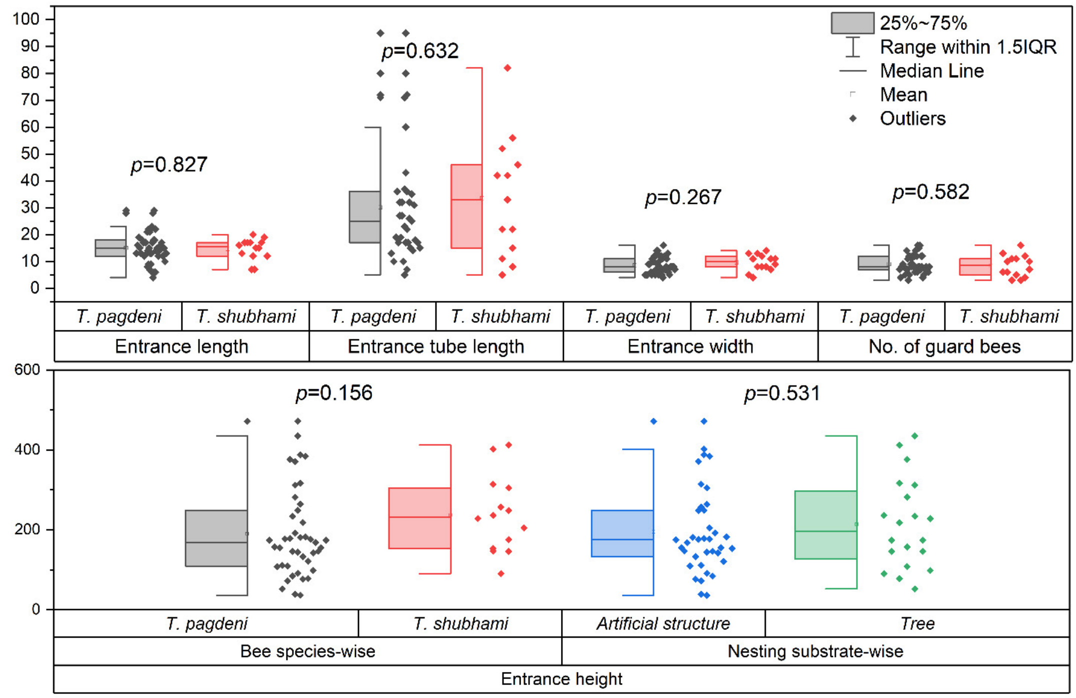

Fig 4. Boxplot representing the variation in the external nest architectural characteristics between both species of stingless bees.

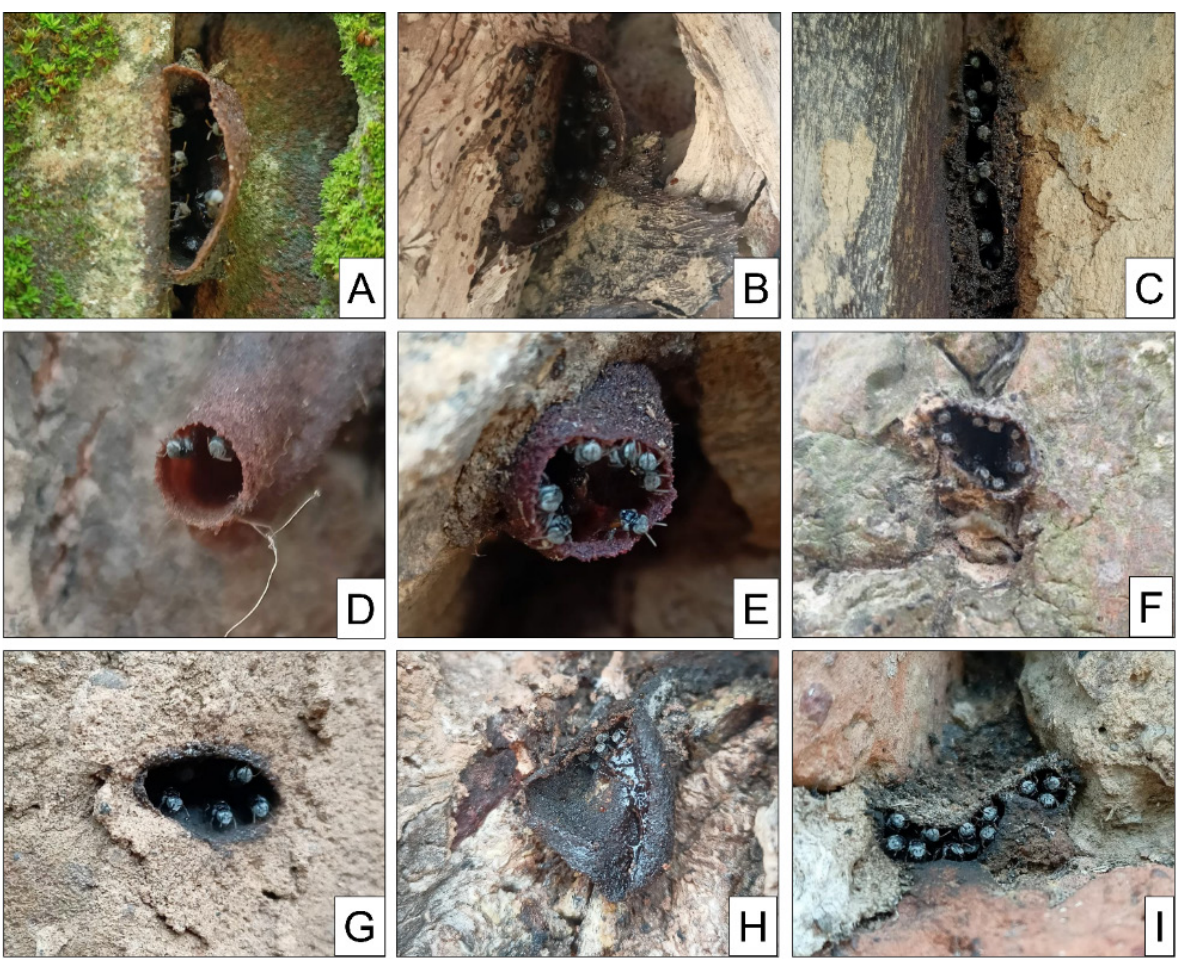

Fig 5. Variation in the shape of nest entrance openings. (A–F) *T. pagdeni* [(A–B) Semi-oval, (C) Slit-like, (D–E) Round, (F) Irregular]; (G–H) *T. shubhami* [(G) Oval, (H) Irregular]; (F) Multiple nest entrances in *T. pagdeni*.

Internal Nest Characteristics

Both species showed similar spatial organization of the nest's internal structures. Brood cells were located at the centre of the nest, and food storage pots were located at the periphery. Both species also build light-brown brood cells and dark-brown honey pots. However, the colour of pollen pots varies quite a bit from species to species, as *T. pagdeni* builds brown to dark brown pollen pots, whereas *T. shubhami* builds light brown pollen pots. Although both species had oval brood cells, the food storage pots were spherical-polygonal in *T. pagdeni* nests and oval in *T. shubhami* nests. Considering the size-related parameters of these structures (*i.e.*, brood cells, honey pots, and pollen pots), *T. shubhami* nests had significantly ($p < 0.05$) greater dimensions as compared to *T. pagdeni* nests (Fig 6; Table 4).

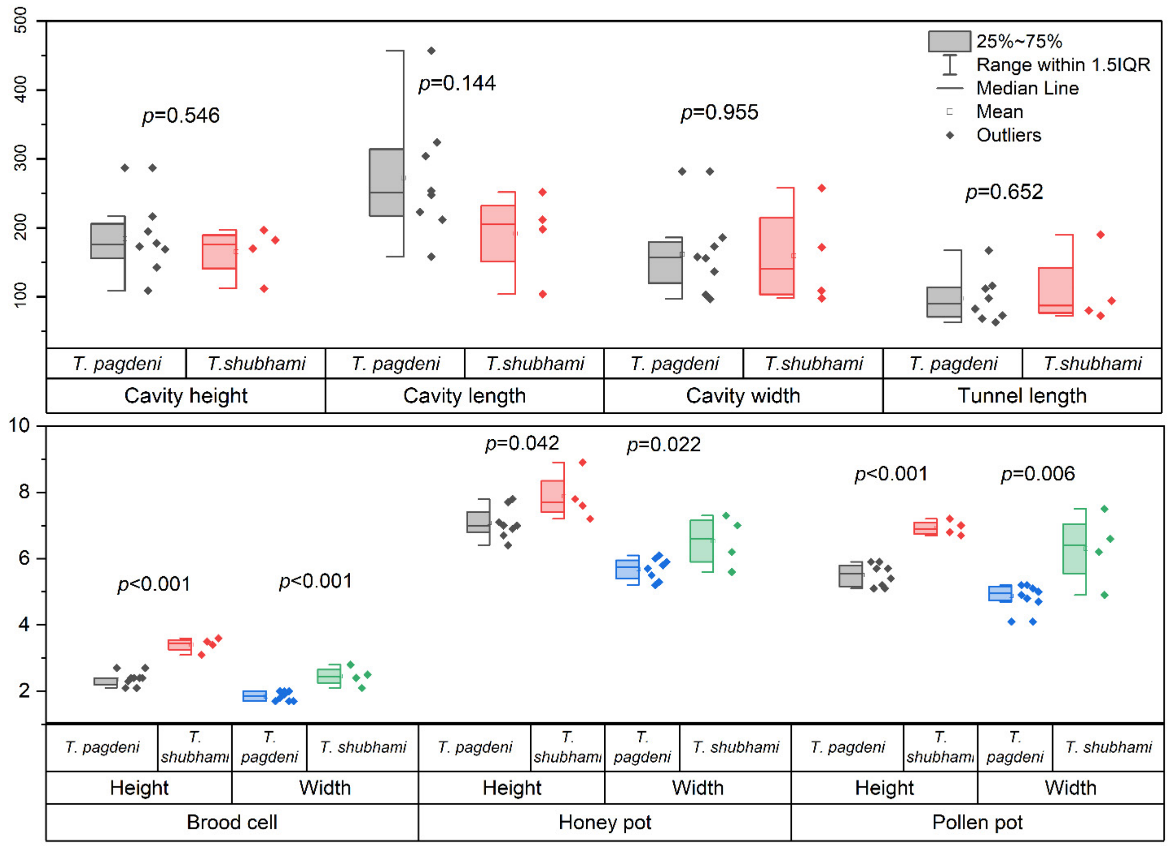

Fig 6. Boxplot representing the variation in the internal nest architectural characteristics between both species of stingless bees.

Table 4. Comparative account on internal nest characteristics of *T. pagdeni* and *T. shubhami.*

Internal characteristics		**Character / Value (mean ± SD) [Range]**	
		T. pagdeni	***T. shubhami***
Internal tunnel length (mm)		97.48 ± 34.42 [63.24–167.44]	109.32 ± 54.62 [72.60–190.14]
Cavity	Length (mm)	272.50 ± 90.91 [158–457]	191.50 ± 62.66 [104–252]
	Width (mm)	161.50 ± 57.91 [97–282]	159.25 ± 73.46 [98–258]
	Height (mm)	183.88 ± 52.79 [109–287]	165.25 ± 37.18 [112–197]
Brood cell	Location	Centre	Centre
	Colour	Light brown	Light brown
	Shape	Oval	Oval
	Width (mm)	1.85 ± 0.14 [1.7–2.0]	2.45 ± 0.29 [2.1–2.8]
	Height (mm)	2.35 ± 0.19 [2.1–2.7]	3.40 ± 0.22 [3.1–3.6]
Honey pots	Location	Periphery	Periphery
	Colour	Dark brown	Dark brown
	Shape	Spherical–polygonal	Oval
	Width (mm)	4.88 ± 0.36 [4.1–5.2]	6.30 ± 1.08 [4.9–7.5]
	Height (mm)	5.50 ± 0.34 [5.1–5.9]	6.93 ± 0.22 [6.7–7.2]
Pollen pots	Location	Periphery	Periphery
	Colour	Brown to dark brown	Light brown
	Shape	Spherical–polygonal	Oval
	Width (mm)	5.69 ± 0.33 [5.2–6.1]	6.53 ± 0.77 [5.6–7.3]
	Height (mm)	7.08 ± 0.47 [6.4–7.8]	7.88 ± 0.73 [7.2–8.9]

The length of internal tunnels was almost similar in both species (109.32 ± 54.62 mm in *T. shubhami* and 97.48 ± 34.42 mm in *T. pagdeni*), without any significant differences ($p = 0.652$). Likewise, there was also no significant variation in nest cavity dimensions, with *T. pagdeni* having little larger cavity size (*i.e.*, 272.50 ± 90.91, 161.50 ± 57.91, and 183.88 ± 52.79 mm length, width, and height, respectively) than *T. shubhami* (*i.e.*, 191.50 ± 62.66, 159.25 ± 73.46, and 165.25 ± 37.18 mm length, width, and height, respectively) (Fig 6; Table 4). Some illustrations of internal nest characteristics are presented in Fig 7.

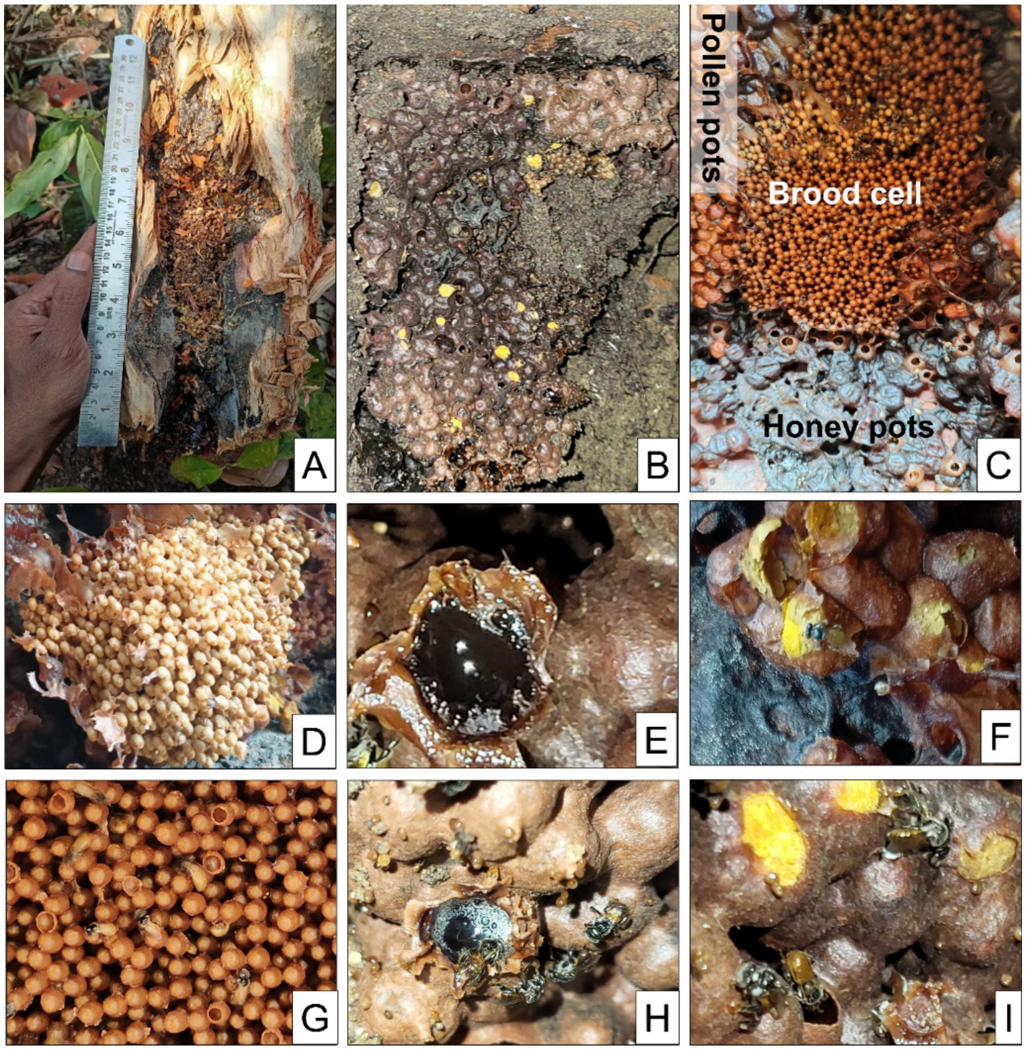

Fig 7. Internal nest characteristics of *Tetragonula* species. (A) Length of internal cavity of a *T. pagdeni* nest within a tree substrate; (B) Internal structure of *T. shubhami* nest inside of a cemented wall; (C) Internal nest contents with differential position of brood cells, pollen pots, and honey pots in *T. shubhami* nest; (D–F) Internal pots in *T. pagdeni* nest [(D) Brood cells; (E) Honey pots; (F) Pollen pots]; (G–I) Internal pots in *T. shubhami* nest [(G) Brood cells; (H) Honey pots; (I) Pollen pots].

Discussion

Understanding the nesting behavior and nest density of stingless bees can provide insights into their ecological adaptation range, which is crucial for their efficient conservation (Roubik, 2006; Chakuya et al., 2022; Engel et al., 2023). Initial estimates of the number of stingless bee nests ranged from 0.15 to 1.30 per hectare in various habitats (Michener, 1946). However, further field research in subsequent decades revealed that this number could be less than one nest/ha in urbanized areas (e.g., Wayo et al., 2026) and could reach 6.0 nests/ha (e.g., Silva et al., 2013) to over 30.0 nests/ha (e.g., Manzanares-Villasana et al., 2025) in some preserved tropical forests. Taken together, the nest density of the two *Tetragonula* species averaged about 1.19 nests/ha in the lateritic zone of eastern India, reaching higher values (*i.e.,* 1.70 nests/ha), especially in areas with less anthropogenic disturbance and greater preserved forest cover. Although several factors can affect the density of stingless bee nests (Hubbell & Johnson, 1977), we can assume that the recorded variation in the forest cover (Mandal & Chatterjee, 2021; Dutta & Chatterjee, 2022; Basu & Basu, 2023) and in the expansion of human activities associated with industrialization (Sarkar, 2011; Malakar et al., 2024) in the lateritic zone explains the variation in nests/ha of *Tetragonula* species on a regional scale. Another fact is that the nest densities of these two species were inversely related, potentially suggesting the influence of one species on the distribution of the other or their differential adaptation to regional variability. Although both species frequently used artificial nesting sites, only *T. shubhami* showed a higher local density in areas with greater human impact and loss of forest cover. In other words, flexibility in the use of cavities for nesting is necessary for the occupation of anthropized habitats but is probably insufficient for the long-term persistence of forest-resident species in landscapes subject to progressive deforestation.

This study documented a wide range of nesting substrates used by *T. pagdeni* and *T. shubhami*, a trait well known in several stingless bees (Roubik, 2006; Engel et al., 2023). In addition to using tree hollows, both *Tetragonula* species frequently nested in man-made structures or artificial cavities. However, there was no evidence of soil nesting in these two species, unlike some Southeast Asian *Tetragonula* species, like *T. kyrdemkulaiensis* Viraktamath and Rojeet*, T. laeviceps* Smith*,* and *T. drescheri* Schwarz (Viraktamath & Thangjam, 2021; Withaningsih et al., 2023). Cavities in walls, including stone, cemented, brick, or mud walls, have generally been identified as good nesting sites for *Tetragonula* bees (Gajanan et al., 2005; Danaraddi et al., 2009; Viraktamath & Thangjam, 2021; Saaivignesh et al., 2023) when providing them with desirable microclimatic stability, physical protection, and structural steadiness (Nayak et al., 2013; Patel & Pastagia, 2016). High frequencies of using wall cavities by *T. pagdeni* (Basanna & Rajanand, 2021), *T. iridipennis* (Choudhary et al., 2021; Sabatina et al., 2024), *T. bengalensis* Cameron (Kunal et al., 2020), and *T. ruficornis* (Hadimani et al., 2024) have also been recorded in anthropized landscapes in India. Colonies in wall cavities and hollow tree trunks may have similar overwintering capabilities (Choudhary et al., 2021). However, nests in artificial structures may exhibit lower persistence rates (due to various factors), even among species with ecological adaptations to anthropogenic habitats, such as *Tetragonisca angustula* Latreille (Batista et al., 2013; Gouvea et al., 2025). Another point to note is that while the formation of multiple nests in the same tree is common in many species of stingless bees (Manzanares-Villasana et al., 2025), including *Tetragonula* species found in Southeast Asia, like *T. laeviceps, T. collina* (Smith)*, T. geissleri* (Cockerell)*, T. melanocephala* (Gribodo), and *T. melina* (Gribodo) (Eltz et al., 2003), this phenomenon was completely absent in our studied bee species.

Key issues for the preservation of different species of stingless bees include understanding their flexibility in using substrates and habitats for nesting (Silva & Ramalho, 2014; Gouvea et al., 2025). *T. iridipennis* illustrates this issue well in India, showing, in some locations, a high association with artificial structures (Choudhary et al., 2021) and, in others, a very high rate of nesting in tree hollows (Layek & Karmakar, 2018). On the other hand, stingless bees that nest in tree hollows and demonstrate fidelity to the forest environment, such as some *Melipona* species in the Americas, tend to be more susceptible to deforestation (Brown & Albrecht, 2000; Silva et al., 2013).

Empirical analysis of nesting site preferences by stingless bees requires some measure of relative substrate availability, even if qualitative (Silva & Ramalho, 2014). For example, *T. iridipennis* showed a high nesting frequency in hollows of the Sal tree (Layek & Karmakar, 2018), a tree also prevalent in the lateritic zone of eastern India (Palit, 2021; Basu & Basu, 2023). This association demonstrates the importance of this nesting substrate in the regional deforestation scenario, but does not necessarily indicate preference. In fact, both *Tetragonula* species nested predominantly in anthropogenic substrates along the lateritic zone, despite the large variation in forest cover among the sampled municipalities. In this case, the most relevant finding is that *T. shubhami* appears to be adjusting to forest cover loss with greater flexibility than *T. pagdeni* at the landscape scale.

The durability and strength of the wood, the internal space of the cavities, etc., are criteria that stingless bees may consider when choosing a tree as a nesting site (Hadimani et al., 2024). For instance, Sal is a hardwood that is strong and durable and can resist insect attacks (Chalise et al., 2022), thus qualifying as a good nesting site for stingless bees. In addition to Sal, the stingless bees have been using various trees common in the lateritic zone of West Bengal [e.g., Akashmoni (*Acacia auriculiformis*), *Eucalyptus globulus*, Ice apple (*Borassus flabellifer*), Palash (*Butea monosperma*), Mahua (*Madhuca longifolia*), Coconut (*Cocos nucifera*), Date palm (*Phoenix dactylifera*), Arjun (*Terminalia arjuna*), Tamarind (*Tamarindus indica*) (Ghosal, 2011; Ghosh & Karmakar, 2012; Mazumder, 2018; Deb, 2022; Basu & Basu, 2023)] that are not necessarily hardwood. This highlights the influence of the abundance of the substrate itself on its use by these bees. Silva and Ramalho (2014) also argued that there would be no preferences for tree species or wood hardness among stingless bees in the Brazilian Atlantic Forest.

Combined information on the architecture of stingless bee nests is useful for understanding their behavioral ecology and for their identification in the field by breeders and specialists. The shape of the nest opening varied within each species, ranging from irregular to rounded, elongated, etc., a condition shared with several other *Tetragonula* species from India, including *T. iridipennis*, *T. ruficornis*, *T. travancorica* Shanas & Faseeh, etc. (Faseeh, 2018; Layek & Karmakar, 2018; Faseeh & Shanas, 2019; Hadimani et al., 2024). In our study, an irregular shape was more frequently encountered in *T. pagdeni* and *T. shubhami* nests. The irregular shape may also be associated with flexibility in adjusting the entrance to the colony's defense needs (Biesmeijer et al., 2007; Syafrizal & Yusuf, 2014). However, some differences are observed in the occurrence of shapes; for example, round-to-oval shapes were more frequent in *T. iridipennis* (Layek & Karmakar, 2018; Sabatina et al., 2024) and *T. srikantanathi* Viraktamath (Viraktamath & Thangjam, 2021) nests in India.

The variation in the size of the nest entrance opening of the two *Tetragonula* species was also within the range recorded for different other *Tetragonula* species in India, including *T. iridipennis* (Roopa et al., 2015; Layek & Karmakar, 2018; Ali et al., 2025), *T. kyrdemkulaiensis,* and *T. srikantanathi* (Viraktamath & Thangjam, 2021). Larger nest openings can facilitate greater forager traffic but necessitate additional guard bees to defend the colonies (Couvillon et al., 2008). In this study, a relationship was observed between the number of guard bees and the size of the entrance opening, indicating a probable trade-off between opening size and defensive capacity (e.g., general colony conditions; Jemberie et al., 2020). That is, more guard bees should also mean more populous colonies, a relationship that could be tested experimentally in the future. The occurrence of multiple entrances in some *T. pagdeni* colonies is a phenomenon that was also reported in other stingless bee species, like in *T. iridipennis* (Jose, 2015) and *T. travancorica* (Faseeh & Shanas, 2019) from India, and *Dactylurina staudingeri* (Gribodo) from Cameroon (Mogho et al., 2016). This behaviour likely serves to disorient predators.

The direction of the nest entrance of stingless bees can also contain ecological information. In fact, south-facing entrances likely facilitate thermoregulatory behavior in nests, particularly in the Northern Hemisphere. There, a south-facing orientation is more exposed to the sun, which could help regulate nest temperature during winter (Kajobe & Echazarreta, 2005; Kajobe, 2007; Choudhary et al., 2021). A high proportion of *T. pagdeni* and *T. shubhami* nests (37.21% and 42.86%, respectively) had south-facing entrances, a trend also recorded in nests of *T. ruficornis* (Hadimani et al., 2024) and *T. gressitti* Sakagami (Chauhan & Singh, 2021) from India. In contrast, *T. iridipennis* showed a higher prevalence of north-to-east-facing entrances in different parts of India (Nayak et al., 2013; Layek & Karmakar, 2018; Choudhary et al., 2021), suggesting a species-specific trait. Given that stingless bees depend on the pre-existing orientation of the cavity entrance, an experimental analysis would be necessary to test cavity choices in relation to entrance orientation and to assess the influence of thermoregulation on this process.

The nest heights relative to ground level indicated a high degree of overlap between the two *Tetragonula* species, although *T. shubhami* reached greater heights. Given the higher occurrence of this species in more anthropized areas of the lateritic zone, it is likely that the avoidance of human disturbances at ground level could have caused bias in the heights of their nests. Previous data on the nest height of *T. pagdeni* (Basanna & Rajanand, 2021) also generally corroborate the results presented here. It is relevant that *T. iridipennis* also establishes its colonies at similar heights throughout this region (Layek & Karmakar, 2018). This similarity in cavity height choice among these *Tetragonula* species points to predation and microclimate (Hora et al., 2023) as likely common selective pressures. This similar 'choice' also exposes them to interspecific competition for nesting sites.

The high frequency of external tunnels/tubes in nests of *T. pagdeni* and *T. shubhami* has also been recorded in *T. iridipennis* (Roopa et al., 2015). In general, the absence of an external tube seems to be more common in nests associated with artificial structures, as seen in the case of *T. iridipennis* (Layek & Karmakar, 2018; Ali et al., 2025) and *T. srikantanath* (Viraktamath & Thangjam, 2021) (Supplementary Tables 1 and 2), but we do not have a satisfactory explanation for this fact. The tube projects the entrance away from the cavity surface, likely increasing the likelihood of retaining invaders while exposing the landing platform to foragers. In structural terms, its length must be a balance between the weight and the resistance of the construction material (wax and/or cerumen); therefore, it would be interesting to test this through interspecific comparisons. Some relationship between the length of the internal tunnel and the size of the cavity or hollow in the tree was also expected, but we do not have enough information to verify this fit. In many cases, the cavities occupied by *T. pagdeni* were frequently larger than those of *T. shubhami*, and yet the internal length of the entrance tube was similar in both species (ranging around 100 mm) and also did not differ from *T. iridipennis* and *T. ruficornis* in various regions of India (Gajanan et al., 2005; Layek & Karmakar, 2018; Hadimani et al., 2024).

Both *T. pagdeni* and *T. shubhami* exhibited an extremely compartmentalized nest internally, where the center was occupied by brood cells and the sides by honey and pollen pots, a very common feature in other *Tetragonula* species, including *T. iridipennis, T. ruficornis,* and *T. kyrdemkulaiensis* (Danaraddi et al., 2009; Layek & Karmakar, 2018; Viraktamath & Thangjam, 2021; Hadimani et al., 2024; Saranya et al., 2024). It is worth noting that the loose clustering of brood cells, common to both species, likely allows better utilization of irregular nesting cavities. Both species exhibited a great variation in the shape and size of the food pots, which are considerably smaller than those observed in *T. kyrdemkulaiensis*, *T. srikantanathi* (Viraktamath & Thangjam, 2021), and *T. gressitti* (Chauhan & Singh, 2021). However, we would still need to empirically assess whether such differences between the two species also imply differences in storage efficiency per unit volume constructed.

Conclusion

Our study provided a first comparative account of the nesting habits of two less studied stingless bee species, *i.e.*, *T. pagdeni* and *T. shubhami*, from the lateritic zone of West Bengal, India. They share several similarities in their nesting habits and are both forest residents that nest in tree hollows. They are also capable of occupying man-made structures, a common phenomenon in this region, which is affected by intense deforestation (Basu & Das, 2021; Mahato, 2021; Basu & Basu, 2023) and increasing human impact. Although less abundant throughout the whole lateritic zone, *T. shubhami* is responding better than *T. pagdeni* to the regional anthropization of landscapes. Despite the flexibility in using cavities for nesting, the long-term regional persistence of these *Tetragonula* species requires preserving their natural habitat (e.g., as a source of swarms and a reservoir of genetic diversity) and conserving native trees for nesting. These bees contribute to regional biodiversity conservation initiatives, as they are important pollinators that influence food production. Even so, this study provides fresh insights into nesting behavior that are pertinent to the conservation and ecology of these two *Tetragonula* species; future study is required to further explore their interactions with other species and the broader ecosystem dynamics, as well as to assess the impact of nest structure on their foraging habits, to ensure their sustainability in changing environments.

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Declaration of Competing Interest

The authors have no relevant financial or non-financial interests to disclose.

Data Availability Statement

The raw data are available from the corresponding author and can be provided upon request.

Authors' Contributions

AL: Conceptualization, investigation, species collection, data curation, writing-original draft.
SS: Formal analysis, writing-review & editing.
RD: Writing-original draft.
SV: Species identification, taxonomic validation.
DS: Manuscript review, scientific editing and critical feedback.
SJ: Methodology, supervision, project administration.

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