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Notes on Taxonomy and Nest Architecture of the Taiwanese Stingless Bee *Trigona (Lepidotrigona) ventralis hoozana*[1) 2)]

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Abstract

Observations on the taxonomy and nest architecture of the Taiwanese stingless bee *Trigona (Lepidotrigona) ventralis hoozana* Strand revealed the following results: (1) The Taiwanese population is subspecifically distinct from the continental ones by developed mesosomal tomenta, pale apical terga and larger body size. (2) Post-emergence pigmentation is distinguished in seven stages. Brood rearing and egg laying activities are mainly carried out by workers of stages Ⅱa - Ⅲa. (3) This bee is now confined to the primary forests in high mountains, where the climate is unusually severe for the stingless bees. Nests are mostly built in aboveground tree hollows. (4) Brood cells are arranged in horizontal complete combs, which are independent from each other and seldom spirally arranged. Combs are completely covered with involucrum of sheeted type. (5) Population size of an examined nest was large, with ca. 10000 adults. (6) Guards are timid, mildly attacking the observers only when nests are opened.

In 1972-73, one of us (S.Y.) was engaged in etho-ecological studies of social wasps in Taiwan. During his survey he found two nests of the stingless bee *Trigona (Lepidotrigona) ventralis hoozana* Strand and made some observations on the nest architecture and oviposition behavior along a plan prepared by the other (S.F.S.), who examined later materials brought by S.Y. taxonomically and anatomically. The present paper deals with the taxonomy and nest architecture as a part of the above results of

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this little known form, which is the northernmost representative of the Indo-Pacific stingless bees. The behavior within an observation hive will be reported in another paper.

Taxonomic Notes

Trigona (Lepidotrigona) ventralis Smith is a widespread Indomalayan species, distributed in N.E.India, Burma, Thailand, Sumatra, Java, Borneo and rather isolately in Taiwan (Schwarz, 1939). Schwarz recognized four varieties, *ventralis* Smith, *flavibasis* Cookerell, *doipaensis* Schwarz, and *hoosana* Schwarz. Comparing the worker specimens from various localities in continental S.E.Asia, Sakagami (1975) could not find any subspecific segregation among *ventralis*, *flavibasis* and *doipaensis*. He also recognized that the body size is smallest in the mountainous areas of central Vietnam, larger in Malaya and Laos, and largest in northern Thailand.

The Taiwanese population was first recorded by Strand (1913). Having mentioned some minor differences from the original description of *T. ventralis*, he gave tentatively the racial name *hoozana*. Sonan (1927) regarded it as a species distinct from *T. ventralis* by the legs and second to fourth metasomal terga black, margins of mesoscutum and mesoscutellum covered with long white hairs and the anterior margin of hind tibia rather straight, not outcurved. Unaware of these studies, Schwarz described this form as a new variety, *hoosana*, being close to var. *flavibasis* but with wings longer (5.0㎜ against 4.5㎜), hairs on mid and hind tibiae and basitarsi paler and terga V apically and VI entirely paler.

The stingless bees are outstanding by the gradual post-emergence pigmentation. Fifty darkest workers were selected from specimens collected from the succumbed nest (N_1) and preserved in 70 % alcohol for taxonomic examinations.

Coloration: Head and mesosoma black; antennal flagella frontally and mandibles blackish brown; extremities of scape brown; metasomal tergum I yellowish with dark brown band along basal depression, terga II - V blackish brown, V apically, VI and venter pale brown to yellow-brown, legs dark chestnut brown. *Pilosity:* Hairs on vertex and scutellum apically ochraceous; mesoscutum apically and metanotum with whitish tomenta in most specimens. Hairs on mid tibia brown to dark brown; posterior corbicular fringe dark to blackish brown. Clypeal hairs relatively dense, tending ochraceous than whitish. *Structure:* No differences from continental specimens, including shape of hind tibia, which is slightly variable in both continental and Taiwanese specimens, but always not so expanded with more distinctly curved contours as in *T. (L.) terminata* Smith. *Size:* ($n=50$) Head width 2.05±0.02㎜, wing length including tegula

Table 1. Comparison of Taiwanese and continental worker specimens of *Trigona ventralis* on some color characters.

Character	No. of specimens examined				
	Taiwan	N. Thailand	Laos	Vietnam	S. Thailand & Malaya
Hairs on vertex					
Ochraceous~pale brown	50	18	14	97	13
Brownish		33		4	3
Dark brown~blackish		191		9	
Total	50	242	14	110	16
Hairs on mesoscutellum					
Whitish~pale ochraceous	50				
Ochraceous~pale brown		8	14	78	14
Brownish		20		13	1
Dark brown~blackish		213		18	1
Total	50	241	14	109	16
Hairs on mid tibia					
Ochraceous~pale brown	20			28	11
Brownish	30	39	3	56	5
Dark brown~blackish		197	11	25	
Total	50	236	14	109	16
Color pattern of tergum I*					
Pale with semicircular dark band	49	4	7	2	14
Apical margin also dark	1	2	2	32	
Much darker		234	5	75	
Total	50	240	14	109	14

* Three degrees correspond to A+B, C+D and E−H, respectively in Sakagami (1975, Fig. 11).

5.24±0.18㎜, wing diagonal (WL_2 in Sakagami, 1978) 1.52±0.04㎜, hind tibial length 1.73±0.04㎜.

Some young males collected from the nest structurally accorded with the description given by Sakagami (1975) based upon three specimens from Dalat, Vietnam. *Size:* (n=5) Head width 2.09±0.04㎜, wing length 5.36±1.02㎜, wing diagonal 1.48

Table 2. Comparison of Taiwanese and continental worker specimens of *Trigona ventralis* on head width.

Localities	No. of examined specimens (16 units= 1 mm)						Head width (mm)
	28	29	30	31	32	33	$\bar{x} \pm$ SD (*n*)
Taiwan				1	23	26	2.05±0.02 (50)
N. Thailand		3	13	59	127	5	1.97±0.44 (207)
Laos		1	8	4			1.89±0.04 (13)
Vietnam	19	43	24				1.82±0.04 (86)
S. Thailand/Malaya		7	9	1			1.85±0.04 (17)

±0.02mm, hind tibial length 1.72±0.02mm.

The Taiwanese specimens were compared with continental ones (Sakagami, 1975) on some characters as follows:

(1) Development of mesosomal tomenta is conspicuous. In 43 out of 50 specimens, even mesoscutellum apically and metanotum are covered with tomenta, though not so conspicuous as in *T. (L.) terminata*. This state seldom appears on the continent.

(2) Metasomal terga V apically and VI were pale brown to pale yellow brown, whereas brown to nearly blackish in continental specimens, sometimes only VI apically pale orange brown.

(3) Hairs are generally paler (Table 1). Particularly mesosomal tomenta are very pale.

(4) Metasomal tergum I exhibits the palest pattern, interestingly, being comparable to the specimens from the southern populations, not the northern ones on the continent.

(5) Head width exceeds even the northern Thai specimens, which are largest on the continent (Table 2). The difference between frequency distribution of Taiwanese and northern Thai specimens is highly significant ($P < 0.001$) by χ^2-test.

Although only the specimens from a single colony were used for comparison, the differences given above are clearer than those among the continental specimens of any areas, particularly as for items (1), (2) and (5). Item (1) is consistent with Sonan (1927) and (2) and (5) with Schwarz (1939). Based upon these differences, *T. ventralis* could be divided at least in two subspecies, *T. v. ventralis* in S.E.Asia and *T. v. hoozana* isolated in Taiwan.

Post-emergence Pigmentation and Task Allocation

As in the other known species, worker pigmentation proceeds gradually. Based on

samples selected from N_1 the following stages were distinguished.

I a. Pale yellow; eyes dark violet, mandibles infuscate. In some individuals head above, mesoscutum partly, mesoscutellum posteriorly, and terga II-III slightly infuscate.

I b. Pale brown semicircular band appearing along basal depression of tergum I.

II a. Head as dark as eyes; mesoscutum, axillae and posterior two thirds of mesoscutellum brown; mesopleura pale brown to brown; scapes and parts of legs pale brown; mandibles brown to dark brown. In some individuals head much darker than mesoscutum and scapes dark brown.

II b. Head, except lower half, or except clypeus and malar area, black; mesoscutum, axillae and posterior two thirds of mesoscutellum dark to blackish brown; metanotum brown to dark brown; propodeum and mesopleura brown to dark brown; lgs brown, apically pale to dark brown, partly brown; bands of tergum I and terga II-IV brown to dark brown.

III a. Head black; antennal sockets, lower two thirds of clypeus and malar area brown; mesoscutum and most parts of mesoscutellum black; mesonotum brown; propodeum and mesopleura except along mesoscutum dark brown; legs dark brown; hind tibia partly and all tarsi brown.

Table 3. Relationship between pigmentation stages and some functional features in workers given by the number of individuals classified into categories explained in the text (p. 41).

Stage	Metasomal swelling (+ or −)	Crop content			Wax plates on terga			Ovarian development		
		+	±	−	+	±	−	+	±	−
I a	all− 5			5			5			5
I b	−11			11			11			11
	+ 4			4			4			4
II a	−17	3	9		8	3	1	2	5	5
	+ 8	5	3		4	1	3	1	4	3
II b	− 2		2		2			1	1	
	+18	16	2		14	3	1	4	10	4
III a	−11	2	9		8	3		1	4	6
	+ 9	7	2		7	2		1	2	6
III b	−12	1	13		7	2	5		2	12
	+ 5	2	3		4		2		1	5
IV	all−50		12	38		4	16			50

IIIb. Head black; clypeus marginally and malar area sometimes dark brown; mesosoma black; mesoscutellum partly and metanotum dark brown; terga and legs dark brown; hind tibia and tarsi sometimes brown.

IV. Described in taxonomic notes.

Distinction of stages does not strictly correspond to stages I - IV recognized in *T. laeviceps* (Sakagami, Inoue, Yamane and Salmah, 1983). In *T. v. hoozana* pigmentation of mesoscutellum seems to proceed earlier than in many other species.

The following features were examined for each stage. (1) Metasoma swollen (+) or not (−), (2) crop filled with abundant (+), medium (±) or little (−) quantity of viscous yellowish liquid (larval food), (3) wax plates on metasomal terga well (+) or moderately (±) developed or absent (−), (4) ovaries with oocytes detectable (+), slightly swollen (±) or threadlike (−).

Table 3 shows that workers of stages IIa-IIIa are chiefly responsible for brood rearing activities such as food provisioning in larval cells and cell building, and also for oviposition.

Distribution and Nesting Sites

Sonan (1927) recorded *T. v. hoozana* from the mountainous areas of 1500-2800m alt. He also noted that this bee nests in tree hollows and the native people living at about 1500m alt. rear it in order to collect propolis from the nests. The propolis is boiled, admixed with petroleum and used as a binding agent or for caulking ship planks. One of us (S.Y.) discovered two nests in 1973 at Kwantau-Shan (at ca. 1500m alt.) located at about 5km south of Kwantau-Shih, the site of the Office of Experiment Forest

Table 4. Climatic records at Hsienyeh* (Experiment Forest of National Chung-Hsing University, Nantou).

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	
Monthly mean air temp. (℃)	14.8	16.1	18.9	22.5	25.7	26.6	27.1	26.8	26.3	24.3	20.8	16.4	Mean 22.2
Precipitation (mm)	61	125	260	218	338	711	509	410	196	46	31	58	Total 2965

* 24° 05′ N, 121° 00′ E, 450m alt. Mean of records taken during 1934 and 1943. Data were given through the courtesy of the Office of the Experimental Forest of Hokkaido University.

of National Chung-Hsing University (24°05′N and 121°00′E, ca. 550m alt.), Nantou, where the dominant vegetation is the primary warm-temperate forest of evergreen oaks, camelias, lauraceous trees, etc.

According to people in the Experiment Forest, most nests are built in hollows of oak trees at heights less than 5m above the ground. But nidification in a bamboo pillar of a house has also been known. Before the Second World War, nests were occasionally found in oak forests at 400-500m alt. At present, however, the primary oak forests remain only at above 1500m alt. along the peaks of the central mountain ridges and the distribution of *T. v. hoozana* also appears to be confined there. The nests are now very rare even within the Experiment Forest. The climate at Hsienyeh, a meteorological observation point in the Experiment Forest near Kwantau-Shih (450m alt.) is characterized by cool and arid winter (Table 4). The minimum air temperature in January drops down to 5-7℃. Applying decrease of air temperature, 0.6℃ per 100m elevation, mean air temperature in January is roughly approximated to 9℃ at 1500m alt., where the two observed nests were collected, and to 1℃ at 2800m, the highest place of collection recorded by Sonan (Mt. Yu-Shan), although the area is located a little southerly near the Tropic of Cancer. Judging from the short flight radius of stingless bees, their vertical shift by flight may not be extensive. Certainly the area may be thermally one of the severest habitats for the tropically adapted stingless bees. It is possible that *T. v. hoozana* is more cool-adapted than the other species. However, its confinement to the coolest zone in Taiwan should have also been brought in part by the extensive deforestation on the island during several hundred years. Actually *T. v. hoozana* is sensitive to the drop of temperature, and ceases foraging even when the honeybees are still continuing their activities.

Guard Behavior

Behavior of guards, which is also group specific, is as follows: Several guards sit on the lower lip of the entrance, slightly and somewhat synchronously retreating on arrival of homing foragers as guards of *T. (Tetragonula) laeviceps* do (Sakagami, Inoue, Yamane and Salmah, 1983). For human observers, the guards are timid, exhibiting no agonism including alert fanning. A number of workers landed on and crawled in the hairs and clothes only when the nests were opened. Interferences such as beating the entrance tube evoked not only withdrawal of guards but also interruption of foraging traffic up to 10 min., followed by mass departures. Aggressiveness was identified as degree 1-2 (cf. Wille and Michener, 1973).

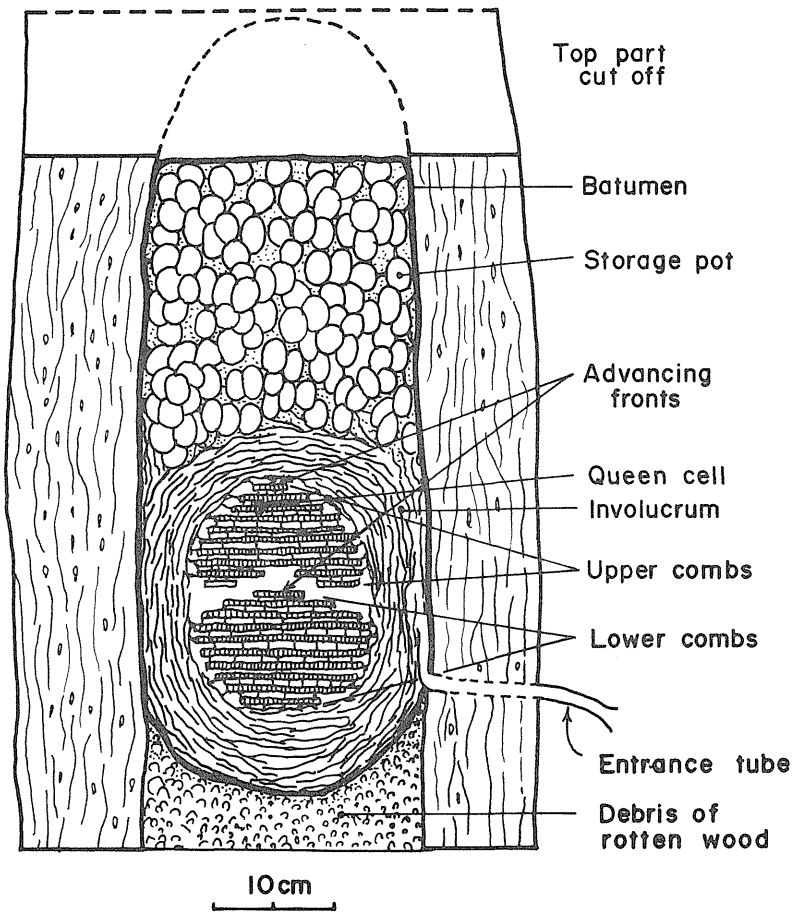


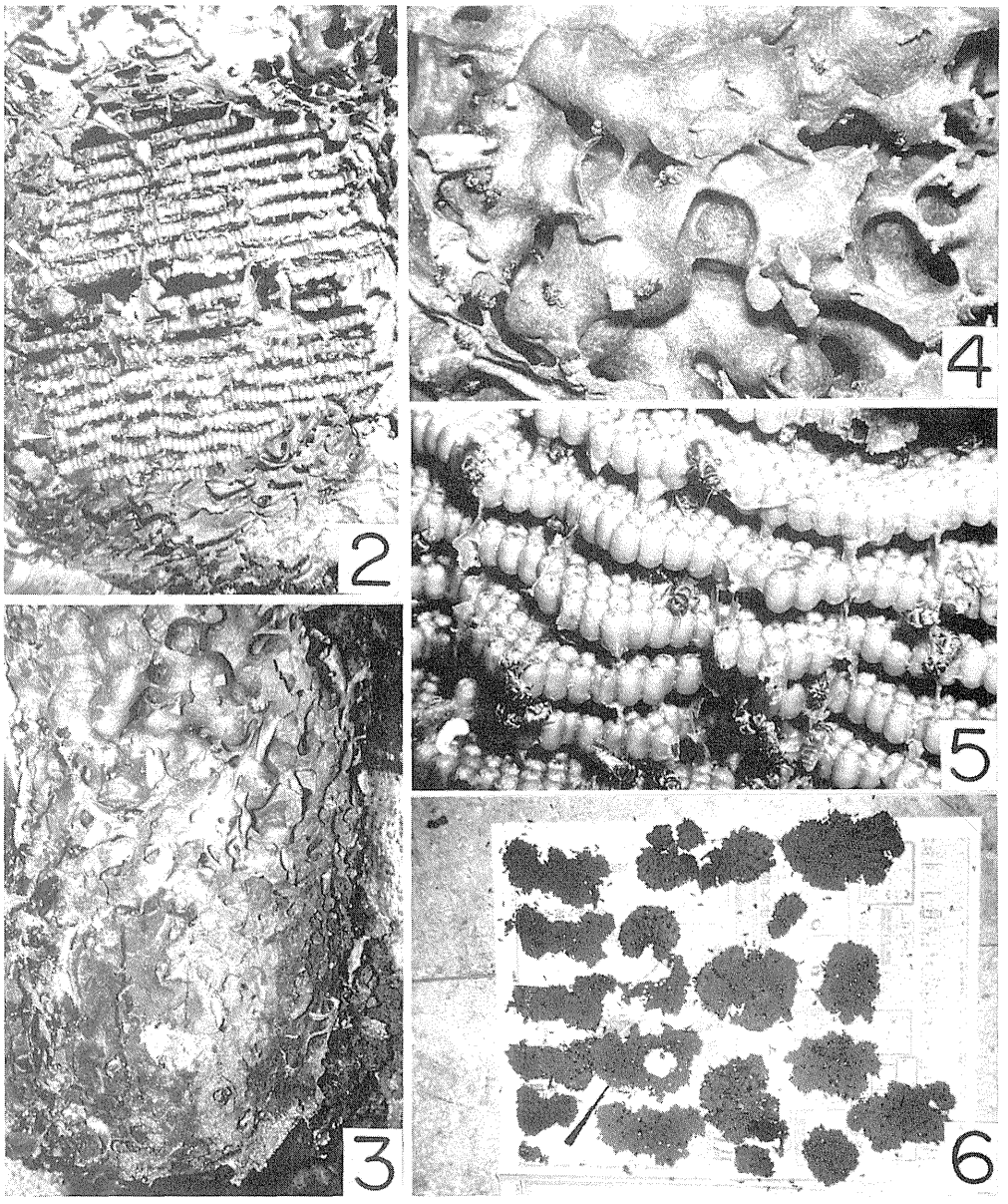
Fig. 1. Cross section of nest N_2 of *Trigona (Lepidotrigona) ventralis hoozana*.

Nest Architecture

Two examined nests (N_1 and N_2) were both built in hollows of oaks (60 and 45cm ϕ, respectively), located at a few meters aboveground. The trees were cut down in a forest and transported to a lumberyard in Hsienyeh, where the presence of the nests was noticed. N_1 was transferred into a wooden box on 14 March 1973. But most part of the nest had been taken away and lost the queen. Therefore the colony succumbed soon. The nest architecture was only superficially examined, but there were no essential differences from N_2.

N_2 was discovered in the same lumberyard on 24 April 1973. The nest was left in a store hut at Kwantau-Shi and the entrance was communicated with outdoor by means of a transparent glass tube, ca. 1cm ϕ and 20cm long. On 4 August the colony was

transferred in an observation hive. On this occasion, the nest architecture was quickly examined (Figs. 1 - 6). The hollow was about 23cmϕ and 60cm long.

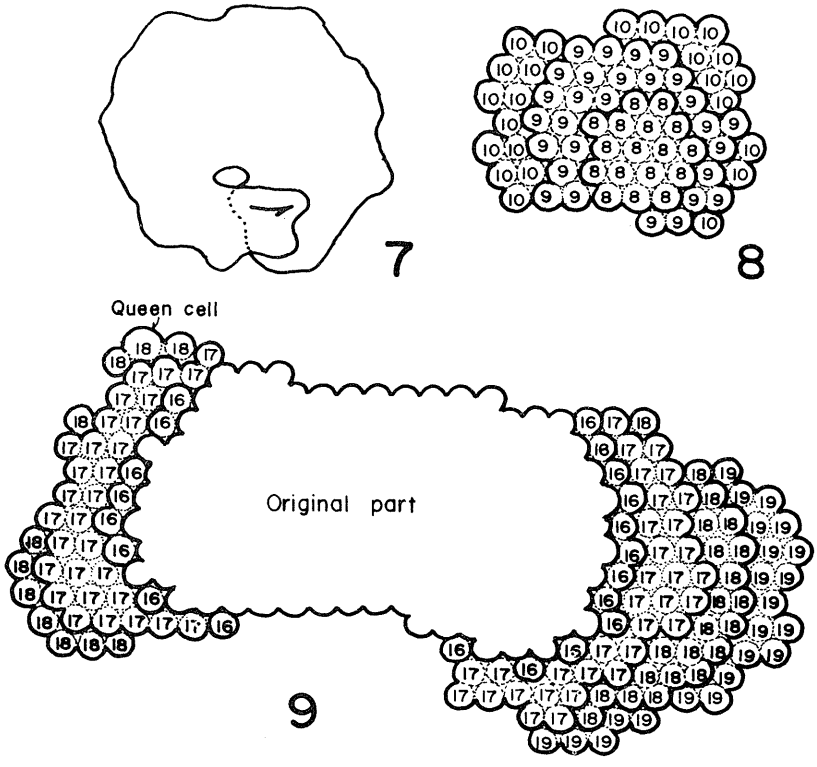


Figs. 2–6. Parts of nest N_2. 2. Brood area with upper and lower comb sections. White arrows indicate queen cells., 3. Storage pots, 4. Ditto, enlarged, 5. Combs enlarged, 6. Combs removed to show various shapes. Black arrow indicates the lowest comb of the upper comb section, with a central hole resulted from emergence of adults.

The entrance tube was broken at cutting the tree, but according to people who helped S.Y., it was 5-10cm long and the tip was slightly funnel-shaped. Since the nest was connected with outdoor by a glass tube, bees only constructed a fringe at the opening, which was blackish brown, soft, pliable and rather smooth. Internal tunnel was not examined.

Batumen plates at top and bottom of nest cavity 2mm thick. Lower part of cavity occupied by brood area completely covered with involucrum 5.0-5.5mm thick. Involucrum brownish, of sheeted type, not of lamellate pillar system, consisting of 5-10 sheets, each 0.2-0.5mm thick, soft and pliable, externally connected with cavity wall by means of short pillars (Figs. 1 - 3).

Brood cells arranged in a total of 20 horizontal complete combs (Figs. 1, 2, 5,



Figs. 7–9. Various cases of comb growth during the rearing in an artificial hive. 7. Spiral growth of comb CIV, 14 days after initiation, 8. Concentric expansion of comb CG-III-4', 9. Bilateral growth of comb CG-III-5'. Numerals in cells of Figs. 8 and 9 indicate dates of construction in August.

6). Successive combs separately built as in vespine nests, not forming spiral continuum even partially, connected each other by several short pillars (Fig.5). Upper and lower surfaces of each comb even (Fig. 2), combs not always typically concentric, some ones with quite irregular contours (Fig. 6), the largest one (15th from top) $14 \times 9 cm^2$ with 1200 cells. Advancing edges at top (first) and middle (11th) combs, each with ten cells which had not yet been oviposited at examination. Cells brownish, 4.6-5.1 mm long ($\bar{x} = 4.9 \pm 0.2$mm, $n = 10$) and 2.7-3.0mm ($\bar{x} = 2.8 \pm 0.8$mm, $n = 10$) with wall 0.8 ± 0.2mm thick. Several queen cells found at edges of combs, about 10mm long and 5.5mm ϕ. Cocoons light yellowish brown.

Upper part of nest cavity occupied by more than 100 storage pots. Pots brownish; their shape variable, spherical to oval or elongate oval, 20-30mm long and 15-20mm ϕ. Adjacent pots either connected with pillars or sharing walls, and coated with copious cerumen cover often extending as lamellae. Consequently, distinction of adjacent pots sometimes difficult externally (Figs. 3, 4). Pollen and honey pots homomorphous and intermingled, though the former prevailing near cavity walls. The brood area of N_1 was also coated with sheeted involucrum and combs (at least 10 were counted) were separately, not spirally arranged.

After transference into an observation hive, some combs were newly started on the top of the older combs and the floor of the hive. One of these combs, C_{IV}, grew spirally (Fig. 7) as observed in *T. (L.) terminata* (Sakagami, Yamane and Hambali, 1983). Expansion of combs was not always concentric, but often partial regardless of spatial conditions, resulting in the irregular shapes (Fig. 8 *vs.* 9) as was under natural conditions. The involucrum was apparently thicker in the non-heated hive than in the heated one, indicating the bees' behavioral response to thermal conditions.

The general architecture does not particularly differ from nests of other comb-builders. There are two distinct differences between *T. ventralis hoozana* and its consubgener *T. (L.) terminata*; (1) Combs are covered with lamellate-pillar system in *T. terminata*, while with sheeted involucrum in *T. ventralis* at least in *T. v. hoozana*, (2) comb arrangement is typically spiral in *terminata*, but consecutive in *v. hoozana*, although spiral arrangement can appear occasionally. These two characteristics are sometimes variable intraspecifically (Wille and Michener, 1973). Whether the mentioned differences are really interspecific or not, particularly the thick sheeted involucrum in *T. v. hoozana* reflects its severe habitat or not, should be clarified by the comparison with nests of *T. v. ventralis* in warmer habitats of S.E.Asia.

The population size of N_2 was quite large. The number of adults was roughly estimated at 10000 and of immature stages at 12,400 (number of closed cells).

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