

AN EXTRAORDINARY CONCENTRATION OF STINGLESS
BEE COLONIES IN THE PHILIPPINES, WITH
NOTES ON NEST STRUCTURE (HYMENOPTERA :
APIDAE : *TRIGONA* SPP.)

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SUMMARY

A bamboo farmhouse on Negros island, Philippines harbored at least 84 colonies of *Trigona* (*Tetragonula*) *fuscobalteata* and *T. (Tetragonula)* *sapiens* in a ratio of about 3 : 1.

Nests were in bamboo stem cavities of 0.7 - 3.0 l volume. In neither species does the nest show specialized features relative to the subfamily. The entrance tube is simple and of medium length. The tube aperture is longer and narrower in *T. sapiens* than *T. fuscobalteata*, although the former species has a greater head-width. Brood-cells are arranged in clusters, not in organized combs, and are not surrounded by an involucre.

There is some indication that within the Philippines stingless bees are more abundant in drier areas.

ZUSAMMENFASSUNG

**Eine Außerordentliche Anhäufung von Kolonien von Stachellosen
Bienen auf den Philippinen, mit Bemerkungen über Neststruktur
(Hymenoptera : Apidae : *Trigona* Spp.)**

Auf der Insel Negros, Philippinen, wurde ein aus Bambus gebautes Bauernhaus entdeckt, das mindestens 84 Kolonien von stachellosen Bienen beherbergte, und zwar der beiden Arten *Trigona (Tetragonula)* *fuscobalteata* und *T. (Tetragonula)* *sapiens* in einem Verhältnis von ungefähr 3 : 1.

Die Nester waren in Bambussegmenten, je mit einem Rauminhalt von 0,7 - 3,0 l. Die Neststruktur entspricht generell dem Typus der Unterfamilie. Die Flugröhre ist einfach und nicht besonders lang. Die Röhrenöffnung ist bei *T. sapiens* länger und enger als bei *T. fuscobalteata*, obwohl *T. sapiens* einen breiteren Kopf besitzt. Die Brutzellen

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sind nicht in Waben angeordnet, sondern bilden traubenförmige Haufen. Sie sind auch nicht von einem Involucrum umgeben.

Es gibt Hinweise, daß stachellosen Bienen in trockenen Gebieten der Philippinen häufiger vorkommen.

INTRODUCTION

Stingless bees are much less diverse and generally abundant in Southeast Asia than the New World tropics. All species known from the Philippines Proper (i.e. the Philippines except for the Palawan group) belong to the taxonomically difficult subgenus *Tetragonula* of *Trigona* (SCHWARZ, 1939, BALTAZAR, 1966). They are characterized by small body size, unaggressiveness, moderate colony size, generalized nest structure relative to the subfamily, and often by anthropophily (WILLE and MICHENER, 1973; SAKAGAMI *et al.*, 1983 a-b).

Bees formerly identified as *T. iridipennis* Smith in Southeast Asia are now treated as *T. laeviceps* Smith (SAKAGAMI, 1978). It appears, though, that this is a composite taxon of at least two sibling-species (SAKAGAMI, unpubl.). Workers of the larger of the two species treated in this paper are indistinguishable from *T. laeviceps*, but where males were available they accorded well with males of *T. sapiens* Cockerell and not *T. laeviceps*. We provisionally treat this species as *T. sapiens* and conclude that all previous reports of "*T. iridipennis*" in the Philippines refer to it.

The other species treated here is unambiguously *T. fuscobalteata* Cameron, the smallest *Tetragonula*. According to present knowledge (SCHWARZ, 1939, BALTAZAR, 1966; SAKAGAMI, unpubl.), the Philippines Proper have at least one other species, *T. biroi* Friese.

There is a fair amount published on *Tetragonula* nest structure. WILLE and MICHENER (1973) reviewed what is known from *T. carbonaria*, *clypearis* (? = *fuscobalteata*), *fuscobalteata*, *hockingsi*, *pagdeni* (as *fuscobalteata pagdeni*), *sapiens* (as *iridipennis* in part), *sarawakensis* and *smithii*. SAKAGAMI *et al.* (1983 a-b) added information on *T. drescheri*, *fuscobalteata*, *geissleri*, *laeviceps* (= *minangkabau*; see SAKAGAMI and INOUE, 1985), *melina* and *pagdeni*. Much less has been written about behavior or colony structure in this group, the main contributions being those of GEORGE (1934), SAKAGAMI *et al.* (1983 a-c) and INOUE *et al.* (1984 a-b). See also ROUBIK (1979, 1983) for extensive treatment of neotropical *Trigona*.

In this paper we describe an extraordinary concentration of two *Tetragonula* species on Negros island, with notes on their nests.

MATERIALS AND METHODS

The senior author found stingless bees more abundant in cultivated areas around Dumaguete, Negros Oriental than any other area visited in the Philippines. Nests are common in coconut trunks and buildings, often conspicuous by the entrance tube and bees entering and leaving. Colonies were located by ordinary search aided by directions from local people. *Trigona* are well known in Negros Oriental by the name *kiyot*.

The main nesting site treated here is the house of coconut farmer Anastasio Umbac at Tabuc-Tubig, Dumaguete. The senior author and Federico P. GODOY on three occasions counted as completely as possible all entrance tubes on the Umbac house with bees entering and/or leaving. The highest count is taken as the best estimate of the number of active colonies and is probably slightly below the true total. Experience with these and other *Tetragonula* spp. indicates that each nest has just one tube.

We examined entrance tubes of 34 *T. fuscobalteata* and nine *T. sapiens* nests near Dumaguete and Valencia, Negros Oriental and one *T. sapiens* nest near Baybay, Leyte. Internal nest features are described based on one *T. fuscobalteata* nest and two *T. sapiens* nests at Dumaguete and four *T. sapiens* nests near Baybay and Inopacan, Leyte.

In estimating the volume of bamboo cavities (i.e. the spaces between nodes), the inner diameter was measured at a cut end if available, otherwise from the outer diameter and an estimate of wall thickness. External internode length was taken as equivalent to cavity length.

Voucher specimens of bees are deposited at the Visayas State College of Agriculture at Baybay, Leyte, Philippines and the Institute of Low Temperature Science of Hokkaido University at Sapporo, Japan (1).

RESULTS

The Umbac house consists of two adjacent structures with a ground area of about 68 m² (fig. 1). The framework is of bamboo, and nearly all *Trigona* nests in the house were inside bamboo beams (fig. 2). The house is typical for the area, though larger than most. Coconut is the dominant local vegetation, broken by occasional second-growth.

A search inside and below the Umbac house revealed very few nests, but they were abundant on the outside walls at heights of about 1-4 m. We estimated the number of colonies in the house as at least 84. We collected bees from 38 colonies, of which 30 (77 %) were *Trigona* (*Tetragonula*) *fuscobalteata* and the others *T. (T.) sapiens*. If this sample is unbiased, the house contained at least 65 colonies of *T. fuscobalteata* and 19 of *T. sapiens*.

We measured volumes of 48 nests which appeared each to occupy one complete bamboo cavity: 26 of *T. fuscobalteata*, seven of *T. sapiens* and 15 unidentified. Twelve of these lay horizontal, the others vertical. The mean volume was 2.1 l in *T. fuscobalteata* and 2.0 l in *T. sapiens* (table I).

(1) Vouchers can be recognized by their nest-series numbers: 654-657, 669, 674, 706-730 and 739-740 for *T. fuscobalteata*; 226, 265, 460, 481-482, 658-659, 731-738 and 743 for *T. sapiens*. See STARR (1984) for remarks on the use of nest-series numbers.

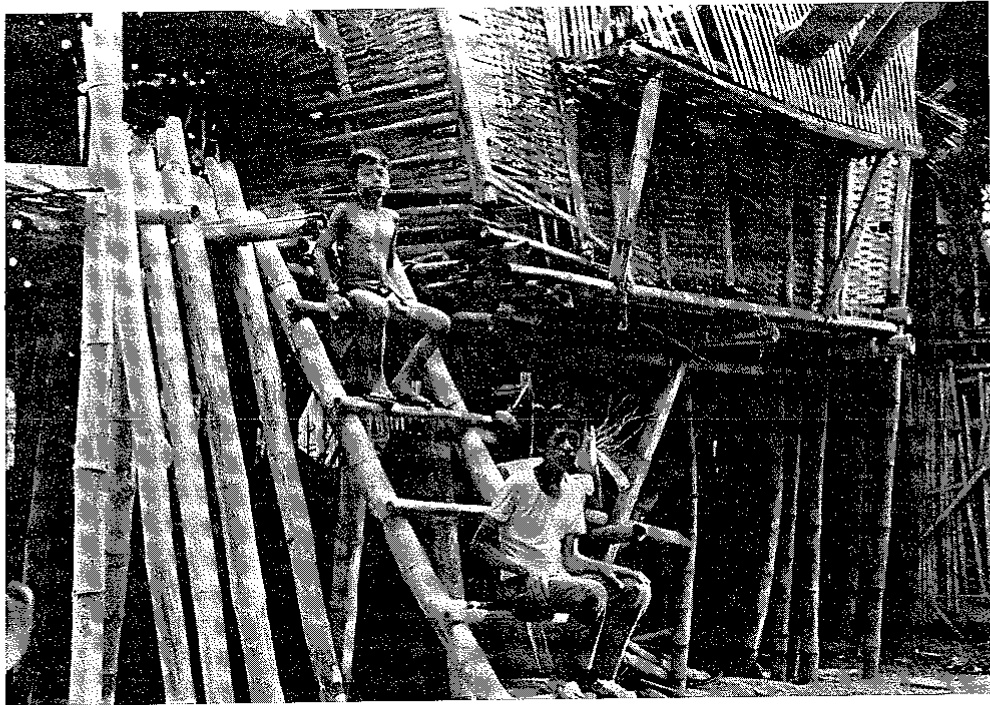


Fig. 1. — House of the Anastacio Umbac family at Tabuc-Tubig, Dumaguete, Negros Oriental.

Abb. 1. — Familienhaus von Anastacio Umbac in Tabuc-Tubig, Dumaguete, Negros Oriental.

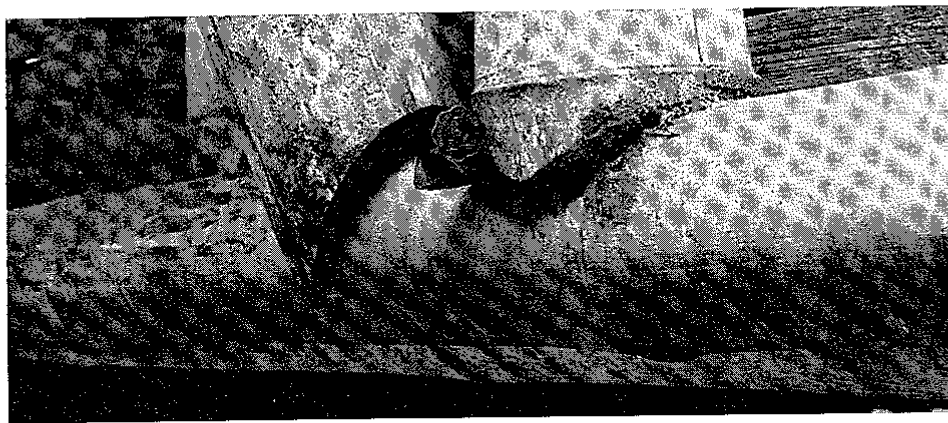


Fig. 2. — Typical bee-inhabited bamboo beam of the Umbac house. Maximum width of the coin is 19 mm.

Abb. 2. — Charakteristischer bienenbewohnter Bambusbalken des Umbac-Hauses. Münzenbreite ist 19 mm.

Table I. — Diameter, length and volume of 48 unbroken bamboo cavities in beams of the Umbac house, each inhabited by a colony of bees. All undetermined colonies can be assumed to be *T. fuscobalteata* or *T. sapiens*.

Tabelle I. — Umfang, Länge und Rauminhalt von 48 vollständigen Bambussegmenten, bewohnt von jeweils einer Bienenkolonie. Alle nicht artenbestimmten Kolonien sind fast sicher *T. fuscobalteata* oder *T. sapiens*.

	<i>T. fuscobalteata</i>	<i>T. sapiens</i>	Undetermined species
No. of nests	26	7	15
Mean diameter (cm)	8.3	7.8	8.1
Range	7.5—9.5	7.0—8.5	8.0—8.5
Mean length (cm)	38.0	41.9	38.7
Range	21.0—44.0	33.0—47.5	28.0—48.5
Mean volume (l)	2.1	2.0	2.0
Range	0.7—3.0	1.7—2.4	1.4—2.4

Entrance tubes of both species lack any of the elaborations known from some other stingless bees (WILLE and MICHENER, 1973, ROUBIK, 1983). They are simple tubes of medium length, mostly of soft, dark brown cerumen (fig. 3 a-c). They may narrow or broaden somewhat toward the end, though not into a distinct trumpet shape. The sole exception to this pattern was a *T. fuscobalteata* tube which flared abruptly at the tip to a maximum width of 45 mm (fig. 3 d).

Some of the variation in entrance tube forme is illustrated in figure 3. We found four main variables :

1. Length, measured along the shortest side. As seen in table II, there is a substantial variation within each species, but virtually none between species.
2. Orientation. Most tubes were approximately horizontal. Exceptions mostly descended distally (e.g. fig. 3 b).
3. Aperture shape and orientation. Apertures ranged from slit-like to elliptical (*T. sapiens*) or approximately spherical (*T. fuscobalteata*). They are distinctly longer and narrower in *T. sapiens* than *T. fuscobalteata* (table II). The length-line is usually close to vertical, but can apparently take any orientation.
4. External texture. The tube wall varies from smooth to coarsely granular. Along with increased roughness go increased wall thickness and rigidity, and it is plain that rough walls are an elaboration on originally smooth ones. Thickness varies from about 1-2 mm.

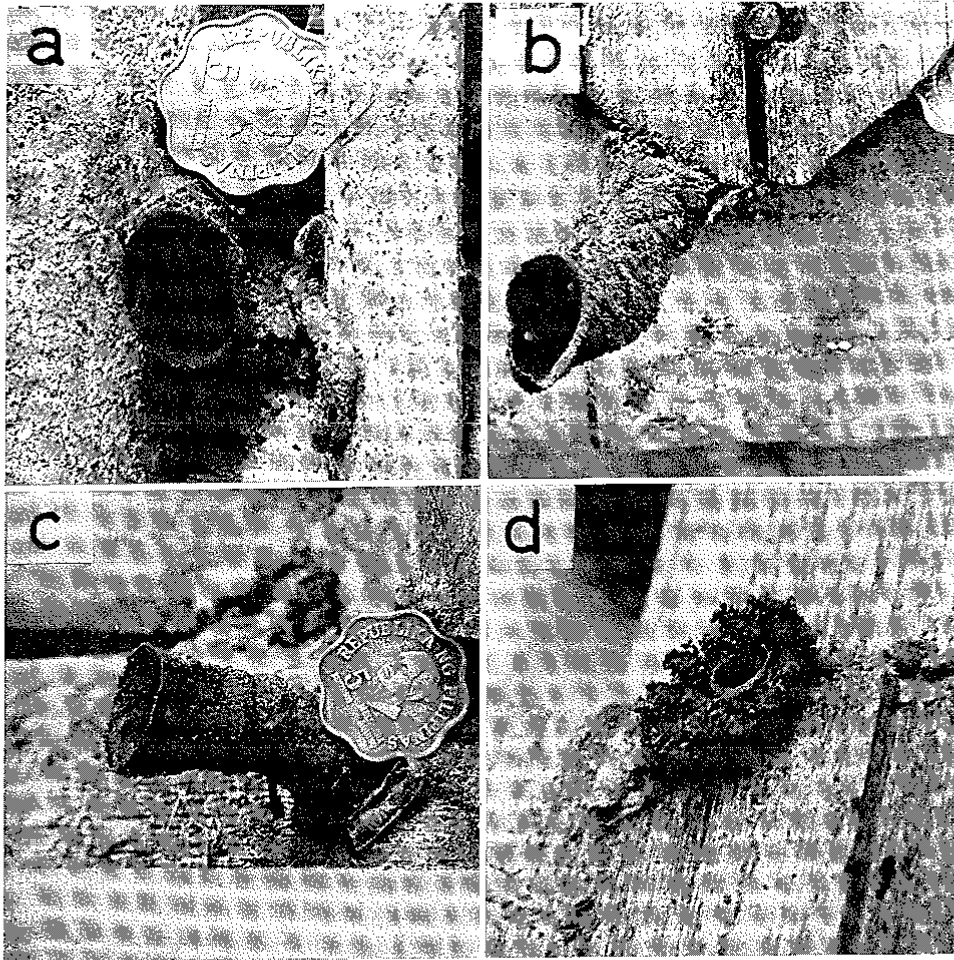


Fig. 3. — Entrance tube of *T. fuscobalteata*. (a-c) Typical tubes, (d) The anomalous tube from colony 674. Maximum width of the coin is 19 mm.

Abb. 3. — Flugröhren von *T. fuscobalteata*. (a-c) Artentypische Röhren. (d) Die sehr ungewöhnliche Röhre von Kolonie Nr. 674. Münzenbreite ist 19 mm.

Both species utilize nest cavities requiring little sealing. The most extensive sealing structure seen was a batumen end-plate of *T. fuscobalteata* of about 37 cm². Sealing cerumen appears to undergo a process of maturation as in entrance tubes. It begins as a smooth, pliable, medium brown sheet, then thickens, darkens and becomes darker and more rigid (fig. 4 a-b).

Most dissected nests were in bamboo or similar cylindrical cavities. Examination of other nests supports the rule that these are constructed in elongate cavities. The most compact seen was a *T. sapiens* nest in a

Table II. — Features of the entrance tube in nests from the Umbac house. By *aperture length* is meant maximum distance across the aperture, while *width* is perpendicular to this across the aperture.

Tabelle 2. — Beschaffenheit der Flugröhre von Nestern am Umbac-Haus. *Aperture length* ist der größte Querabstand des Fluglochs, während *aperture width* dazu senkrecht ist.

	<i>T. fuscobalteata</i>	<i>T. sapiens</i>
Mean minimum tube length (mm)	11	13
Range	0 — 31	0 — 40
n	32	9
Mean aperture length (mm)	15	20
Range	9 — 21	10 — 45
n	34	10
Mean and modal aperture width (mm)	9	5
Range	5 — 15	5 — 7
n	34	10

cavity about 8 cm high and 23 by 26 cm wide. The smallest nest cavities measured had volumes of 0.7 l in *T. fuscobalteata* and 1.7 l in *T. sapiens* (table I); note, though, the small sample size for *T. sapiens*. One other *T. fuscobalteata* nest had a volume of less than one liter.

Measurements of two *T. sapiens* suggest that preferred nest cavities are considerably larger than those given in table I. In each of these there was both ample space and the opportunity to limit it. In one, the bees had available one bamboo cavity and most of the adjacent cavity, through a break in the node-plate (fig. 5 a). They had closed the cavity about 15 cm from the outer end, limiting nest volume to 3.6 l, about 80 % of that available. The other colony, in a tree-fern hollow (fig 5 c), similarly limited its nest cavity to 7.3 l. In each case the closure was with a dark, brittle batumen plate about 2-3 mm thick.

No nest of either species had an internal entrance tube, so that the external tube opened directly into the nest cavity.

Three *T. sapiens* nests each had a perforated batumen plate inside (fig. 5 b-c), similar to end-plates but with numerous holes of just the size to let a bee pass. This suggests that each was originally an end-plate, perforated when the nest was expanded.

The nest-lining batumen is very thin and often discontinuous.

The small, oval brood cells and cocoons are connected with each other and the nest walls by a network of narrow, cylindrical pillars and are compactly clustered in an apparently unstructured manner (fig. 4 c). They are not surrounded with an involucre.

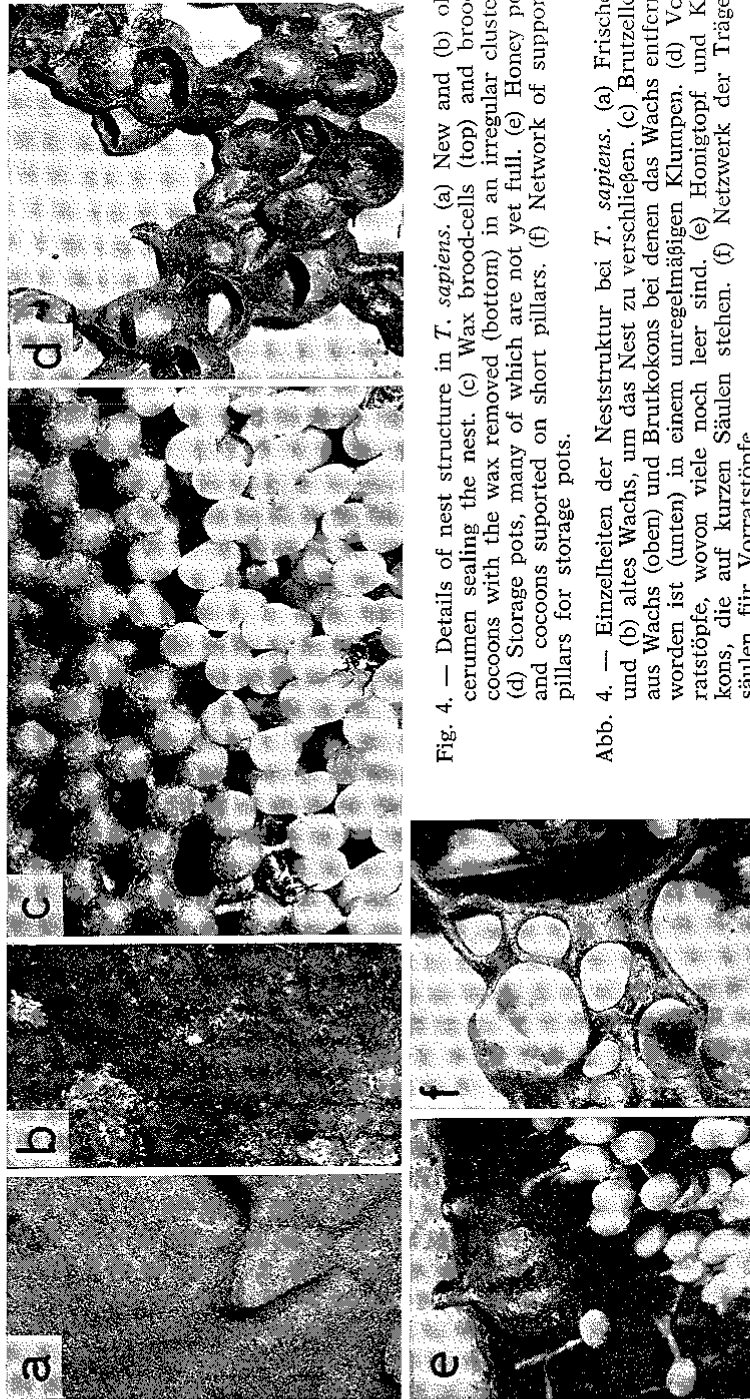


Fig. 4. — Details of nest structure in *T. sapiens*. (a) New and (b) old cerumen sealing the nest. (c) Wax brood-cells (top) and brood-cocoons with the wax removed (bottom) in an irregular cluster. (d) Storage pots, many of which are not yet full. (e) Honey pot and cocoons supported on short pillars. (f) Network of support-pillars for storage pots.

Abb. 4. — Einzelheiten der Neststruktur bei *T. sapiens*. (a) Frisches und (b) altes Wachs, um das Nest zu verschließen. (c) Brutzellen aus Wachs (oben) und Brutkokons bei denen das Wachs entfernt worden ist (unten) in einem unregelmäßigen Klumpen. (d) Vorratstöpfe, wovon viele noch leer sind. (e) Honigtopf und Kokons, die auf kurzen Säulen stehen. (f) Netzwerk der Trägersäulen für Vorratstöpfe.

Storage pots for honey and pollen are of a single, roughly spherical type. Like brood cells, they have thin walls of soft, brown cerumen (*fig. 4 d*). At the edges of the storage zone, individual pots may be fairly discrete, connected by pillars (*fig. 4 e*), but more centrally they form a single, continuous mass. This appears to begin as a network of pillars (*fig. 4 f, 5 a*) which serves as a framework on which storage pots are built until all inner spaces are filled.

The honey is medium brown, of similar viscosity to raw non-commercial *Apis cerana* or *A. breviligula* honey, but much sourer than these or *A. mellifera* honey. The pollen is consistently wetter than that from *Apis* nests and is sour, as if mixed with acetic acid. The number of filled pollen pots in one *T. sapiens* was estimated at 1,360, based on a count of what appeared to be about 5 % of the total. The total volume of pollen in these was estimated at 0.9 l, based on the volume in water of 20 pollen masses.

Figure 5 shows the gross internal structure of nests, i.e. the placement of brood cells, cocoons and storage pots. The first two occupy a distinctly bounded zone, and where space allows they form a single mass. Development proceeds such that same-aged brood form cross-sectional bands within the zone (*fig. 4 c, 5*), which must move along it in waves. One *T. sapiens* nest had a peculiar gap of about 2 cm across the brood zone (*fig. 5 c*).

Honey and pollen are stored in separate pots, but the pots are often interspersed. The storage zone in one *T. sapiens* nest was largely divided into a honey area and a pollen area (*fig. 5 c*), while in two others no such division appeared (*fig. 5 a-b*). In the *T. fuscobalteata* nest a brood zone separated a zone of mostly pollen from one of mostly honey (*fig. 5 d*). The area next to the entrance was in each case a storage zone.

In the simplest case, then, the nest has a single storage zone next to the entrance and a single brood zone beyond this (*fig. 5 c*). In some nests there is a second storage zone beyond the brood zone (*fig. 5 a*), and one *T. sapiens* nest and the *T. fuscobalteata* nest had a second brood zone beyond this (*fig. 5 b-d*).

In one *T. sapiens* colony we counted 2,775 adults. This is certainly an underestimate, but probably not very far below the true total.

DISCUSSION

The abundance of stingless bees in the Dumaguete area cannot be definitely explained, but climate appears to have something to do with it. With an average annual rainfall of 1,306 mm, Dumaguete is among the driest places of the Philippines (unpublished data from PAGASA, the national weather service). On the other hand, Borongan, Eastern Samar, where the senior author found only one *Trigona* colony during 2½ weeks, is one of the wettest places with 4,244 mm of rainfall. The tentative conclusion from this

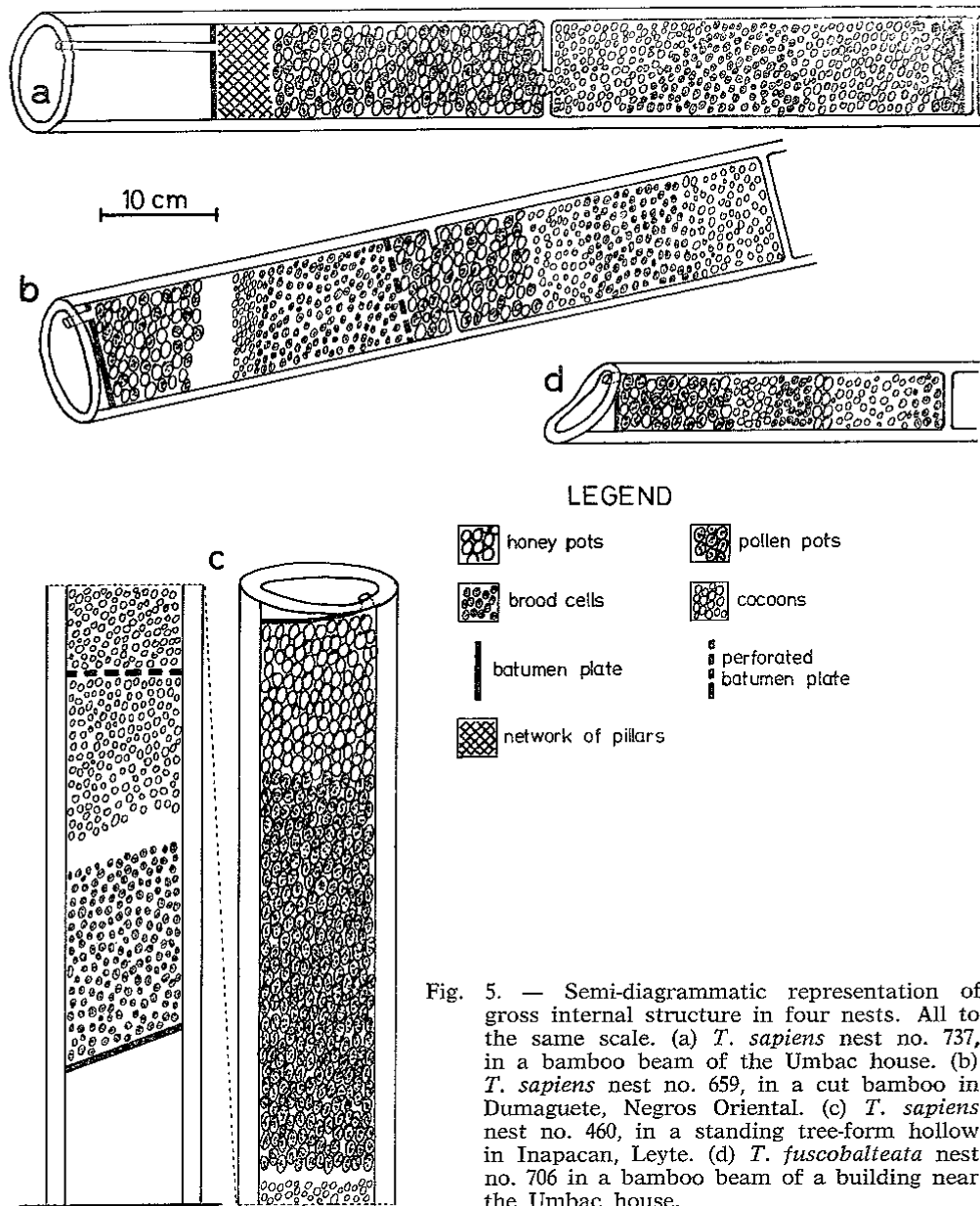


Fig. 5. — Semi-diagrammatic representation of gross internal structure in four nests. All to the same scale. (a) *T. sapiens* nest no. 737, in a bamboo beam of the Umbac house. (b) *T. sapiens* nest no. 659, in a cut bamboo in Dumaguete, Negros Oriental. (c) *T. sapiens* nest no. 460, in a standing tree-form hollow in Inapacan, Leyte. (d) *T. fuscobalteata* nest no. 706 in a bamboo beam of a building near the Umbac house.

Abb. 5. — Teilweise schematische Darstellung der inneren Struktur von vier Nesterne. (a) *T. sapiens* Nest Nr. 737, in einem Bambusbalken des Umbac-Hauses. (b) *T. sapiens* Nest Nr. 659, in einem Bambusstamm in Dumaguete, Negros Oriental. (c) *T. sapiens* Nest Nr. 460, in der Stammhöhle eines Baumfarnes in Inopacan, Leyte. (d) *T. fuscobalteata* Nest Nr. 706, in einem Bambusbalken eines Gebäudes neben dem Umbac-Haus.

is strengthened when six other comparable coconut-growing areas of the Philippines familiar to the senior author are ranked for rainfall and apparent *Trigona* abundance. All six are intermediate between Dumaguete and Borongan in both rankings, in which they are strongly negatively correlated.

The concentration of colonies in the Umbac house has no obvious connection with food sources and is most likely a simple result of long-term availability of good nesting sites. The house was built in 1938 and so has presented a great many bamboo cavities for more than 40 years. Like most Filipinos, the Umbacs are quite willing to have *Trigona* nesting in their house and do not take honey or cerumen from them. Given the short swarming distances of *Trigona* and their tendency to remain long at a nest site (INOUE *et al.*, 1984 b), the time factor is significant. We were told that the *T. sapiens* nest dissected from the Umbac house had been continuously occupied for more than 10 years, which may not be unusual for undisturbed *Tetragonula* colonies.

The slight amount of sealing needed to close the cavity is consistent with what is known from other *Tetragonula* spp., none of which builds even a moderately exposed nest.

The only previously described *T. fuscobalteata* entrance tube (SAKAGAMI *et al.*, 1983 b) was within the range described here, and tube lengths of both *T. fuscobalteata* and *T. sapiens* reported here are similar to those of other *Tetragonula* spp.

The slit-like apertures of many entrance tubes suggest a defensive tactic, a means of forcing all entering insects to walk in and of passively excluding all but small insects. It is peculiar, though, that the smaller bee species has the wider aperture. The modal head-width of *T. fuscobalteata* workers, measured in units of 0.04 mm, is 1.60 mm, against 1.88 mm for *T. sapiens* (SAKAGAMI, unpubl.), yet *T. fuscobalteata* has a significantly wider aperture (table II; $p < 0.001$, t-test).

Internal nest features reported here are mostly consistent with those known from other *Tetragonula* spp.: simple batumen plates of pure cerumen, thin lining layer, no involucrum, brood cells elongate and opening upwards, brood cells in unstructured clusters, and honey and pollen pots similar. Only two Australian species are known to depart significantly from this pattern (MICHENER, 1961).

It is usual in stingless bees for honey to lie next to the nest entrance, with brood farther away and pollen in between. The apparent rule in *Tetragonula* is also to have storage pots next to the entrance, but it is unclear whether honey and pollen pots are usually separate or interspersed. They are separate in *T. carbonaria*. When *T. minangkabau* has two storage zones, the one nearer the entrance typically has both honey and pollen, while the other has only honey (SAKAGAMI *et al.*, 1983 a). This is also the pattern in the *T. fuscobalteata* nest examined, but we have not seen it in *T. sapiens*.

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