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NOTES ON THE BIOLOGY AND WAXES OF FOUR SPECIES OF
AFRICAN *TRIGONA* BEES (HYMENOPTERA : APIDAE).

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IN the Preliminary Report on *Trigona* wax (Smith, 1951) it was shown that the wax of stingless bees of the genus *Trigona* was used as an adulterant of beeswax, and was sometimes sold as beeswax. The samples of *Trigona* wax which were analysed were obtained from traders, and while it was believed that some of them were reasonably pure *Trigona* wax, there was always some element of doubt.

In order therefore to obtain samples of *Trigona* wax of known purity, a search was made throughout Central and part of Eastern Provinces for the nests of *Trigona*. Twenty-eight nests of the larger *Trigona* species were collected and examined, as well as numerous nests of the minute *Trigona* of the sub-genus *Hypotrigona*. As the quantities of wax present in *T. (Hypotrigona)* nests are insignificant, this sub-genus is not dealt with in this paper.

Of the larger *Trigona*, four separate species were found, and the adult insects and their nests are described herein. The wax obtained from these nests was sent to the Government Chemist in Dar-es-Salaam for analysis. Some samples were also supplied to Dr. Raymond, of the Colonial Products Advisory Bureau, and to Professor Tenniswood of the Department of Chemistry, Makerere College, for more detailed examination. Samples were also supplied to overseas firms, in order that they could determine whether there was an industrial use for *Trigona* wax.

In the descriptions of the species, particular attention has been paid to the nest, in particular to the formation of the brood nest. This is of the utmost importance when considering sub-generic divisions. Further, examination of adults found in nests has thrown much light on the question of varieties and sub-species. In the past, specimens caught on the wing having different coloration have been allocated to different varieties and sub-species, and in some cases to different species. Examination of nest material has shown that one queen can produce a wide range of colour variation in her progeny. 7

In nest material it is found that the newly emerged bees are pale. What will eventually be black areas are pale brown. Queens are usually in an intermediate stage. Further, these young bees will be found to have swollen abdomens which are believed to be due to the development at this stage of the wax glands. The older foraging bees, which normally find their way into the collector's net, are usually fully coloured and their abdomens shrunken. 9

Meloboris *Trigona denoiti* Vachal. - - -
Trigona "A."

<i>Locality.</i>	<i>Local Name.</i>
Kifiumi . . .	Sache, Baarusehre.
Kiirangi . . .	Ituvia.
Sandawe . . .	Torongome.
Kinyamwezi . . .	Ugaga.
Kigogo . . .	Pula.
Kichagga . . .	Nzii.

Distribution.

This is a common species, widespread throughout Eastern and Central Africa. It is reported from the Belgian Congo, Bechuanaland, and northern Transvaal, in addition to all parts of Tanganyika.

The nests were collected at Bonga in Mbulu District, Bereku, Chandama, Changalo, Mrijo and Kwa Mtoro in Kondoa District. Specimens of workers have been found in *Trigona* wax samples from Manyoni, Singida, Dodoma and Handeni.

Nests.

Near Bonga and Bereku the nests were in termite mounds on hill slopes. Soil, red to brown loam. Elsewhere in various soils, usually, but not necessarily, in termite nests. Entrances may be merely a hole approximately one centimetre in diameter, or a vertical waxy pipe, or a horizontal pipe along the surface of the ground made of wax, resin and earth particles. Up to eight nests have been observed in one termite mound and natives report that they have found up to twelve.

The termites appear to treat the *Trigona* as indifferently tolerated guests or synoekets. When the nests have been disturbed both the termites and the bees rapidly build protective walls of earth round their respective nests. If a bee should fall among the termites it is immediately attacked. The termites do not seem to attack the exposed *Trigona* nest, though stray termites may wander in, only to become entangled in sticky wax.

The nests are frequently located three-quarters to one and a half metres from the surface in close proximity to the brood and fungus galleries of the termites. It is possible that such a situation is chosen to ensure that a constant temperature is maintained in the bees' nest. The nest is connected at the top to the surface by means of a vertical or sloping pipe, average diameter one centimetre. From the bottom of the nest another pipe descends half a metre or more and finishes in a dead end. This pipe appears to act as a drain for any water that might enter or be produced by condensation inside the nest. The nest space and the entrance and drainpipes are lined with a hard black resinous material approximately 1 mm. thick. As a rule, the older the nest the thicker the lining.

The nest is an elongated pear shape, varying in size but normally about 15 by 20 cm. The narrower end is either at the top or to one side, and contains most of the honey and pollen pots. The more bulbous end contains the brood nest. The brood nests encountered contained up to fourteen combs surrounded by a labyrinthine involucre of thin leaves of brown wax. The under side

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of the involucreum above the drainpipe area has a slightly mildewed appearance. The nest may be as much as two and a half metres below ground.

The honey and pollen pots are composed of thin brown wax and are either closely appressed or separated by pillars of wax. They are all of one approximate size, being oval, 1.5 cm. high and 1.0 cm. in diameter, when complete. The pots are irregularly arranged, pollen and honey being located at random. Among the food pots were observed two or three pots containing debris, probably discarded larval skins. Numerous white mites were seen among the debris.

Large elongated plugs of sticky wax are located just inside the nest close to the entrance and drain pipes. The largest is by the entrance pipe. It is thought that this sticky wax is used either for plugging the entrance in an emergency, or for plastering on to invaders, thus glueing them to death. Sticky wax plugs were found in position in the drainpipes in some nests.

The brood nest is composed of ten to fourteen combs separated by pillars of wax. The combs are round and frequently of spiral formation. The smallest and newest combs are at the top. Usually there is a central vertical hole, containing queen cells if these are present. Pillars in this axial region are dichotomous. Queen cells are also found at the outer edges of the brood combs. Brood cells containing eggs and young larvae are composed of brown wax. Cells containing older larvae and pupae have the wax removed from the ends, which are at that stage composed of larval skins. Most of the cells containing young brood are sealed, but occasional cells containing small larvae are left open. It is suspected that these are drone larvae. Brood development in each comb is rotational. As mature bees emerge, the cells from which they come, composed of larval skins, are removed. A gap is thus left in the ring of the brood comb. At the other side of the gap new cells of wax are built and provisioned. Continuing in an anti-clockwise direction round the comb, brood in increasingly advanced stages of development is encountered until return to the point where the bees are emerging. Brood development is not at the same stage in the other combs at points vertically above and below. The lower combs are always a little more advanced than the upper combs, so the gap between emerging brood and new brood cells proceeds in an anti-clockwise direction as it ascends. It is on this spiral stairway of new cells that the queen performs her task of egg laying. The largest brood combs are about 100 mm. in diameter. The vertical axial hole is 10 to 12 mm. in diameter, unless queen cells are present, when it may be up to 20 mm. Each comb is 5 mm. thick, this being the depth of the brood cells. In a straight run of 50 mm. on the surface of the comb there are 17 to 17.75 worker or drone cells. Queen cells are between 8.5 and 10.0 mm. long.

In one nest at Chandama there was no brood at all present though an involucreum had been constructed. The drones were engaged in massed flights. The presence of a virgin was suspected but not confirmed. There was no sign of a fully developed queen.

Diagnostic Characters.

Nest subterranean, generally in termite nest. Brood nest having spiral stair-case development. Workers with variable yellow facial maculations, thorax black, abdomen variable in coloration. Mandibles with two teeth; teeth not prominent and are separated

by a wide shallow cleft. Hind tibia with simple hairs; sub-triangular in shape; apical corners acute.

***Trigona togoensis* Stadelmann.**

Trigona erythra var. *togoensis* Stadelmann.

Trigona "B."

<i>Locality.</i>	<i>Local Name.</i>
Kigogo . . .	Mrego.
Kirangi . . .	Mbuju.
Kinyamwezi . . .	Upula.
Sandawe . . .	Isna.
Kichagga . . .	Rungu.

Distribution.

In addition to East Africa this species is reported from Kabinda in the Belgian Congo. The writer has encountered nests in Kondoia and Manyoni Districts of Central Province of Tanganyika. Specimens were caught on Mango blossom at Illonga, Killosa District, Eastern Province, and the species is well known in the woodlands of Western Province. Workers have also been found in *Trigona* wax samples from Dodoma, Singida, Kondoia, Handeni and Tabora Districts.

Nests.

Normally found in the hollow trunks and branches of large trees. Morstatt (1921) reports that the Wachagga on Kilimanjaro sometimes find them in their beehives. The entrances are not normally conspicuous, but the hole may be surrounded by resinous matter.

The entrance is connected to the nest by a resinous tube to the nest cavity. The nest is very variable in size and shape, according to the space available in the tree. Generally the food cells surround the nest and the pollen and honey pots are arranged at random. The food pots vary in size between 1.5 and 2.0 cm. in diameter and between 2.0 and 2.5 cm. in height. In these nests were found one or two heavy irregular lumps of cream coloured material, whose composition has not yet been determined.

The brood nest is surrounded by a waxen leafy involucre and contains up to fifteen horizontal combs, each of a single layer of brood cells. The largest comb measured was 10 cm. in diameter. The comb spacing, centre to centre, is approximately 9.0 mm. The thickness of the combs, which is the same as the depth of the worker cells, is between 5.7 and 5.8 mm. In a straight run of 50 mm., there are an average of 14 brood cells. The queen cells, which are located either at the edge of the brood comb or in the involucre, are 9.0 to 9.2 mm. long.

The brood development differs from *T. denotii* in that there is no spiral formation of the brood comb, and that egg laying commences in the centre of each comb. The largest and most developed combs are at the bottom, and each one above is successively smaller, the eggs and youngest larvae always being round the outside of each comb. The development of the brood nest therefore proceeds upwards in a conical form. The new cells are added to the top and sides of the cone. This continues until the fully developed brood commences

to emerge from the centre of the lowermost comb. When a space is formed by the removal of the old larval skin cells, the queen returns to the bottom of the nest and commences a new cone of brood combs in the space. A gap is left between the rings of emerging brood and the cone of young brood. This space often has, in addition to the usual waxen pillars, a partial involucrem screening the old brood from the new.

That this species is well able to defend itself in spite of lack of an effective sting was demonstrated by a colony that had been transferred from a tree and put in a box in the writer's garden. Honey bees, *Apis mellifica*, attempted to rob the stingless bees' nest. However, they did not succeed, as the *Trigona* set upon the honey bees, seizing the leading edges of the bees' front wings with their mandibles. The bees were unable either to sting or bite the *Trigona*, which hung on like bull dogs until the honey bees retreated.

Diagnostic Characters

Nest arboreal. Brood nest having horizontal combs with conical development. Head and thorax of worker black and pitted. Mandibles with two prominent teeth, separated by a deep cleft. Hind tibia broad, with simple hairs and a spoon-shaped excavation. Posterior apical corner rounded.

→ ~~*mellifica*~~

***Trigona beccarii* Gribodo.**

<i>Locality.</i>	<i>Local Name.</i>
Kiirangi . . .	Itula ngombe.
Sandawe . . .	Terengombe, Nachto.
Kikonyonga . . .	Kwimba.
Kikimbu . . .	Ipilia.
Kisumbwa . . .	Kililu.

Distribution.

A common species widespread throughout East and Central Africa. The type of this species was collected by Beccari at Keren. Other specimens have been collected in Martini's Concession, Eritrea. Varieties are reported from the Belgian Congo, Nyasaland, and Benguella. The writer has collected workers in Kondoia, Iringa and Songea Districts of Tanganyika, in addition to nests at Lalta, Kondoia District. Although the above species and varieties would appear to be races of *T. beccarii*, examination of nest material is required to establish true relationship.

Nests.

Found in the ground down to one metre. Some are so close under the surface that cattle put their feet into them, sometimes breaking their legs. The honey badger, *Mellivora sagulata* Hollister, is said to dig up the nests for the honey and brood.

A black tunnel leads down from a simple entrance hole to the top of the nest cavity. The storage pots surround the brood nest, but are mostly on top. The storage pots are between 2 and 2.5 cm. in diameter and 3 cm. high. The involucrem contains horizontal brood combs showing the same conical form of development as with *T. togoensis*. The largest brood combs encountered

were 9 cm. in diameter. The thickness of the combs is 7 mm. Queen cells 9.5 to 10 mm. long. In a straight run across the surface of the brood comb of 50 mm. there are 12.5 brood cells. Inside the involucre, at the bottom of the brood nest, was found the nest rubbish, larval skins and other bits and pieces. Rubbish pots, as found in nests of *T. denoiti* were not seen. Queen cells were found hanging from combs suspended by wax attachment.

Diagnostic Characters.

Nest subterranean. Brood nest having horizontal combs with conical development. Yellow maculations on face and lateral margins of mesonotum and on scutellum. Yellow marks and bands on abdomen interrupted dorsally. Reddish hairs on head and thorax. Wings with reddish tinge. Mandibles with two teeth which do not protrude beyond the line of the straight cutting edge. Excavation in hind tibia flat and extending over the apical three quarters.

Trigona staudingeri Gribodo.

<i>Locality.</i>	<i>Local Name.</i>
Kilosa . . .	Pumi.
Kiirangi . . .	Mbosho.
Kichagga . . .	Inyeri.

Distribution.

Highly local in its occurrence in East and Central Africa. In the places where it does occur it appears to be abundant. Outside Tanganyika it has been reported from Kabinda in the Belgian Congo. The writer has collected nests at Ilonga, near Kilosa, Eastern Province, and has seen a nest near Korogwe. Nests of this species had been reported by natives near Morogoro, at Arushachini, south-east from Kilimanjaro, and on the Makonde Plateau, Southern Province.

Nests.

The nests of this species are found externally on the undersides of the branches of trees. The nest itself is externally coated with plates of cerumen. Within the outer skin is a labyrinthine wall of cerumen, 3 to 5 cm. thick. The entrance area is towards the bottom of the nest. The entrance merely consists of a thickening of the labyrinthine wall and absence of outer plates. The brood nest, which is surrounded by a thin involucre of brown wax, is located in the upper part of the nest. The honey, pollen and gum pots are at the sides and below the brood nest. The pots are fairly small, often no more than 1 cm. high.

The form of the brood nest shows the highest degree of development in the genus *Trigona*, assuming that *Apis* has reached the highest state of all bees. The brood combs hang vertically, are built from the top downwards and are double sided. This form is unique among the Meliponidae. The New World species, and as far as is known, all the other Old World species, build either single layer horizontal combs or merely irregular clusters of brood cells. The combs do not hang parallel to each other but in irregular folds. The brood nest does not develop in the form of a rough sphere extending outwards in concentric layers as in *Apis*. Instead, the queen starts laying at the top in the newly built cells, and at the same horizontal level in each comb. The bottoms of the combs are

therefore level and contain the newly laid eggs. The upper parts of the combs contain more advanced brood, all at the same stage of development at each horizontal section. As the fully developed bees emerge from the uppermost cells of each comb, the cocoons of larval skins are removed and replaced by an open structure of branching wax pillars. Above this pillar structure new brood cells are built and provisioned. The horizontal space containing the wax pillars is thus constantly moving downwards as mature bees below it emerge and new cells above it are being built. When the brood at the top of the brood nest starts emerging, the queen returns to the top of the brood nest and begins again. The double sided combs are approximately 1 cm. thick. In a straight run of 5 cm. on the surface of the comb there are 14.5 worker cells. Queen cells are found in any part of the brood nest and are 7 to 8 mm. long and about 5.5 mm. in diameter.

In addition to the thick labyrinthine wall of cerumen surrounding the whole nest, there are a number of wax pots containing a brown sticky waxy substance. When disturbed, the bees arm themselves with pellets of this sticky substance on their hind tibia and fly to the attack in large numbers. The foe is well bitten by their tiny but sharp mandibles, and smeared with sticky ammunition. Even human beings find this treatment highly demoralising as not only is the skin covered with sticky biting bees, but also ears, nose and eyes are fully investigated. The sticky wax is also placed on the surface of any damaged portion of the nest, thus presenting an effective barrier against ant attack.

Diagnostic Characters.

Nest extra arboreal. Brood combs vertical, double sided, horizontal downward development. Bees black, thin, elongated. Legs very thin except for wide rounded hind tibia. Plumose hairs on legs.

TRIGONA WAX.

As the laboratories of the Beekeeping Research Station are not yet completed, most of the nests were sent to the Government Chemist, Dar es Salaam for analysis. Nest material was also supplied to the Colonial Products Advisory Bureau (Plant and Animal), in London, and to Professor Tenniswood of the Makerere College. The results of the analysis are summarised below.

The wax of sixteen nests of *Trigona denoiti* was analysed, and found to fall within the following ranges :

	(1)	(2)
Saponification value	8.3-39.5	
Acid value	5.6-8.5	7.5
Ester value	2.7-30.5	36.9
Iodine value	47.5-54.8(a)	73.8%(b)
Specific gravity	0.952-0.975	.
Setting-point	62.5-66.5	.
Melting-point	66.4
Refractive index 80° C. n_D	1.4687
Weinwurm test	Positive	.
Sterol group test	„	.

Column (1) shows the range within which the 13 nests analysed by the Government Chemist fall. Column (2) shows the results obtained by the Colonial Products Advisory Bureau from a cake of wax obtained from these nests.

(a) Hanus $\frac{1}{2}$ hour. (b) Wijs 3 hours.

The wax of two nests of *Trigona togoensis* gave the following results :

Saponification value	31.0-53.5
Acid value	2.8-8.5
Ester value	28.2-45.0
Iodine value	48.2-50.6(a)
Specific gravity	0.958-0.970
Setting-point	57.7-65.0
Weinwurm test	Positive
Sterol group test	"

Two nests of *Trigona beccarii* were as follows :

Saponification value	44.4-46.8
Acid value	6.15-9.9
Ester value	34.2-40.65
Iodine value	54.6-55.6(a) 98.3%(b)
Specific gravity	0.962-0.965
Setting-point	61.0-64.0
Melting-point	64.6°
Refractive index at 80° C. N_D	1.4625
Weinwurm test	Positive
Sterol group test	"

(a) Hanus $\frac{1}{2}$ hour. (b) Wijs 3 hours.

Analysis of one nest of *T. staudingeri* produced the following results :

Saponification value	49.9
Acid value	12.9
Iodine value	55.8(a)
Specific gravity	0.972
Setting-point	61.3°
Weinwurm test	Positive

The Sterol group test used is that of Liebermann-Burchard. *Trigona* wax gives a red to reddish brown colour, while beeswax gives a greenish colour.

There were insufficient results to show any significant difference between the waxes produced by the different species of *Trigona*.

The range of values into which pure *Trigona* wax would appear to fall is as follows :

Saponification value	8.3-53.5	Average.
Acid value	2.8-12.9	7.0
Ester value	2.7-45.0	27.1
Iodine value	47.5-60.9(a)	50.1
Specific gravity 15.5/15.5° C.	0.952-0.975	0.963
Setting point	57.7-66.5	63.8
Ratio No.	0.5-10.0	4.4
Refractive index 80° C. (2 samples) N_D	1.4625-1.4687	.
Weinwurm test	Positive	.
Sterol group test	"	.

(a) Hanus $\frac{1}{2}$ hour.

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