THE SCUTELLUM NEST STRUCTURE OF TRIGONA (*TRIGONA*) *SPINIPES* FAB. (HYMENOPTERA: APIDAE)

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ABSTRACT

T. (*T.*) *spinipes* (= *ruficrus*) is a neotropical stingless bee living in Brasil, Paraguay and part of Argentina (Misiones). It builds an external nest, upon branches of trees.

Inside the nest there is a huge and massive structure, basin or shield-like in shape, the scutellum. It is made chiefly of prepupal dejections and adult bee excrements. It also contains dead bees, cerumen, propolis, Acarina, remains of brood cocoons, etc.

Besides other lesser roles, it is here suggested that the scutellum serves chiefly as a strong supporting wall for the nest's internal constructions. The author thinks that the presence of a strong wall of some sort—preexistent or bee made—is characteristic of all Meliponinae nests.

INTRODUCTION AND LITERATURE

Trigona (*Trigona*) *spinipes* Fab, commonly known as Irapuá or Arapuá, is a stingless bee found in large areas of Brazil, where it ranges from the State of Ceará to the State of Rio Grande do Sul. It exists also in Paraguay and Misiones Province, Argentina. On its geographical distribution see Schwarz (1948: 271).

Most authors, including Schwarz, called it *T. ruficrus* Latriella. However, Moure (1960: 155) examined a Fabricius type in the Zoologiske Museum, Copenhagen, and arrived at the conclusion that *spinipes* is the correct name.

This bee builds external nests, on branches of trees, first described by Seabra (1799: 104). It is also well known because of its habit of cutting flowers, leaves, bark, etc, for building material or for easier access to nectaries of some flowers. For a discussion of its destructive and nesting habits, see Schwarz (1948: 267–270).

As Seabra (1799: 101), F. Muller (apud H. Muller 1875: 43), Peckolt (1894: 223–225), H. von Ihering (1903 (1930: 77–78)), and other authors state, this is a vicious bee, biting an intruder fiercely and in great numbers. A single bee is sufficient to annoy. Even when the observer wears a protective net over his face, an attack of hundreds of these bees is almost unbearable.

Inside the nests of this species there is a huge and massive structure, first described by H. von Ihering in 1903 (1930: 66–70, 81), who gave it the name of scutellum.

Silvestri (1904: 136), Mariano Filho (1910: 18–21; 1911: 127–128), Bertoni (1912: 142), and Ducke (apud Schwarz 1948: 268) also wrote briefly about this structure. Schwarz (1948: 25, 268, pl. 6) summarized the knowledge existing concerning the scutellum.

R. von Ihering (1940: 403) said that in Northeastern Brazil, in the São Francisco valley, this "compact part of the nest" is used in fishing. It is triturated, cooked and placed inside baskets, that are put in the water. It is extremely toxic to fish. Sawaya and Aguiar (1960: 93–94) wrote that the material they examined had a high content of acetylcholine, which they believed to be one of the fish killing substances present.

The study of the origin of the scutellum may reveal a better understanding of its properties as a fish poison.

Among other species of bees the scutellum is not definitely known altho the same structure may exist in the nests *T.* (*T.*) *corvina* and, in a different form, in the nests of *T.* (*T.*) *amalthea*. On *amalthea* there are short nest descriptions made by Bertoni (1912: 142), Salt (1929: 438), Myers (1935: 132), and Weyrauch (1942: 63–64). Michener (1946: 193–194) wrote more extensively on a nest of *corvina*.

Materials and Methods

Nests A and E were from São Paulo city, State of S. Paulo, Brasil. The other nests were found in Cosmópolis, in the same State.

In order to observe the nests of this fierce bee, a variety of head masks, made of nylon and plastic were used. A lightly tied piece of wire over my coat sleeves was also used in order to stop the bees from crawling under my clothes. However, *spinipes* is not a large bee, and always gets inside the clothing and torments the observer. It was easy to examine nests on cold mornings, but frequently they had to be observed during warmer periods, when the bees were active.

Pieces of scutellum, and soil samples, were examined in the laboratory using a Zeiss stereoscopic microscope, with magnifications of 6 ×, 10 ×, 16 ×, 25 × and 40 ×.

OBSERVATIONS

NEST A In 1961, I had the opportunity of examining a nest of *spinipes* collected in the woods of Cidade Jardim, in the city of S. Paulo. The nest was pear-shaped, and on a trunk or branch of only 6 cm of diameter (measured just under the nest). During a storm, the nest fell to the ground and broke and gave me the chance to examine its interior.

At the base of the nest I found a large, thick and compact structure, shield or basin. This scutellum was 12–13 cm thick, and 35–40 cm across, in one direction. In the opposite direction it was broken, at the time I took the measurements. Unfortunately, when the nest fell, the position of the scutellum in relation to the tree branches and to the other structure of the nest was not recorded. The inside of the broken nest had been exposed to rain, during the storm.

I could see that the shield-like structure was made of several layers, that in some places were breaking apart, probably because of their exposure to rain. Aware of the observations made by Salt in *amalthea* (a related species), a close inspection of these layers revealed sheets of exoinvolucrum between the layers. The involucrum is a structure composed of many irregularly spaced membranes that involves the brood combs and sometimes the honey and pollen pots. I apply the term exoinvolucrum to the harder or more brittle and exterior part. By probing carefully on the more compact part of the shield, sheets were observed that probably belonged to the exoinvolucrum. Between them was a yellowish or brownish material.

What seemed to be the more recent part of this material, faced the brood region of the nest. It was yellowish and friable. Many legs and other parts of dead bees could be detected in it. As I went through the compact mass, it became difficult to dig and uncover the primitive involucrum sheets.

The structure of this nest's scutellum was not studied in detail since long exposure to rain probably altered its characteristics.

NEST B On July 21, 1962, a nest was collected from a tree located in a ravine, in Saltinho, Usina Ester, Cosmópolis, State of S. Paulo. It was built on a fork, at approximately 6 meters above ground. When the tree was felled the nest was partially broken but the scutellum suffered little.

The nest measured approximately 48 cm (diameter) × 60 cm (high). The scutellum had a general U form and was built along both sides of two branches. The scutellum, from its lower part, to both higher parts of the U, measured 39 and 45 cm. The inside floor of the U had a width of 21 cm. The base of the scutellum was a little below the tree fork. Within 20 cm of this base, it gradually increased in bulk, until it reached the "valley" floor (the lower inside part of the U). This 20 cm comprised the bulkier part of the scutellum. The whole scutellum weighed 11.90 kg.

Both arms of its U shape were at the sides of the nest. What seemed to be a dead liana, went thru one of these arms. There were three or four membranes of the brittle exoinvolucum covering the outer part of the scutellum. Near its inside surface, were storage pots and brood combs.

After rasping the surface of the scutellum that was in contact with the tree branches, three samples of material were taken and examined (#1—near the valley-floor region; #3—near the base; and #2—midway between both places).

Sample 1 appeared granular, yellow-orange in color, with many Acarina, parts of dead bees and remains of bee cocoons. There were also dark masses which broke up and showed a granular structure when prodded with a needle. These dark masses were much softer than in the other two samples. I found, too, large cocoons and bacillus-shape black excrements. These cocoons and excrements belonged to an inquiline that lived in the scutellum.

Sample 2 was generally granular, dark brown in color. There were fewer Acarina than sample 1, but included remains of dead bees, small sheets of bee cocoons and 2 or 3% of small crystals, hyaline or yellowish. These crystals fractured easily, upon slight pressure of a needle tip. There were also other hyaline grains, somewhat different in appearance and very hard. These were sand grains. Altho far less numerous than other crystals, they were not uncommon. Vegetal fibers were plentiful. Some sand grains were in actual contact with such fibers. Some areas were covered with a white material. Dark masses were present. When rasped with a needle, they formed whitish ''ribbons'' with many granules.

Sample 3 also was granular in structure, with many brownish-red granules. Its appearance was clearer than that of sample 2. Some stratified, thin deposits of clear yellow granules alternated with a dark substance. When proded with the tip of a needle, this dark substance broke up, showing a somewhat granular structure. A few hyaline crystals were present which were easily fractured. Remains of bee cocoons and dead bees were found. A quantity of what seemed to be white mycelia were seen. No Acarina were present in this sample.

One of the arms of the U-shaped scutellum was examined inside. Much loose granular material, of a brownish color, was found. In many places there were deposits of clear yellow granules. White and cream colored ones were also common. The granules, size was about the same as the brown ones. A gradient in color could be seen, between the yellow and white grains. Sometimes this occurred also in the same deposits. In other places, there was a similar transition between clear yellow and orange-rose grains, or between clear yellow and bordeaux color grains, passing thru pink tinges. Live Acarina and remains of dead ones were seen. Many dark and nearly always flat masses were found.

In some places there were many white filaments, apparently fungi mycelia. In other places, chiefly where the scutellum had contact with the tree branches' small puffs of varying size were found. They were light yellow, with a somewhat cotton-like consistency. In some places they were larger and of irregular form. The nature of this substance was not determined.

Some of the primitive outer exoinvolucrum membranes of the nest, could be recognized among the varied materials found inside the scutellum. These membranes had a core of small pieces of vegetal matter. By this characteristic they were found and traced in the scutellum. The interior of the scutellum had a stratified appearance, altho the strata varied and were not always present.

In several places it was possible to see some insect larvae, in silk-lined tunnels. Inside these tunnels, were dark excrements of bacillus-like shape. The larvae are now being reared, for identification.

The surface of the scutellum varied. The outer part of it was of a darker color and in places it had a thin coat of propolis. The inside surface, i.e., the surface near the brood combs, was lighter in appearance and mostly covered by a thin cerumen. Near the tips of the U, the inside surface was lighter in color which in several places was covered by white granular material, over a dark substance. Scattered over this white layer were the remains of the cerumen coat. It seemed that the bees had removed much of the superficial cerumen, leaving the white granular material exposed. The surface, in such places, was pitted, showing the marks of the bee mandibles that removed much of the cerumen. There were many small grains ranging from white below, to yellow-orange above, but it seemed that in this case the orange color was due to the cerumen of the upper strata.

Outside and inside surfaces had spots of clear yellow granular material. Over both surfaces, some of these spots were elongated and sometimes became progressively brownish over their extension. These spots certainly were the dejections of moving bees. [Five or six hard hyaline grains, possibly sand, were found.]

It must be stressed that on the inner and outer surfaces of the scutellum, as well as inside it, numerous dark, flat, relatively small masses could be seen. Removing them with a needle's tip, the remains of cocoon walls could be found. These flat masses made up nearly all of the scutellum's outer surface and a greater part, if not most of its inner surface. When prodded, they produced numerous orange or cream colored and brown small grains.

In order to study the nature of the excrements of this bee three young bees were caught. A slight pressure on their abdomen resulted in voiding their feces. Upon drying, the clear yellow granular material found on the scutellum was found to be the bee's excrements.

NEST C This nest was at a height of 4–5 m, upon a tree fork having three branches from the banks of the Pirapitingui river (Saltinha, Usina Ester, Cosmópolis, S. Paulo State). Under the fork supporting the nest, the tree trunk had a diameter of 12 cm. I was told that the nest was a relatively new one, about 6 months old.

The nest was 54 cm high and had a diameter of 35 cm.

The whole nest, including the scutellum, was enveloped by several sheets made chiefly of vegetal matter (exoinvolucra). Between each sheet was a large empty space. On the scutellum's inner side, one or two of these membranes were visible in some places.

The scutellum was a continuous structure, but two regions could be recognized. One, below and in front of the nest, had a valley or U shape. The other, at the back of the nest, showed a shield-like form. Two lianas or small branches passed thru the scutellum near the floor of the "valley."

The front and under region of the scutellum had a U or valley shape. Each arm of the U was along one of the two more extreme branches of the fork. From its narrow base, below the tree fork, the scutellum went upward, in 10 cm, increasing progressively in thickness until the "valley" floor which was 9 cm. wide. From the valley floor upward, both arms of the U became increasingly slender. From the tips of the U, to the scutellum's base measured 18 and 19 cm Between both tips, the distance was 21 cm. This part of the scutellum weighed 450 g.

The "valley" portion of the scutellum was connected to the shield-like upward region, which started at the back of the "valley" or U. One of the arms of the U was built around the outer side of one of the tree fork branches. After flanking this branch, it, too, contacted the shield.

The shield region was made between and along both extreme branches of the 3 branch fork. The middle branch nearly divided this part of the scutellum in two, and was to a large extent encased by it.

On the tip of one of the arms of the U. near the place where it contacted the scutellum's shield region, were 3 long plates. The central one was about as thick as the membrane of the exoinvolucrum, but the others were much thicker, up to 16 mm approximately. Breaking one of these thicker plates showed the primitive membrane of vegetal matter in the center of the plate. Covering it, in both sides, were deposits of hard material. Over the surface of one of the plates was a white finely granular material. Under it was a dark layer. When prodded with a needle, this dark material gave up a white granular substance. It is possible that primitively there was another layer over the white grains, but this was not as evident as in Nest B.

Inside, the broken arm of the U region the primitive exoinvolucrum membranes made chiefly of vegetal matter were recognizable. Other membranes of the exoinvolucrum, near but outside the scutellum, appeared to be in process of thickening.

On the internal surface (that nearer the brood combs), was a large quantity of the clear yellow granular substance, as well as many flat, small, dark deposits, commonly contiguous. In some places the clear material predominated, but in others the dark deposits were dominant. Under them, some remains of the combs' cocoons could be found. Over this side of the escutellum surface, was a thin and irregular coat of cerumen and propolis. In some places the deposits of both substances were thicker, but still thin. A much larger and thicker deposit of transparent propolis covered an area of approximately 1 × 1 cm. The twin marks of both bee mandibles could be seen everywhere on the surface, showing that some material was rasped and taken elsewhere. Some of the superficial cerumen apparently was removed. Parts of dead bees were common on this inner side of the scutellum.

The surface of the outer side of the scutellum's lower part was far darker than that of the upper and inner sides. This surface was coated with propolis, mostly thin, but of varying thickness. Under it, there was far less yellow granular material than that found on the upper and inner surfaces of this U part of the scutellum. The flat, small, dark deposits, generally contiguous, were even more common than on the scutellum's inner side, comprising most of this outer surface, and contributing greatly to its darker appearance. Under them, remains of brood cocoons were found. At the back of the scutellum's shield-like region, the surface was coated with a brighter, more transparent propolis than that found in the U region. Under it the masses of yellow small grains were clearly visible. Some lumps of shiny green propolis (or perhaps propolis embedded with a green material) were found in some places, on the outer surface (seldom on the internal surface). Rarely were there parts of dead bees on the outer surface, contrary to what was found in the inner one. Dispersed over the outer surface of the scutellum, a few brownish granules were seen even though there were no deposits of them. Possibly their presence was accidental, scattered during the manipulations of the escutellum.

Inside one of the scutellum's arms, and inside the shield region, 50% of the content was, in many places, made of the clear-yellow granular material. There were also whitish and brownish-red small grains, and hues (including cream) intermediate between these colors as well as between them and clear-yellow. Often, in the same deposits these color transitions could be observed. The brownish-red granules were in part loose. Some of them were being carried over the bodies of the many Acarina present. Many small, dark deposits, generally forming strata, were found. Among them some remains of brood cocoon walls were seen. White filaments (mycelia?) were present in some places. There was a cavity lined with silky threads. In a sample from inside the shield-like portion of the scutellum, one sand grain was found, as well as a small black hard grain, not identified. Remains of dead Acarina were plentiful. Dead bees were also found. This inside part of the scutellum had a general stratified appearance (although an irregular one) due to the succession of dark deposits and clearer granular material.

The small, dark, flatish deposits found everywhere, when prodded with a needle, broke up showing numerous small grains, orange to brown, or cream colored.

NEST D This nest was on a tree near the Jaguari river (Ilha, Usina Ester, Cosmópolis, State of S.Paulo). It was 50 cm high. In a lateral view, it had a maximum width of 42 cm. Seen in front of the entrance, its width measured 29 cm.

The scutellum extended almost from the base to the top of the nest, on its rear side. The scutellum was not entirely removed, and so its shape could not be studied in detail. However, it was easy to see that it was shield like. It's upper part was taken away, for a closer examination. It had to be chopped out. This was not easy because of its hardness. Most of the scutellum was left intact to avoid endangering the nest.

The scutellum was covered on its outer side by an exoinvolucrum of 4–6 membranes (in all nests there is always a space between the scutellum and the membrane next to it). On the inner side of the scutellum, the brood combs confined it. There were also a few sheets of the exoinvolucrum near this inner side of the scutellum.

Directly connected with it or near the uppermost part of the scutellum, were several thick and hard plates. When cut, they showed the core of vegetal matter characteristic of the exoinvolucrum, with propolis outside it. They had only a little granular material. Over the surface of the scutellum's upper part, as well as over the surface of some membranes near it, there were many places with a layer of a white, granular material. This white layer was not continuous, but rather spotty. There were remnants of cerumen and of a granular material impregnated with cerumen, in a higher position in relation to the white layer. In a few cases, propolis was present, instead of cerumen. It seems, by the twin marks of mandibles, that the bees removed in such places much of the original cerumen, uncovering the white layer.

The inner surface of the scutellum had also plenty of soft cerumen, partly lining it or present in small lumps. Under this coat, in some places, there was plenty of dark, apparently flat deposits. Propolis was far less common. Relatively few spots of clear yellow granular material were seen.

The outer surface of the scutellum was well covered with cerumen and little propolis. A few brownish-red small grains adhered. Several big cracks were lined with cerumen. In general this outer surface was dark and composed of many small, dark, flat, continguous deposits, under the cerumen coat.

Some primitive membranes of the exoinvolucrum on the inside part of the scutellum were recognizable by the vegetal fibrous matter that makes their core.

Most of the bulk of the scutellum consisted of a brownish-red granular material. Clear-yellow granules were far less numerous than in colonies B and C. However, in some places they comprised about 50% of the materials present. White and cream colored granules were seen, too. Sometimes, in the same deposits, colored granules ranging from clear yellow to white, clear yellow to brown, and white to brown occurred. Small hyaline crystals easily fragmented upon slight pressure of a needle tip. Many layers of dark, nearly always flat deposits, alternating with other materials gave a stratified general appearance to a cut of the scutellum. Together with these layers were found remains of the walls of the brood cocoons. When prodded with a needle, the dark deposits broke up into brown or cream colored granules.

Several tunnels or cavities lined with silk were found. Among them were dark excrements, with a bacillus-like shape (far more numerous than in colony B) obviously associated with some immature insect living there.

Remains of dead bees and dead Acarina were observed inside the scutellum. One grain of sand was found near the inner surface of the scutellum.

NEST E Several years ago, in S. Paulo, a colony of *T. spinipes* established itself voluntarily, at the top of a *Cariniana estrellensis* (Raddi) O. Ktze. tree. The nest was at a height of 6–7 m. and reached with difficulty. Since I did not wish to remove nor to destroy the nest, observations were made with me perched near it. In such circumstances, the nest was not examined as thoroughly as would have been possible in another situation.

The nest was 50 cm high with a lateral width of 36 cm. and started at a tree fork. The upper part of the trunk went approximately through the middle of the nest. Other tree forks were inside the nest. Just under the nest, the tree trunk had a diameter of 6 cm. The largest lateral branch had only more or less 1 cm of diameter.

The scutellum began at the tree fork, surrounding the tree trunk. It had two portions. One was a half ring or belt, with a thickness of only 5 cm. encircling part of the tree trunk. This half ring merged, on both ends, with the base of the shield-like part of the scutellum. This shield, starting at the tree trunk, extended almost to the top of the nest which was inclined slightly backward. Below, it rested in part on the chief lateral branch of the tree fork at the rear of the nest, opposite to the nest's entrance.

The distance from one margin of the scutellum, to the margin of the other side was 19 cm. Its shield-like form only protected the nest's back, leaving the nest's frontal area unprotected. In this region, cutting through some membranes of the involucrum, were a cluster of honey pots.

The scutellum was completely covered by two sheets of the exoinvolucrum. On the inner side of the scutellum, exoinvolucrum membranes also occurred. The scutellum's upper region had a plate, under which there was an empty space, followed by the main part of the scutellum. This plate was merely an extension of the scutellum which on both surfaces was limited by sheets of exoinvolucrum. They could be recognized by their core of fibrous plant material, between layers, on both sides, of propolis. Unfortunately, samples from the central region of the scutellum's inner side were unobtainable. Those I could take were mostly at the scutellum's edge.

One of the samples from the lower part of the scutellum showed a relatively large region of dry, brittle, red-brown bright glass-like propolis. Elsewhere, similar propolis was found as small layers, at the surface, or as small deposits, under it. This lower region of the scutellum contained innumerable small brown and cream colored grains, and many dark masses.

Deposits of yellow granules were relatively few, but white or cream ones, mixed with the brown small grains were common. A sheet of the exoinvolucrum was recognizable inside this part of scutellum, because of its core of fibrous plant material. Remains of dead bees were common. Also found was a relatively large broken part of what was probably a quartz grain which was hard to fracture. Acarina were covered by cream and brown granules as well as small pieces of dry propolis.

Inside the tabular expansion of the scutellum, already mentioned the brown small grains predominated. However, from 5 to 10% of all granules had a yellow-orange hue. Some granules were between this color and brown. Many dark deposits were seen. They were mostly thick, but in general appeared stratified with some thin clearer strata or empty sheet-like spaces between the dark deposits. Remains of dead bees and dead Acarina were common. The dead bees were in great part inside the dark masses.

Inside another sample, also taken at the scutellum's upper edge region, the brown small grains predominated. Three sand grains were seen. There were countless Acarina and two insect larvae. Some zones had white mycelia.

At the edge of the "shield", or slightly inside the nest's upper region, the surface was covered by a predominantly white, salt-like, finely granulated material, over dark strata. This white layer was patchy and of irregular thickness. In places it still had over it some cerumen or granular material impregnated with cerumen. Often there was a color gradient between the light brown cerumen and the white layer. A color range was also seen in one place, between clear-yellow (above) and white (below).

In other samples taken at the surface's outer portion, or slightly on its inner and lower side, the surface was almost black, soft, and flat, although by no means even. It was apparently made by adding relatively small, dark and flat deposits, the limits of which were far less clear than in the surfaces of other nests In places, a few areas of propolis and some cerumen could be seen. The remains of dead bees were also found on the surface, covered by cerumen or by the dark deposits. These dark deposits were found not only at the scutellum's surface, but also made up most of its interior. In some places they showed a decidedly stratified aspect, but not in others. When prodded with a needle, the dark material broke into a mass of brown and cream colored small grains, or with a yellowish hue (more rarely). Among the dark deposits it was possible to see some remains of the bees' brood cocoons.

An elongated bee excrement, laid over the outer surface of the scutellum, was partly granular and clear yellow, and partly dark, not visibly granular. However, when this dark portion was prodded with a needle, it also broke up into clear yellow granules.

The samples taken from this nest were small, and not much stratification was seen.

SOIL SAMPLES

The scutella of nest B and C, at first seemed to consist largely of clay or earth. Examination of samples of soil was then made under the stereoscopic microscope (6×– 40×).

In the region of Cosmópolis, the soils are of glacial, permo-carboniferous (Setzer 1949: 55) or diabasic-basaltic, triassic origin. Several samples were collected near nests B and D.

Two samples of glacial soil appeared granular with a great amount of sand grains of different sizes. Some of them were not hyaline. Another sample, possibly of mixed origin, when prodded with a needle gave off a finely divided material, probably clay.

The samples of soil of diabasic origin had much less quartz grains, although they were still common. A great part of this soil was a finely divided, non-granular material, clear reddish-brown ("purple") in color. There were also some shiny black grains. In other places, the diabasic soils frequently have much more sand.

In Jardim Guedala, S.Paulo City, where nest E is located, the tertiary red soil is rich in sand grains.

For a discussion on the soils of the State of S.Paulo, see Setzer (1949).

DISCUSSION

When referring to the papers of other authors, I have placed between parenthesis, following the Latin name I have adopted, the original nomenclature used by the authors cited.

SHAPE H. von Ihering (1903 (1930: 66–70, 81) called scutellum a structure of *spinipes* (=*ruficrus*) nest . . . "with the form of a basin or shield". One of the pictures he published (see Schwarz 1948, plate 6), shows the scutellum only at the side of a nest. Another picture (1903 (1930: 66–70)) presents the same structure as one large L, which is in part under and in part at the rear of the nest. H.von Ihering also said that the scutellum is . . . "generally compact, yet it presents here and there some irregular corridors, full of dead bees".

Silvestri (1904: 136), said that the scutellum of a nest he examined in Misiones, Argentina . . . "circuncated completely the tree bifurcation on which it rested: it is a true and solid foundation". It seems to me, by the pictures he published, that this nest also extended itself to the sides of the nest (his picture 8 should be viewed upside down). If this is done, at the lower right is a space that probably was occupied by one arm of the scutellum; and at the picture's lower left there seems to be another arm, the upper part which possibly was concealed by the exoinvolucrum. From Silvestri's words, and from the pictures, I presume that this scutellum had a U shape.

Mariano Filho (1911: 127) wrote that the scutellum—at the nest base—was a "globular mass . . . sometimes extending itself a little to the sides". The "globular mass" concept is difficult to understand, in view of his additional description in which he states that the scutellum had ". . . a position in form of shield or rampart". Possibly he meant that the scutellum was in an upward position, as that in which a shield is held. At any rate, it is impossible to consider a shield as a "globular" structure.

In a previous paper (1910: 21), Mariano Filho wrote that the scutellum "was situated in the [nest's] base, extending itself upper on" . . . In that paper, he also published a picture presented by H.von Ihering, that shows the scutellum as an oblique, nearly vertical wall (Schwarz 1948, plt 6). It seems to me that Mariano Filho used the expression "globular mass" only because the scutellum's outer surface is rounded. At any rate, no truly globular scutellum was found by myself or other authors.

In all nests described in the present paper, the scutellum or its major part had a general shield-like or a U shape, or both.

In nest B, the scutellum had a definite U form. It was built along both branches of a tree fork. In fact, this scutellum was nearly divided in two U's, each half being at opposite sides of the tree fork.

In nest C, the shield-like portion of the scutellum was in an upward position, at the back of the nest, among three branches. The middle branch nearly divided it in two, in its upper region. This scutellum extended forward and downward, at the base of the nest. There it formed a U or "valley", mostly under the nest and partly encircling it. Both arms of this U were built along the two more forward branches of the tree fork. In short, this interesting scutellum had a shield-like or C shape at the back of the nest, and U or valley form in the lower frontal region of the nest.

Nest D and E had a scutellum with only a shield-like form, in an upward position.

Nests A, B, C, D, E showed that the scutellum's form can be variable. However, in all five cases, the chief structure was rounded, convex, in the nest's outer side; and rounded, concave, on the inner side.

SIZE AND WEIGHT In nests B, C, D, E, (the ones in which size was measured), regardless of shape, the scutellum extended from the base of the nest to its upper region. However, the scutellum is always shorter than the whole length of the nest, because it is enclosed by a few membranes. The presence of such outer sheets was first noted by H.von Ihering (1903 (1930: 69)).

In nests C, D, E, in side view the scutella's widths were less than the entire widths of the nests. However, when seen from the rear, these scutella occupied most of the nests' widths since in such cases it was shield-like and situated at the nests' back.

One of two nests of this species, described by H. von Ihering (1903 (1930: 66–70)), had a remarkable scutellum. As mentioned, it was somewhat L-formed, occupying not only most of the nest's rear, but nearly all of its lower half too. I cannot understand how it measured only 32 cm (height) × 10 cm (width).

The largest scutellum examined was nest B. It weighed 11.90 kg and had a maximum height of 45 cm and a width of 21 cm (measured in a direction parallel to both U arms of it). It was nearly double the weight of the one examined by Silvestri (1904: 136), which was only 6 kg.

Mariano Filho (1910: 21) said that . . . "the older the nest, the bigger the scutellum and, (singular thing!) the fewer the number of the hive's inhabitants". I cannot see why this should be. Nest B had the largest scutellum I saw, and it also seemed to be the most populated nest.

PROTECTIVE EXOINVOLUCRUM COVER The scutellum is never seen from the exterior. In its outer side, as shown by H. von Ihering (1903 (1930: 69, 81)), it is always enveloped by a few sheets of the involucrum. In the nests I examined, the outer part of the scutellum was covered with 2 to 6 membranes. Between each sheet and also between the scutellum and the sheet next to it, there is a relatively large space, where the bees may circulate. This part of the involucrum is brittle and made chiefly of a core of vegetal matter lined on both sides (except outside the nest) with at least some propolis, and at times with plenty of it. I think that it should be called exoinvolucrum, in contrast to what could be named the endoinvolucrum (the inner sheets made of cerumen).

Silvestri (1904: 137) stated that "the substance that constitutes most of the peripheric part [of the nest], in its major part seems to be dung of herbivorous [animals]".

Mariano Filho (1911: 127) wrote that the plant fibrous material used to make the "peripheric involucrum" was collected by this bee from dry cattle dung.

Michener (1946: 194), writing on the brittle peripheric membrane of *T. corvina,* said that "This arrangement must serve a useful purpose for at the attack of an enemy (e.g. the author) the outer thin coating is promptly broken and bees can swarm out from many parts of the nest to attack the intruder".

In my opinion, one of the chief roles of the exoinvolucrum is to protect the scutellum's surface, and that of the whole nest, against rain. Since propolis is a water soluble substance, the outer surface of the exoinvolucrum does not have it.

Lindauer (1957: 71) stated that *spinipes* (= *ruficrus*) and *T. (T.) hyalinata* . . . "adapt around the nest a cap of manure and mud, that resembles very well the cracked bark of a tree". In fact, *spinipes* nests viewed from the ground, seem to covered by mud. I was deceived, too, until I could closely examine the exoinvolucra.

INSIDE AND OUTSIDE CONSTITUTION H. von Ihering (1903 (1930: 81)) thought that although the scutellum is "built chiefly of clay, it however contains such a proportion of wax, that the whole thing forms a solid mass. . .".

Silvestri (1904: 136) and Bertoni (1912: 142), said that the base of the nests of *spinipes* (= *ruficrus* for them), was made of "vegetal earth."

Mariano Filho (1911 : 127) stated that the scutellum . . . "consists of a globular mass of resistant clay, much propolized." . . .

Salt (1929: 438) wrote of the nest of *amalthea,* a related species: "by receiving the dirt and the waste of the nest above, this network might successively be transformed into the hard, cellular mass found below it." The network was probably what I call the exoinvolucrum. The work of Salt was important to the present research, because it stimulated me to investigate the possibility of similar origin of the scutellum.

In nests B, C, D, the outer surface of the scutellum was well covered with propolis. In all nests here examined in detail, the scutellum's inner surface had patches of propolis and cerumen, but more commonly there were small, flatish (altho not even), more or less rounded deposits of a dark material. The limits of each of these dark small deposits generally were unclear, but in many cases it was possible to see that they were separately laid down and incorporated in the scutellum's surface. Remains of dead bees and spots of clear yellow granules were not rare at the scutellum's surface.

These spots of yellow granular material were found mostly on the scutellum's inner side. Some of them were elongated and partly dark in color. However, when prodded with a needle, the dark portion broke up, transforming itself into a yellow granular mass. The roundish spots of yellow granules certainly were the dejection of resting bees, flattened by the workers.

In order to confirm the origin of this material, three young bees of nest A were captured and their excreta examined. It was easily seen that this excreta is the clear yellow granular material found in all nests.

Near the upper part of the scutellum, a finely white granular substance, salt-like, was frequently found. It was always over a dark layer. However, this white material must have been under a stratum of cerumen, the remains of which were seen sometimes over the white layer, and partly impregnating it. Why this happens, is not known.

The inside, that is, the bulk of the scutellum consists of several materials grouped in four categories: A—dark deposits, often in strata, together with the remains of the bee cocoon's walls; B—more or less free granules; C—remains of dead bees; D—Acarina, alive and dead.

Inside or outside the scutellum, the dark material, when prodded with the tip of a needle, broke up into a mass of small grains, yellowish or cream-brown in color. On the surface of nest E, the dark substance was soft, but on the other nests it was generally firm. In both cases, their granular nature was the same.

The deposits that exist on the base of the cocoons of prepupal and pupal brood cells of *spinipes* showed also the same granular structure when prodded with a needle.[1] Moreover, among the dark deposits that exist in the scutellum, it was possible to find the remains of the bee's brood cocoons. These were frequently still adhered to the dark deposits, as they always are on the bottom of the cocoons. All this demonstrates, unmistakably, that the dark material constituting most of the scutellum, comes from

[1] Observations of this will be published in another paper on brood cells and combs.

the bottom of the brood cocoons of *spinipes*. In other words, this dark material is the excreta of prepupae, which void them after making their cocoons. H. von Ihering (1903 (1930 : 87)) said that excrements and larval skins were found on the bottom of the brood cocoons of meliponins. However, he did not mention the presence of this material in the scutellum.

In nest C, the granular materials was chiefly a clear yellow color (50% of total matter present) ; this was also true in parts of nest B, and apparently in much of nest A (which was the only one not examined with the stereoscopic microscope). In the other nests, altho not so common, small yellow grains were present, too.

There was a large proportion (the predominant one in nests B, D and E), of small grains more or less reddish-brown in color. In nests B, C, D, E (the ones examined in detail) there were also many white and cream colored granules and even some bordeaux and pink ones (nest B). At first, it was thought that perhaps the reddish-brown ones were earth. However, a comparison with samples of soils taken near the original nests sites, showed that this was not the case. For one thing, sand grains were a rarity in the scutella. Yet, sand was common in the soils examined. True, the scutella had other hyaline crystals, but these were not of quartz since they were easily smashed by a slight pressure of a pin's tip.

The scarcity of sand in the scutella, shows that earth is either not normally present, or is of very little importance there.

The origin of the reddish-brown, and cream colored granules seen in the scutellum is substantiated by the fact, that they are easily obtained by prodding with a needle the dark deposits made of prepupal excrement. In many places the small grains were loose with many Acarina among them. It seems that the Acarina or more probably the insect larvae also found inside the scutellum, were responsible for freeing the granules from the dark deposits.

The alternation of layers of dark material with layers of yellowish granules, and also the presence of exoinvolucrum sheets, gives a general stratified look to a cut thru the inside of the scutellum. Yet, this is not always the case, inasmuch as sometimes the deposits were irregular in form.

Writing briefly on the nests of *spinipes* (=*ruficrus*), Silvestri (1904: 136) and Bertoni (1912: 142) said that there was, at the nest's base, a "thick" or a "compact" mass of "vegetal earth." Probably such "vegetal earth" was, in fact, the scutellum and granular material.

In short, contrary to what was thought, the scutellum of *T. spinipes* is not made up of mud or vegetal earth. The conclusion that the scutellum is predominantly derived from the bees' excrements—prepupal and adult—is an entirely new concept. It also shows that this species gives a building destination to a matter that most melliponins simply throw away.

LOCATION—Nest A arrived at my home in a tree trunk cut just below the nest. Possibly the tree fork at the nest's base was lost. It is not certain, however that there was one on the nest's base. Yet, higher up, the nest incorporated other tree forks.

All other nests examined were built over a tree fork, which had two or three branches. Not only these lower branches and some upper ones, but even lianas were wholly or partly incorporated into the nests and scutella. This incorporation of tree branches was a common characteristic of all nests examined. Obviously, the heavy scutellum must always contain or rest upon branches capable of supporting it.

Silvestri (1904: 136) referred to such structure on a tree bifurcation.

Mariano Filho (1911: 127–128) also saw a scutellum at a tree fork, . . . "a fact generally common when the nest inplants itself in little developed trees. In such cases the interior of the nest is frequently transversed by small secondary branches, that help in giving more stability to it."

It is interesting to notice that most nests are built on trunks or branches of relatively small diameter. Just under the nests here examined, diameters of the tree trunks were as follows: A = 6 cm; B = 13 cm; C = 12 cm; D = 4, 5 cm; E = 6 cm.

It seems amazing that such heavy structures are often made on thin branches. One would even think that *spinipes* build their homes on the most slender branches capable of supporting their heavy nests. A possible explanation is that the scutellum would be of little use, as a defense, if an enemy could attack from above. On slender trunks or branches it seems very difficult to attack from above because such branches are at tree tops or at the sides of trees, in places generally difficult to reach from neighboring branches capable of sustaining a medium size mammal. Yet, this hypothesis does not seem to explain the case of nest B, where the branches were not so thin. It must be considered, however, that nest B was an old one and when first built, certainly the tree branches were thinner.

FUNCTION Mariano Filho (1911: 127) wrote that . . . "it is because of the scutellum's heavy weight that the monstrous nest maintains itself in most complete stability." This theory of the "stability" function was also adopted by Ducke (apud Schwarz 1948: 268) and R. von Ihering (1940: 402–403).

When examined in relation to their position, the scutella generally (but not always) had their outer convex surfaces directed against the place from where a climbing enemy could menace the nest. On the opposite side, their inner concave surfaces somewhat protected the vital parts of the nests: the brood combs and the storage pots.

In my opinion this shows that the scutellum has a defensive role. Yet, this "defensive" function does not tell the complete story. In nest D, for instance, the tree trunk was at the back of the nest, but not fully incorporated into it. The scutellum was mostly at one side of this trunk. On the other side the nest was not so well protected by the scutellum. In nest E, the situation was even more revealing. The upper part of the tree trunk passed thru the middle of the nest. From the place of the trunk where the nest began, the scutellum went upward in a somewhat inclined and outer direction. Its shield-like shape left a space, between the shield margins, of 19 cm. Thru this region, not protected by the scutellum, a mammal climbing the trunk could easily attack the nest. In fact, after removing a few sheets of the exoinvolucrum, I came upon some honey pots. True, at the base of the nest, even in this little protected region, there was also a belt of scutellum some 5 cm thick, around the tree trunk. However, this was manifestly insufficient to stop or to delay an attack by a climbing mammal.

Lindauer (1957: 71, 73, 78) wrote that "The stingless bees do not make cleaning flights as our *Apis* does, but leave the excrements in their own nest, in special places, where other refuse is also put. This garbage heap is removed from time to time, but they [the bees] always let some remain, in order to leave a disagreeable odor to ward off nectar and pollen thieves.'' Lindauer did not mention any permanent refuse heap. He did not speak of the scutellum of *spinipes* (= *ruficrus*), which in all probability was not seen by him.

In my opinion, the prevailing smell inside the nests of nearly all species of meliponins, is decidedly good. True, the scutellum has a slightly disagreeable odor, but it certainly would not repel an enemy with approximately the same olfactory reactions as man.

Another possible role of the scutellum would be as a reservoir of heat. This huge structure is always thermally isolated from the outside by 2–6 membranes of the exoinvolucrum and by the spaces between them.

Weyrauch (1942: 64) wrote that a similar external involucrum, in a neighbor species serves to . . . ''maintain in the interior of the nest a higher temperature than that of the ambient.'' This was a nest of *amalthea* (= *trinidadensis*, identified by Schwarz 1948: 252), in which the existence of the scutellum is not yet known.

The scutellum certainly absorbs and keeps some of the nest's heat. On cold nights, part of the heat received during the day would then be transferred to other parts of the nest. However, the intensity of this exchange of heat must be very small (it was not measured).

H. von Ihering (1903 (1930: 81)) stated that, in his opinion, the scutellum . . . ''seemed destined to give greater solidity and resistance to the nest.'' This certainly must be true, and one is easily convinced by the scutellum's massive structure. However, H. von Ihering's statement is a general one, and must be further elaborated.

Silvestri (1904: 136) said that this structure was . . . ''a true and solid foundation'' at the base of the nest he examined. As told here in the discussion of its shape, it seems to me that this scutellum had a U shape. At any rate, Silvestri's pictures showed the scutellum to have at least one inclined wall. Therefore, it was not, in my opinion, a mere base foundation.

Mariano Filho (1911: 127) called the scutellum ''a globular mass,'' and this might imply an absence of walls. However, when the shape of that structure was discussed, it was shown how his own words were at variance with that ''globular'' concept.

In view of Mariano Filho's conflicting considerations on this matter, it seems advisable not to take his words as meaning an absence or near absence of walls in the *spinipes* (= *ruficrus*) nests he saw. In the nests of *spinipes* which I observed, the scutellum always could—or at least a part of it—be considered as a wall. One may say the same in relation to the nests described and pictured by H. von Ihering (1903 (1930: 66–70); in Mariano Filho 1920: 21).

Obviously, this huge structure must have an important adaptive role, or it would not be formed in the course of evolution. Actually, *spinipes* is a very successful bee and even resists man's persistent efforts to eradicate it.

In my opinion, the nest construction (storage pots, brood combs, etc.) of the Meliponinae must always be directly or indirectly fixed on a strong wall. In all nests of well known species, this is a common constant. Of course, not all individual pots or combs are directly anchored to a wall, but they are connected to other pots, combs, etc., that in turn are firmly attached to a wall. In some cases the wall may be built by the bees themselves. The scutellum is an example of this. The presence of a strong wall is—I think—a general rule or ''law'' of the nests of the Meliponinae. The same cannot be said of the nests of other bees as, for instance, the Bombinae (bumblebees).

As stated, the nests of *T. spinipes* are located on relatively thin branches, mostly at the tree tops or sides. Obviously such small round branches do not afford the wide and large wall surfaces that seem so necessary to the nests of meliponins. I believe that the shield-like scutellum is well suited to provide the supporting walls these bees need. This is, in my view, the scutellum's chief role.

In nest B, the branches of the tree fork were larger than those of the other tree forks here mentioned but still not to be considered large branches. In this case, the scutellum had a U shape. Both arms of the U greatly increased the surface that the two branches could offer.

SIMILAR STRUCTURES IN OTHER SPECIES In the nest of a related species, the Central American *T.* (*T.*) *corvina,* Michener (1946: 193–194) described a structure that probably was also a scutellum. Inside the nest of this bee, he found several thick (¼″–¾″) layers of hard material. It . . . "required a hatchet and considerable prying to cut and remove large pieces." In places the layers, when . . . "not distinct formed a total thickness of two and one half to three inches." There was an outside brittle thin layer. The nests were built on tree branches.

The general shape of this structure was not described, but probably *T. corvina* has a scutellum, too. In fact, sometimes *T. spinipes* also makes such thick layers, near or connected to the scutellum (see obs. of nest C and E). And besides, Michener found a massive structure 2½″–3″ thick (approximately 6.5 cm–7.5 cm). It has a comparable one, among the nests of bees: the scutellum of *T. spinipes.* There are other points of similarity between the nests of *corvina* and *spinipes.* The "stratified or laminated" "yellowish solid material" "among the inner layers of hard wax" in a *corvina* nest, resembles the condition found inside the scutellum *spinipes.* Also the construction of nests upon branches and the covering of the nests by an outer brittle layer, were found in both species (Michener, o.c.; Schwarz 1948: 276–279).

In the opinion of Schwarz, *corvina* is a "near relative" of *ruficrus,* here named *spinipes.* However, both bees were considered by Cockerell to be two varieties of the same species (Schwarz 1946: 276).

The presence or absence of some kind of scutella should be investigated in *amalthea* (= *trinidadensis* and/or *silvestriana*). Inside hollow trees, Bertoni (1912: 142), in Paraguay, found in this species a thick structure at the nest's base. Salt (1929: 438), in Colombia, said that "Upward from the lower batumen, for 15 cm, extended a hard, brittle, coarsely cellular mass of cerumen . . ."

Myers (1935: 132), in Trinidad, found that an external nest of *amalthea* (= *silvestriana* Vach.) had the outside . . ." covered with exceedingly hard, small chambered resinous material, incorporated with much earth. This layer was very thick at top and bottom" . . . It must be remembered that some authors thought that the scutellum of *spinipes*, too, was made of propolis or cerumen, and earth.

Weyrauch (Schwarz 1948: 252) wrote that a nest of *amalthea* (= *trinidadensis*), captured at San Ramon, Peru, had an "outer envelope consisting of a thick mass of coarsely chewed leaves." "This envelope is thoroughly compact and contains no hollow spaces." In a previous paper, describing another external nest of this species, Weyrauch (1942: 63–64) did not mention any strong wall. However neither did he deny its presence. Possibly it escaped his attention.

It seems that when *amalthea* builds external nests, it has periphereal walls that perhaps may have some points of similarity with the scutellum. As already mentioned, the internal nests of *amalthea* may also have a related structure. For the time being, the name scutellum should be used only in connection with the internal massive walls of *spinipes* and—probably—*corvina*.

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