

OBSERVATIONS ON THE BIOLOGY OF A LEAF-CUTTER BEE "*Megachile frontalis*," IN NEW GUINEA

CHARLES D. MICHENER * AND J. J. H. SZENT-IVANY †

Megachile frontalis (Fabricius) (usually known in the past as *M. lachesis* Smith, see Liefinck, 1958) is the most conspicuous and probably the commonest leaf-cutter bee in the Territory of Papua and New Guinea. It is a large, elongate, black species that is sometimes of considerable importance because it cuts leaves of plants. It may also be a significant pollinator of certain plants. Aside from its economic significance, this species is of special interest because it is one of the rather elongate, parallel-sided species of *Megachile*, most of which do not use leaves in nest construction. *M. frontalis*, however, has cutting edges between the mandibular teeth of the female and cuts leaves for use in making its cells. Its systematic position will be discussed in a subsequent paper by one of us (Michener).

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DISTRIBUTION

MEGACHILE *frontalis* and *M. atrata* Smith are closely allied species, if indeed they are specifically distinct, which together range from Malaya and Sumatra for over 4,500 miles across the Malay Archipelago to the Solomon Islands. *M. atrata*, which differs from *frontalis* by having yellowish rather than dark infuscated wings, is generally more western in distribution. Dr. M. A. Liefinck has kindly reported (*in litt.*, 10th August, 1959) this form from Malaya, Sumatra, Borneo, Java, and the lesser Sunda Islands of Bali, Flores, Sumba, Roti, and Timor. It is also known from the Philippine Islands (Luzon, Samar, Mindanao). *M. frontalis* is found, as shown by the localities listed below, for the most part east of the range of *M. atrata*. However, on Flores and Sumba, the two species, or at least forms with the two wing colors, both occur. This is the principal evidence now available, suggesting that the two forms are distinct species. Detailed anatomical studies have not been made.

The distributional data for *M. frontalis* (FIG. I) given below were gathered from the literature, from various collections, and from our field observations. Those data pertaining to the Territory of Papua and New Guinea are given in detail and summarized in FIG. II ‡ and those from other areas are sometimes given in a rather general manner, according to the details available. *M. frontalis* was found in all districts of the Territory of Papua and New Guinea, visited by Szent-Ivany during the past five years. In the list, localities not followed by any information in brackets are (except as otherwise noted) for specimens collected by Szent-Ivany (1954-1959) or by Michener (1959). This material is in the collection of the Department of Agriculture, Stock and Fisheries (Port Moresby), the Bishop Museum (Honolulu), and the Snow Entomological Museum, University of Kansas (Lawrence, Kansas). In brackets after other localities may be found (1), authors and dates, referring to publications listed in the "Literature Cited", or (2), the letter "L", referring to information provided by Dr. M. A. Liefinck (*in litt.*, 10th

* Watkins Professor of Entomology and Chairman of the Department of Entomology of the University of Kansas, Lawrence, Kansas, U.S.A.

† Senior Entomologist, Department of Agriculture, Stock and Fisheries, Territory of Papua and New Guinea, Konedobu, Port Moresby.

‡ The following places mentioned by previous authors could not be located or identified, thus they are not shown on FIG. II.: Urikituru, Kinigunang, Sinai and Suavi.



FIG. I.

August, 1959), or (3), letters referring to museum collections in which specimens of *M frontalis* were examined. These letters are B, Bishop Museum, Honolulu; AM, Australian Museum, Sydney; SAM, South Australian Museum, Adelaide; HSPA, Hawaiian Sugar Planters Experiment Station, Honolulu; USNM, United States National Museum, Washington; AMNH, American Museum of Natural History, New York; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

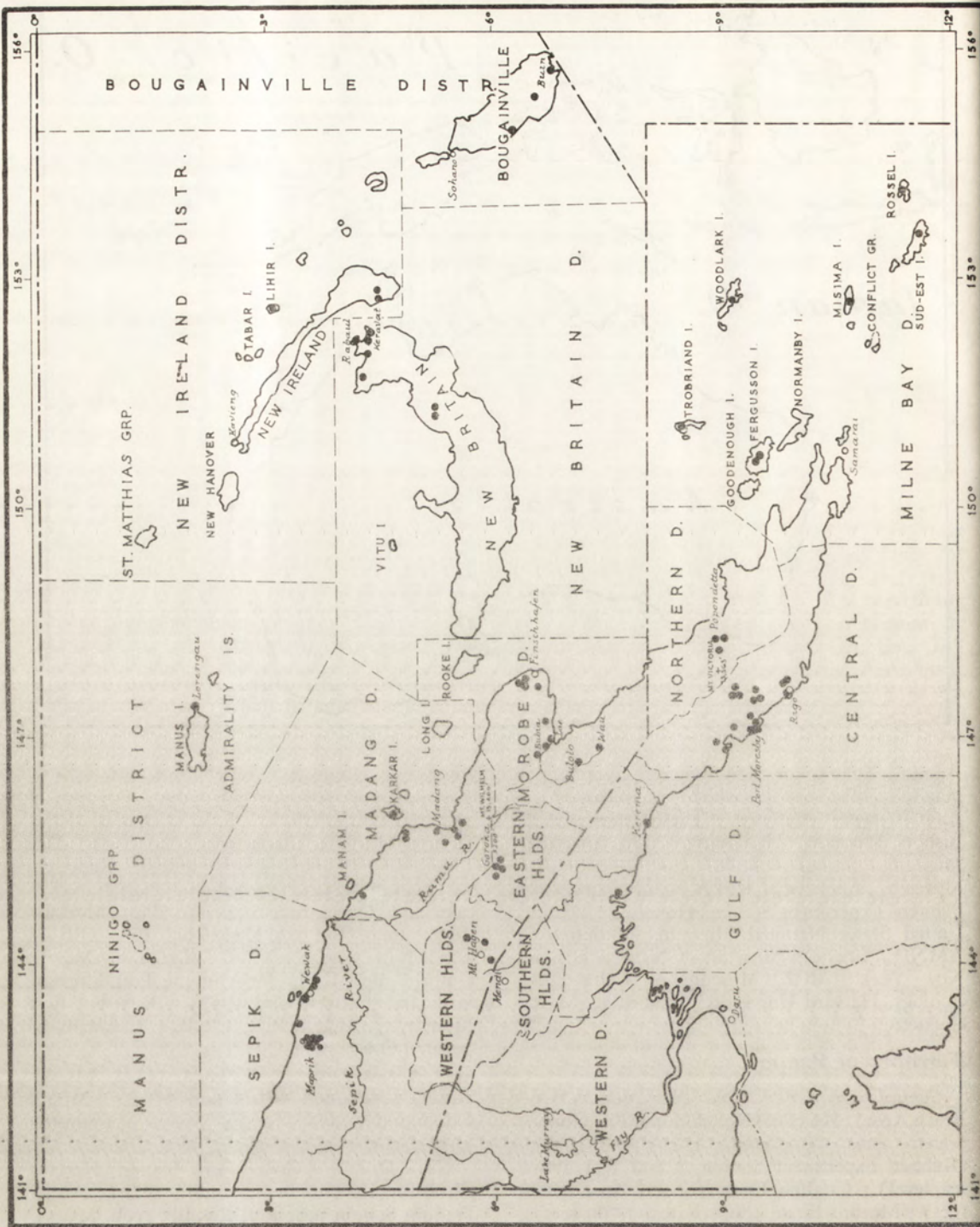
Territory of Papua

Central District: Aroa Plantation (Hisiu Beach Area); Koitaki (Koitakinumu Plantation), Sogeri Area [Cockerell, 1929]; Bisianumu (Rubber Experiment Station, 1,600 feet above sea level); Catalina Estate (Sogeri Area, 1,600 feet); Mororo Estate (Sogeri area, 1,700 feet); Gardens of the Corrective Institute and the War

Cemetery, Bomana (near Port Moresby); Experimental Blocks of the Department of Agriculture, Brown River; Daradai Plantation (Musgrave River area, 900 feet); Doa Plantation (Galley Reach area); Kapogere (Agricultural Station); Laloki (Plant Introduction and Quarantine Station); Port Moresby Town area (Boroko, Konedobu, Paga Hill—a number of specimens was collected by Mr. E. Guthrie and Mr. L. Jones in the Port Moresby town area in 1946 and 1947); Bisiatabu, Port Moresby [SAM]; Rigo; Roku; Urikituru to Sogeri [Cockerell, 1929].

Northern District: Kokoda (Coll. Mr. J. Healy); Mamoo Plantation (near Mount Lamington, 1,000 feet); Mount Lamington [AM, SAM].

Gulf District: Government Station, Kerema [Probably Kevema of Cockerell, 1929]; Aimei Trading Station near Port Romilly (coll. Mr. G. Rio).



Milne Bay District: Murua (Woodlark) Island and Kulumadaw Hill, Murua Island [B, AMNH]; Fergusson Island [USNM]; Misima Island [SAM]; Mt. Sisa, Misima Island, 1,050 feet [AMNH]; Lusancay Islands; Kiriwina Island, Trobriand Islands; Rambuso, Sudest Island, sea level to 325 feet [AMNH]; Jinju, Rossel Island, sea level to 325 feet [AMNH].

Territory of New Guinea

Sepik District: Aitape [SAM]; Brandi (Intermediate School area), But (Friese, 1912 b), Mandi and Tanbada villages in the Wewak Subdistrict; Bainyik Agricultural Station, Maprik (Government Station) and the areas of the following villages in the Maprik Subdistrict: Amahop, Apangai (No. 1), Aupik (No. 2), Bali (Garden of the South Sea Evangelical Mission), Bunahoj, Imbia, Kulabu, Kuminibus, Numakum, Numango, Wingei (No. 1), Wora (No. 1), Yamigum, and Yanago.

Madang District: Amele village cocoa plantation; Dugamoor Plantation (Bogia Subdistrict, coll. Mr. K. Mayer); Dylup Plantation; Kulili Plantation, Kar Kar Island; Madang (Friedrich-Wilhelmshafen) Agricultural Station; Reapi village; Bogadjim (Stephansort), S.E. of Madang [Friese, 1909]; Erima (harbour of Bogadjim) [Friese, 1909]; Astrolabe Range [SAM].

Morobe District: Bubia (Agricultural Experiment Station), Lae (Botanical Garden and secondary forest near "Didimans Creek"); Nasawampum village (20 miles N.W. from Lae); Busu River, east of Lae, 325 feet [B]; Boana Mission, Huon Peninsula [B]; Wau ("The Homestead" Coffee Plantation, 3,500 feet); Finschhafen [SAM]; Wareo, near Finschhafen [SAM]; Sattelburg (25 miles W. of Finschhafen) [Friese, 1909]; Bulolo, 3,300 and 3,900 feet [B]; Komba [SAM]; Mount Gyifrie [SAM].

Western Highlands District: Kinjibi Plantation (Wahgi Valley, about 5,000 feet); Korn Farm (Agricultural Station, near Mount Hagen, 4,700 feet); Tsenga, upper Jimmi Valley, 3,900 feet [B].

Eastern Highlands District: Goroka (town area and coffee plantations of G. Pentland and R. & J. Frame); Koffena Plantation; Kori-teigu village; Lunapieve Plantation (Asaro Valley). Altitudes of these localities are 5,200-5,700 feet.

Manus District: Loniu Village (Los Negros Island).

New Britain District (Neu Pommern): Keravat (Lowlands Agricultural Experiment Station); Kokopo; Baining, St. Pauls, Gazelle Peninsula, 1,140 feet [B]; Rialla, north coast [B]; Talalo, Nakanai Mountains, 2,925 feet [B]; Kinigunang [Friese, 1909]; Ralum [USNM] (Cockerell, 1911).

New Ireland District: Lagakot Plantation, Lihir Island; lower Kait River [B]; Gilingil Plantation [B].

Bougainville District: Kangu Hill (Buin, southern tip of Bougainville Island opposite Shortland Island of the British Solomon Islands Protectorate); Simai [AM]; Borioka, 975 feet [B]; Naval Air Base [Krombein, 1951]; Suavi [Cockerell, 1929].

British Solomon Islands

Guadalcanal: No further locality [B]; Tenaru [Krombein, 1949].

Florida: Siota [Krombein, 1949, 1951].

Tulagi: [Cockerell, 1936].

Malaita: Suu [Cockerell, 1936].

Dutch New Guinea

Djamna [MCZ]; Hollandia [Friese, 1912 a]; Humboldt Bay (near Hollandia), [Friese, 1909]; Manokwari [Friese, 1909]; Pim, Jutefa Bay, sea level to 100 feet [USNM]; Misool Island [L]; Sabron, Cyclops Mountains, 930 feet [USNM]; Kaimana [USNM].

Indonesia

Kei Island.

North Moluccan Islands: Halmahera (Gilolo) [Lieftinck, 1958]; Ternate [L]; Batjan (Bachian) [Smith, 1860; L]; Obi [L].

South Moluccan Islands: Buru (Bouro) [Alfken, 1926; Lieftinck, 1958]; Ambon (Amboina) [B, L]; Ceram (Piru) [HSPA]; Saparua [Lieftinck, 1958].

Lesser Sunda Islands: Flores [L]; Sumba [L]; Tanimbar (Timorlaut) [L].

Celebes: Samanga [Friese, 1909; L].

Friese (1909) also records the species from Cairns, Queensland. Subsequent collecting in the area has not rediscovered it, but it may well occur there.

VARIATION

As indicated in the section on distribution, *M. atrata* may be only subspecifically distinct from *M. frontalis*. Even among forms currently referred to as *frontalis*, considerable variation exists. The Philippines form, which has received the subspecific name *nigrolateralis* Cockerell (1914), is probably the same as *atrata*. According to Dr. M. A. Liefstinck (*in litt.*, 10th August, 1959), specimens from Celebes have paler wings (grey, not fuliginous) than typical material.

Specimens from the Eastern and Western Highlands districts of New Guinea, collected at altitudes of 4,700 to 5,500 feet, and, curiously, also those from near sea level on the Lusanay Islands and Kiriwina Island in the Trobriand group, differ from those found elsewhere in New Guinea by the brownish-red rather than black scopa of the female and by the more extensive reddish pubescence on the apical terga of the male. Only one female out of nearly 100 studied from the highlands has a black scopa, but males are less consistently different. We know of no biological differences between these forms, but the biological observations described below are identified by localities and could thus be segregated in case differences appear after more-detailed study.

It is interesting to note that, according to Dr. Liefstinck, the red scopa reappears on the island of Sumba, in the Lesser Sunda group. He says that on that island the scopa may be red, black, or intermediate, but that red predominates. There are also specimens of *M. atrata* from Sumba and Timor with red scopal hairs. Except for this material and the populations from the New Guinea Highlands and the Trobriands, all known specimens of both *atrata* and *frontalis* have a black scopa.

TERRITORY OBSERVATIONS.

Seasonal Occurrence

There seems to be no marked seasonalism in the flight of *Megachile frontalis*, specimens having been taken in every month of the year. Not only have adults been taken at all seasons, but at Kerema on 8th May, 1959, and at Bisiapuru on 12th May, all stages from eggs to young adults were found in cells. Continuous activity throughout the year is not surprising in an area all of which is less than 10 degrees from the equator.

Sleeping

At Goroka and Kerema "sleeping" individuals of both sexes were observed (by Michener). Occasional bees of both sexes were observed alone, on grass leaves, but the majority of those noted were resting on dead weeds rising above the general level of surrounding tall grass. The bees flew to these favoured locations between 4 p.m. and 6 p.m. (observations made 28th April to 1st May at Goroka), earlier if the day was rainy. They alighted, turned head downward on a small stem (or grass blade), grasped the stem with the mandibles and within half a minute to one minute became "asleep" so that they could be put into a bottle with little danger of their being disturbed and flying off. If dropped on the ground, some lay there while others flew off sluggishly. Even on the most densely occupied weeds, the bees were not crowded together. Each was a centimeter or more from its nearest neighbours. While the sexes often mixed, there was an obvious tendency for females to sleep in some groups and males in others. In the morning the bees took flight between 7 and 9 o'clock as they were dried by the sun.

On 28th April, 1959, a rainy afternoon, all the individuals which could be found in an area of 20 by 20 metres at Goroka were taken. There were about 30 of each sex, mostly on three tall dead weeds but a few were scattered elsewhere. The next evening, a similar number was in the same area, mostly on the same dead weeds. Perhaps they failed to reach their usual resting places on 28th April before heavy rain immobilized them. On 30th April and 1st May only two were seen. Apparently there were about 122 individuals sleeping in the area, 120 of which were taken in the first two nights. In nearby similar areas, no *Megachile* could be found sleeping.

One would expect that bees sleeping outside of nests in this way would be mostly males (as is the case with many species) or young females that had not yet started to nest. This is not the case with *M. frontalis*. Most individuals of both sexes had tattered wings, indicating considerable wear.

The sleeping places studied at Goroka and Kerema were not near nesting places, nor were they near leaves or flowers used for making and provisioning the cells.

At Madang, males only were observed by Szent-Ivany sleeping in a field of *Mimosa pudica*. The bees were not resting on these rather low plants but on two higher ones. One was *Stachytarpheta javanica* (Verbenaceae), the other *Paspalum conjugatum* (Gramineae). Thirty-seven were caught in one sweep of the *Stachytarpheta* plant at 6.20 p.m.

Flowers visited

Adults of *Megachile frontalis* were found on flowers of plants belonging to 10 different families. However, they seem to prefer flowers of Leguminosae, both woody and herbaceous species. The names of the plants visited are:

- Acanthaceae :
Alysicarpus intrusa.
- Caricaceae :
Carica papaya.
- Compositae :
Cosmos sulphureus.
Tagetes erecta.
Zinnia elegans.
- Convolvulaceae :
Ipomoea sp.
- Euphorbiaceae :
Euphorbia pulcherrima.
- Labiatae :
Ocimum basilicum.
Ocimum canum.
Hyptis sp.
- Leguminosae :
Cajanus cajan.
Cassia allata.
Centrosema pubescens.
Crotalaria anagyroides.
Crotalaria goreensis.
Crotalaria mucronata.
Crotalaria retusa.
Leucaena glauca.
Mimosa pudica.
Pueraria phaseoloides.
- Myrtaceae :
Eugenia malaccensis.
- Polygonaceae :
Antigonon leptopus.
- Sterculiaceae :
Commersonia bartramia.
Kleinbovia hospita.

No collection of pollen was observed on plants in families other than Leguminosae and it is probable that these are only nectar sources. In fact, pollen collecting was only observed on *Cajanus cajan*, *Crotalaria mucronata*, *Leucaena glauca* and *Mimosa pudica* but it is likely that the other Leguminosae are also pollen sources. Competition for visits by *Megachile* between

Mimosa pudica and *Leucaena glauca* was observed at Bisianumu, where *Megachile frontalis* was observed in large numbers collecting pollen from the flowers of *Mimosa*, but was not on those of *Leucaena*. However, *Leucaena* flowers were visited for pollen at Kapogere where *Mimosa pudica* was absent. Much more decisive evidence of competition among flowers for visits by bees has been gathered elsewhere (see, for example, Linsley and MacSwaine, 1947).

Injury to Leaves

Cutting of pieces of leaves for the construction of cells by *Megachile frontalis* was observed repeatedly in the Territory of Papua and New Guinea. The following plants were affected:

- Combretaceae :
Terminalia catappa (Madang).
- Leguminosae :
Cassia allata (Port Moresby). (See Plate 1.).
Cassia fistula (Port Moresby).
- Lecythidaceae :
Planchonia timorensis (Kulabu).
- Lythraceae :
Lagerstroemia indica (Goroka).
- Myrtaceae :
Eucalyptus deglupta (Goroka). (See Plate 1.).
Psidium guajava (Doa plantation, Brandi Intermediate School area). (See Plate 1.).
- Rosaceae :
Rosa spp. (Goroka, Kokopo, Wau). (See Plate 1.).
- Rubiaceae :
Coffea arabica (Goroka, Lunapieve Plantation). (See Plate 1.).
Gardenia sp. (Goroka).
Timonius sp. near *rufescens* (Kulabu).
- Sapindaceae :
Pometia pinnata (Madang).
- Sterculiaceae :
Commersonia bartramia (Government Station, Madrik).
Theobroma cacao (Lagakot Plantation, Lihir Island).

The extensive damage to *Eucalyptus deglupta* at Goroka has been described in two previous papers (Szent-Ivany, 1958; Szent-Ivany and Womersley, 1958). As a result of cutting of more or less symmetrical pieces from the leaves, the whole appearance of the trees was changed, the shape of the leaves resembling that of deciduous species of *Quercus*. (See Plate 1.).

Besides *Eucalyptus deglupta*, three ornamentals (*Lagerstroemia indica*, *Rosa* spp. and *Gardenia* sp.); and one fruit tree (*Psidium guajava*) were found severely damaged by *Megachile*



PLATE 1.

frontalis. Extensive damage to rose bushes was caused in the manager's garden at the Animal Industry Station at Goroka, in July to October, 1955. It was observed that the bees had their nests at a distance of several hundred yards from this garden. The nests were built in the side of a ditch which formed the western boundary of the airstrip. Hundreds of nests were found here. Several nests were examined and most of them had parts of rose leaves in the cells. There were no rose bushes between the area of the nests and the Animal Industry Station.

The female bees were very active between 9 and 11 a.m. on a bright sunny day and it was easy to follow the route of their flight between the rose garden and the drain. Bees coming out of their nests flew straight in the direction of the station garden and most of them came

from that direction back to their nests. All the way from the ditch to the garden one could see the bees flying rapidly back and forth.

Some *Gardenia* trees in the Goroka town area were almost stripped by females of *Megachile frontalis*.

Minor damage in patches was observed on *Theobroma cacao* at Lagakot Plantation and on *Coffea arabica* at Lunapieve Plantation and at Mr. R. Frame's Plantation at Goroka, where some young coffee trees were severely stripped, causing a slight setback in growth.

Chemical control is not easy. The most successful treatment is to apply BHC in the form of "Gammexane 10" dust. The application has to be repeated at intervals of two or three days. However, the dusting of coffee and cacao bushes with Gammexane is not recommended, because it appears to cause an "off-flavour" to the beans.

Near Kulabu *M. frontalis* was observed attacking leaves of two secondary forest trees, *Timonius* and *Planchonia*.

NESTING AND BREEDING

Nest Locations

A. R. Wallace (*in* Smith, 1871) noted that this species "makes a small round hole in hard clayey ground." L. J. Toxopeus (*in* Alfken, 1926) recorded observations on a large number (thousands) of nests in an earth bank. He observed the bees carrying pieces of leaves as well as pollen into these holes. Szent-Ivany (1958) recorded the species (under the heading "*Megachile* sp.") nesting in large numbers in lawns and tennis courts in New Guinea (Kinjibi Plantation, Western Highlands).

We have observed nests at Port Moresby (Paga Hill), Bisianumu, Kerema, Goroka, and several places in the Maprik subdistrict (Sepik District).

As reported by the authors cited above, the nests consist of burrows in the ground. Scattered ones are found in flat ground, either bare or covered with short grass. Bare village squares in the Maprik subdistrict were found to be favourable sites (Plate 2). However, nests often occur in much larger numbers in earth banks, e.g., roadside banks near the villages of Kulabu and Kuminibus, Maprik subdistrict (Plates 2 and 3, Figure III), the sides of roadside ditches at Kerema and near the village of Kulabu, the side of a ditch along the airstrip at Goroka and small roadside banks at Bisianumu. At Kerema, there were about 100 nests in a bank about 18 inches high along a ditch 10 yards in length. At Bisianumu, many old cells were exposed by erosion of banks, indicating that they had been in use for a long time.

At all locations mentioned, the nests of the *Megachile* were in heavy soils. This preference is emphasized by the following observations made at Kulabu. A shallow ditch (Fig. III) about two feet wide separated a road from a clayey roadside bank. The ditch was full of sand, probably brought from the nearby river when the road was constructed. Large numbers of *Bembix melancholica* Sm. but no *Megachile* were nesting in the sandy soil. In the clayey soil were large numbers of nests of *Megachile frontalis* but no nests of *Bembix*.

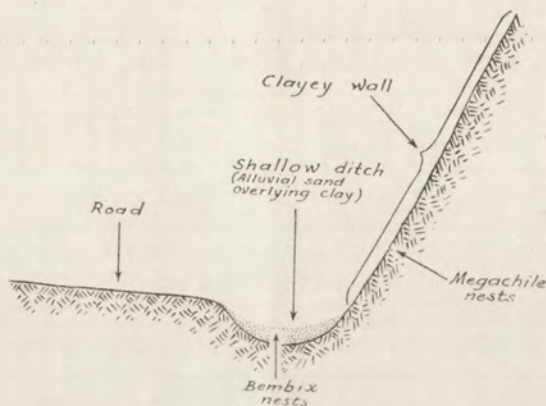


FIG. III.

Construction and Activities Around Nests

Unlike most species of *Megachile*, *M. frontalis* digs its own burrows. Females have been seen starting burrows where there was no previous hole, both on flat ground and in vertical banks. In digging, the females work largely with their mandibles. In rather moist soil at Kerema, excavating females were observed to carry out a pellet of earth once every 45 to 90 seconds (average, about once a minute). The pellets are irregular, up to about 3 mm. in diameter. The bee comes out of the nest head foremost, carrying a pellet in her mandibles, and flies 150 to 300 mm., drops it, and returns to the nest.

In bright, sunny weather both male and female *Megachile frontalis* were very active around the nests in the roadside banks near the villages of Kulabu and Kuminibus. However, the males settled down on nearby plants as soon as clouds covered the sun. The females continued cutting leaves, carrying leaf sections and pollen into their nests even in rainy weather. They stopped flying when the rain became strong or during sudden tropical downpours. Similar observations were made at Kerema.

In May, when observations of groups of nests were made at Kerema and Bisianumu, females were more abundant about nests than males. At Kulabu and Kuminibus in July, however, the number of males around the nests was much larger than that of the females. The proportion of females and males at the clayey wall near Kulabu village was estimated to be one to three. The males were actively flying

around the nests and up to three males were seen following a female (carrying pollen or leaf sections) into the nest. The females, which were actively building their nests or carrying pollen into them, appeared to be rather hostile towards the males. Males were often seen crawling into a nest which was not occupied at the time by a female. When a leaf-carrying female arrived at the entrance of a nest out of which a male was crawling, she appeared to be disturbed and vigorously chased the male away.

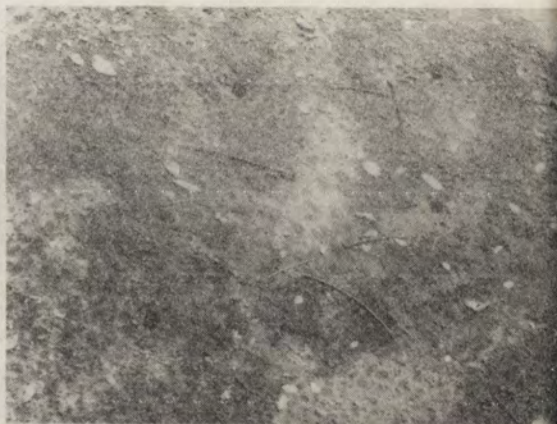
The parasitic bee, *Coelioxys intrudens* Smith (det. G. E. Nixon), was observed in large numbers hovering around the nests. Szent-Ivany often saw the head of a female *Megachile* in the entrance of a nest when a male *Megachile* or a female *Coelioxys* tried to enter it. Two or three quick vertical movements of the large head of the female *Megachile*, accompanied by horizontal movements of its large mandibles were enough to frighten away the smaller male *Megachile* or female *Coelioxys*. On one occasion a large brown gryllid (*Acheta* sp. ? Det. P.M. Stock) was observed entering a *Megachile* nest.

When half of the body of the gryllid was in the entrance hole, the female *Megachile* which occupied the nest pushed it out with a quick movement. The cricket stopped in front of the entrance and did not leave until the female *Megachile* attacked it several times. On attacking the large cricket, the female *Megachile* did not use her sting—she attacked only with the mandibles.

Mating

Males of *Megachile frontalis* were frequently seen on grass stems next to entrance holes as though waiting for females returning to or leaving the nests. Males usually attacked any female leaving the nest. On several occasions three or four males were seen to attack a single female. Sometimes they pushed the female down to the ground and one of the males copulated with the female on the ground. Several matings were watched and copulation was estimated to last 20 to 25 seconds. While they copulated, several other males were seen hovering around the mating pair. On one occasion Szent-Ivany put a cyanide killing bottle over a copulating pair and left it there until both were dead. As soon as the killing bottle was lifted and the

PLATE 2.



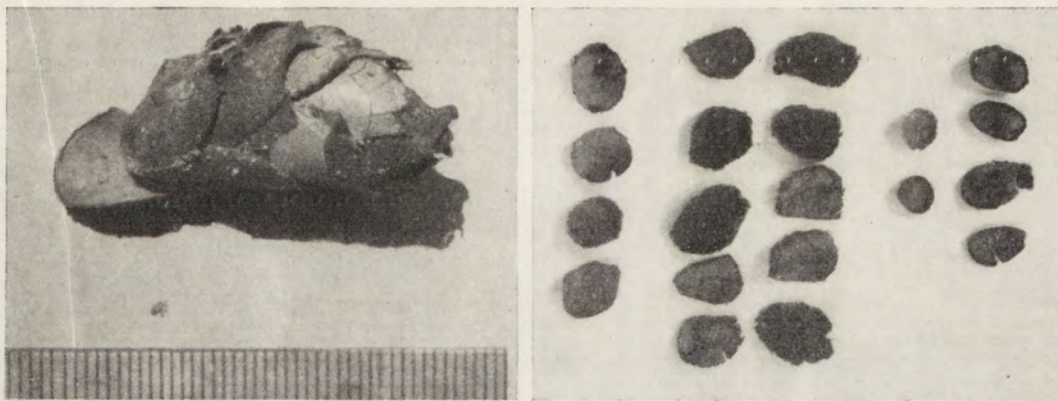


PLATE 3.

dead male was removed from the ground, another male lit on the back of the dead female and tried to copulate, while two other males were hovering above.

Nest Structure

Burrows examined ranged from 40 to 150 mm. deep. In soft moist soil at Kerema none (except those being constructed) was under 100 mm. in depth. The shallowest burrows studied were in hard, dry soil at Port Moresby. In diameter, burrows ranged from 14 to 16 mm., often irregularly larger near the entrances, perhaps due to washing by the heavy rains.

Burrows were sometimes simple, although deeper ones were often branched. From relative ages of larvae, it seems that each bee (at Kerema) makes a rather deep burrow, fills the inner portion with two to four cells end to end in a series, then often makes one or two short side branches starting at the cap of the last cell and sometimes bending back toward the entrance of the burrow. Each side branch is filled with one or two cells. The existence of short burrows (Port Moresby), deep enough for only one or two cells, indicates that a bee may make more than one nest during her life.

In a bank, burrows may be horizontal, but often slant downward. In flat ground, they always slant down; they are not vertical.

Cells

The cells are found in horizontal or slanting positions. In outside dimensions they are 23 to 32 mm. long, 12 to 16 mm. wide (Plate 3). The outer layer of leaves usually consists of 11 to 16 thick pieces, rather irregularly shaped,

each 13 to 16 mm. long by 11 to 13 mm. wide. The piece at the bottom of the cell, presumably the first put in place, is nearly round. Inside the outer layer of leaves is a layer, 0.5 to 1.5 mm. thick, of fine mud, well-smoothed on the inside. Female bees, presumably collecting mud, have been seen beside muddy puddles at Goroka. Inside the mud is a thin layer of leaves which must be soft and pliable when put in place, for each is neatly concave in inner aspect. There are about four elongate pieces (11 to 15 mm. long, 7 to 9 mm. wide) forming the side walls of this inner layer and a single round piece, bowl-shaped, about 7 mm. in diameter, forming the bottom of the inner layer. The inside dimensions of the cell are 13 to 16 mm. in length, 8 to 10 mm. in width.

The provisions consist of firm, rather dry, pollen, filling the bottom 5 to 6 mm. of the cell. The egg (Plate 4 and Fig. IV) is placed on top of the provisions. One end is inserted at the edge of the food mass, while the other extends beyond the middle of the surface of the provisions but does not touch it.

The cap of the cell consists of one or two inner, irregularly round leaf fragments about 9 mm. in diameter. They may be, but are not always, of thin, soft material like the inner layer of the cell. Outside of this is a layer (1 to 2 mm. thick) of masticated leaf material, followed by two or three more round leaf pieces, 9 to 10 mm. in diameter. Outside this is a thin layer of mud or mud mixed with masticated leaf material. A sectional view of a cell and its cap is shown in Fig. IV.



FIG. IV.

If the cells are in series, the base of the next cell rests against this mud layer, which is concave externally to fit the convex base of the cell. The cells are all similarly shaped, the first not more convex at its base than the others.

When the larva reaches maturity it covers the inner walls of the cell, except for a small space in the center of the cap, with a layer of yellowish faeces one fourth to one half of a millimeter thick. No evidence was noted of faeces being deposited before the larva reached maturity, as in other *Megachile*, but further observations should be made on this point. The cocoon is very thin, whitish, one layer thick, made of fine, white fibres with an amorphous substance filling the spaces between them. In texture, the cocoon is soft, delicate, flexible. Often there is a small hole in it at the anterior end, and the inner leaf of the cap may be chewed at this point. The tendency for the mature larva to chew the centre of the cap has also been noted in *Megachile brevis* Cresson (see Michener, 1953).

Associates

Females of *Coelioxys intrudens* Smith (det. G. E. Nixon) were found about *Megachile frontalis* nests at Kūminibus, Kulābū, and Wēwāk, all in the Sepik District, and at the former village a *Coelioxys* was seen to enter a *Megachile* nest, in which she remained for two minutes.

At Kerema, two adult females of *Milto-gramma species* near *fasciata* Meigen (det. F. G. Fennah) were found about the nest openings, and in some old cells some puparia, possibly of the same fly, were found. These sarcophagids probably feed on the food stored in the cells of the *Megachile*. Adults and puparia of a presumably different species of *Milto-gramma* were found in similar situations at several localities in the Sepik District.

In the latter area adults of *Plagiostenoptera aenea* (Wiedemann), a dipteran of the family *Platystomatidae*, were also found around the nests.

A mutillid, *Timulla (Trogaspidia) fervida* Smith, was found crawling in and out of nests at the Catalina Estate.

On many of the bees, especially on the propodeum and base of the abdomen, were numerous hypopi of a glyciphagid mite, probably belonging to the genus *Chaetodactylus* (det. J. H. Camin).

SUMMARY AND CONCLUSIONS

Megachile frontalis (Fabricius) is a common species in the Territory of Papua and New Guinea, as it is in most of the rest of the eastern half of the Eastern Archipelago. It is active throughout the year, visits a wide variety of flowers, apparently preferring legumes as pollen sources, and cuts leaves of many species of plants for nesting material. It is sometimes a significant pest because of destruction of leaves of *Eucalyptus* and other plants. It is a parallel-sided species. Most such species do not cut leaves.

Noteworthy features of the behaviour of *M. frontalis*, by which it differs from most other species of *Megachile* whose biology is known to us, are enumerated below:

1. It constructs its own burrows in the soil, often in aggregations. Most megachilids, and particularly species of *Megachile*, make use of pre-existing cavities or construct cells in the open. It is interesting that one other megachilid that digs its own burrows, the European *Anthocopa cristata* (Fonscolombe), also carries the excavated soil away from the nest in pellets (Ferton, 1893). This contrasts with most burrowing bees, which leave the



PLATE 4.

excavated soil near the nest entrance. Other species of *Megachile* are known which usually dig their own burrows [e.g., *octosignata* Nylander (Ferton, 1909), and *circumcincta* Kirby (Ferton 1908)].

2. The cells consist of two layers of leaves separated by mud. Some other, quite unrelated species also use mud between layers of leaves or petals [e.g., *M. azteca* Cresson (Friese, 1924)].

3. Round pieces of leaves are used at the bases of the cells as well as in the caps. Chewed leaf material is also used in the cap, together with mud. The use of chewed leaf material or vegetable paste is very common in species of other megachilid genera (e.g., *Hoplitis*) and some *Megachile* use such paste in conjunction with pieces of leaves [e.g., *M. sericans* Fonscolombe (Ferton, 1901)].

4. The cocoon is thin and delicate, without coarse fibres in the anterior end, and is surrounded almost completely by a thin layer of faecal material.

5. Mating occurs, at least part of the time, not on flowers but near the nests.

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EXPLANATION OF FIGURES

Fig. I. Map showing the range of *Megachile frontalis* (prepared by Mrs. M. L. Szent-Ivany).

Fig. II. Map showing the range localities where *Megachile frontalis* has been found in the Territory of Papua and New Guinea (prepared by Mrs. M. L. Szent-Ivany).

Plate 1. Leaves cut by *Megachile frontalis*. Top left, injury to climbing rose (*Rosa*) in garden near Wau; top centre, injury to *Cassia fistula* in garden, Port Moresby; top right, injury to coffee (*Coffea arabica*) in plantation near Goroka; lower left and lower right, injury to *Eucalyptus deglupta*, Goroka; lower centre, injury to guava (*Psidium guajava*), Doa Plantation, Central District of Papua.

Fig. III. Diagram of nesting site of *Megachile frontalis* and *Bembix* sp. near Kulabu village, Maprik subdistrict, New Guinea.

Plate 2. Nesting sites of *Megachile frontalis* in the Maprik subdistrict, New Guinea. Upper left, typical village showing flat, trampled ground in which many *Megachile* nest; upper right, nest holes in village square shown at left; lower left and right, roadside banks near Kulabu and Kuminibus villages showing many nest entrances.

Plate 3. Left, a cell of *Megachile frontalis* removed from the soil. The scale at the bottom is in millimetres. Right, leaf fragments from cells of the same species, showing, from left to right a, the lowermost

(rounded) fragment from four cells; *b*, ten of the irregularly-shaped fragments from the outer layer; *c*, the round pieces forming the bottom of the inner lining of two cells; and *d*, four of the elongate pieces forming inner linings. Two of the last were unavoidably torn in separating them for photography.

Plate 4. *Megachile frontalis*. *Left*, larva in process of pupating, small prepupa, large mature larva, small larva, and egg; *centre*, pupae, males above and

below, female in middle; *right*, adults, male above, female below.

Fig. IV. Diagrammatic sectional view of a cell of *Megachile frontalis*, with base of next cell in the series above it. Heavy lines represent thick leaves, light lines, thin pliable leaves. The dotted area represents the food stores on top of which is the egg; areas shaded with slanting lines represent mud; the cross-hatched area represents masticated leaf material.