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Biology, Immature Stages, and Phylogenetic Relationships of Fideliine Bees, with the Description of a New Species of *Neofidelia* (Hymenoptera, Apoidea)

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INTRODUCTION

The family Fideliidae contains but three genera, *Fidelia* and *Parafidelia* from the xeric regions of southern Africa and *Neofidelia* from the southern part of the Atacama Desert in Chile. Hoping to obtain new information on the phylogeny and systematic placement of fideliine bees, I undertook two field trips, one to the Republic of South Africa and to South-West Africa in 1968 and the other to Chile in 1969. The results of these trips, presented here, represent the first account of the life history, larva, and pupa of fideliine bees. The description of a new *Neofidelia*, the second species for the genus, is appended.

The taxonomic and phylogenetic relationships of these bees with other bees have been enigmatic ever since the group was discovered. Friese (1899), the first person to describe a fideliine, named the genus *Fidelia* and placed the bee near the *Eucera-Anthophora* complex because of its long tongue and long scopa-like hairs on the hind legs. At the same

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time, Friese recognized that its abdominal scopa and male terminalia were similar to those of megachilids. Brauns (1926), describing the second genus, *Parafidelia*, reiterated Friese's concept of the relationship of the fideliines to the Anthophoridae. Shortly thereafter, Cockerell (1932) elevated the group to family status because of the abdominal scopa, the three submarginal cells, and the male armature, which was like that of *Anthidium* (Megachilidae); he regarded it as "an offshoot from the ancient stem from which the Anthidiinae were derived." Popov (1939) maintained the group as a distinct family and pointed out that the seventh metasomal sternum was surprisingly similar to that of lower bees (the Colletidae, Diphaglossidae, and Panurgidae, *sensu* Popov). He concluded, therefore, that the group was "a highly specialized oligotropic family of bees closely approaching the family Colletidae" and argued that the characteristics it shared with the higher bees were an "example of independent convergent development." Michener (1944), re-evaluating Popov's evidence, concluded that the many similarities between the Fideliidae and the higher bees (the Apidae, *sensu* Michener, 1944) were "more than mere convergence" and placed the group as a subfamily of the Apidae, which he interpreted broadly to include also the Apinae, Anthophorinae, and Xylocopinae. However, when Moure and Michener (1955) described the third genus, *Neofidelia*, they pointed out that, in addition to the unusual characteristics mentioned by previous authors, the fideliines lacked basitibial plates and possessed a long labrum, both suggestive of the Megachilidae. Unlike the megachilids, however, these bees had three submarginal cells and a preepisternal suture above the distinct scrobal suture. Furthermore, in contrast to all of the "higher" bees, the fideliines had horizontal volsellae with cuspides and digiti. Moure and Michener concluded that the fideliines were "as different from the Apidae as are the Megachilidae" and that they had certain features more primitive than those in any of the Apidae or Megachilidae. "If the latter [Megachilidae] is to have the status of a family, the Fideliidae must also." In summary, the difficulty in determining the relationships of the Fideliidae rests in their possessing an incongruous mixture both of seemingly primitive and specialized characters and of characteristics that are intermediate between those of other families of bees.

I would like to express my appreciation to Mr. Edwin Martinez, Department of Living Invertebrates, the American Museum of Natural History, for his excellent assistance during the field studies in Africa. The Chilean trip was possible because of the help of Mr. Luis E. Peña G., the eminent Chilean naturalist who served as guide and

companion. The following people permitted me to examine collections in their charge and aided me during my stay in southern Africa: Dr. A. J. Hesse, South African Museum, Cape Town; Mr. C. G. Coetzee, State Museum, Windhoek, South-West Africa; Dr. C. Jacot-Guillarmod, Albany Museum, Grahamstown, Republic of South Africa; and Dr. L. Vári, Transvaal Museum, Pretoria, Republic of South Africa. A number of people assisted me in a similar fashion in South America: Dr. Luciano Campos, Universidad de Chile, Santiago; Miss Fresia Rojas A., Museum Nacional de Historia Natural, Santiago, Chile; Mr. Haroldo Toro, Universidad Católica, Valparaíso, Chile; and Mr. Rodolfo Wagenknecht Huss, La Serena, Coquimbo, Chile. The Compton Herbarium Kirstenbosch, Cape Province, Republic of South Africa, kindly provided identifications of the African pollen plants.

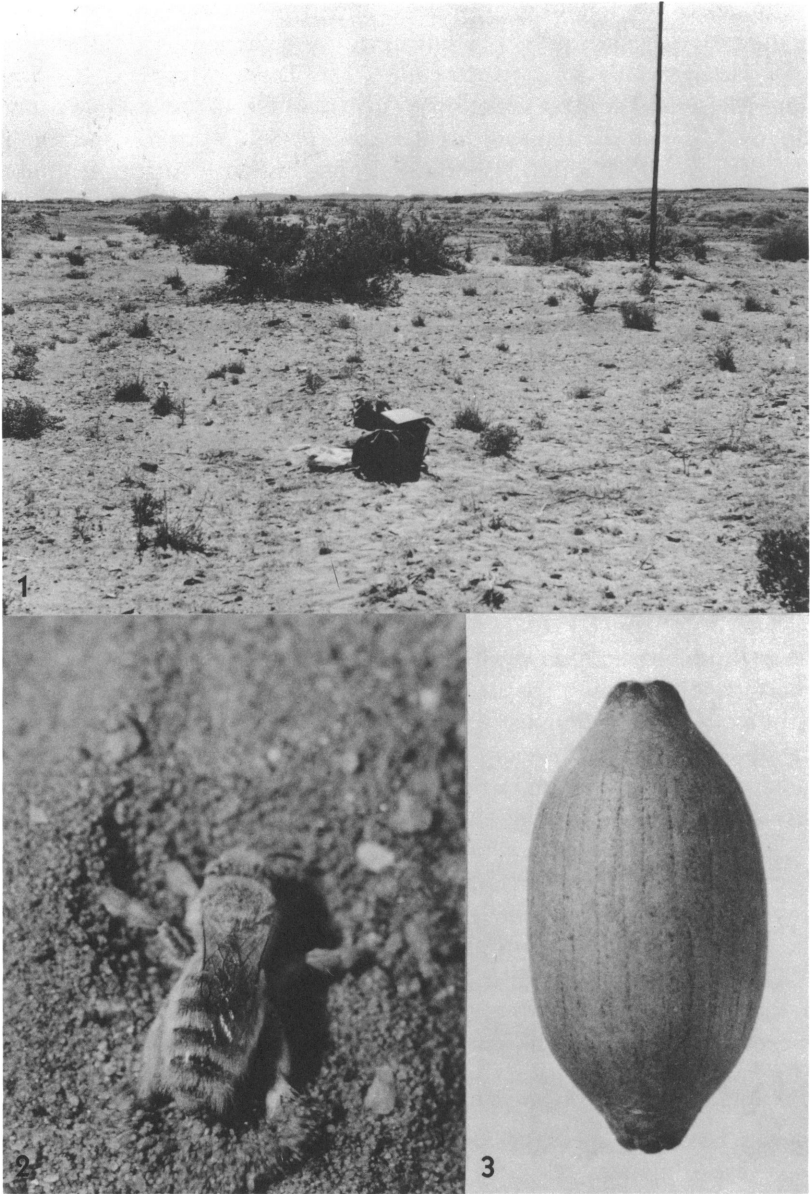
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FIDELIA

BIOLOGY

DESCRIPTION OF NESTING SITE: An extensive nesting area of *Fidelia villosa* Brauns was found by Edwin Martinez on October 30, 1968, in a desert region 30 miles southeast of Keetmanshoop, South-West Africa, with scattered xerophilous vegetation. The site (fig. 1) was approximately 75 meters from a dry sandy wash lined with trees and shrubs, and the nests were situated in an open, undisturbed, essentially flat area, not in danger of flooding in heavy rains, and not subject to wind erosion. The nesting area, more than 30 meters in diameter, was about 10 meters from a low sand dune. Scattered bushes and small clumps of grass grew on and near the site, but the ground was primarily bare; almost none of the nest entrances was shaded.

The pollen plant of both *F. villosa* and *paradoxa* Friese, which occurred in the same area, was *Mesembryanthemum*, possibly *fenchelii* (Aizoaceae). It grew sporadically adjacent to the site and was abundant over a broad area for hundreds of meters along the dry wash. A species of the bee *Capicola* (Melittidae) commonly gathered pollen from the same flowers, but other species of bees infrequently visited the plants. *Fidelia villosa* was observed collecting pollen at other localities from additional species of *Mesembryanthemum*-like plants. *Fidelia paradoxa* visited another species of *Mesembryanthemum* 12 miles west of Steinkopf, Cape Province. *Fidelia kobrowi* Brauns obtained its provisions from *Ruschia grisea*, a relative of *Mesembryanthemum*, near Steytlerville, Cape Province. The



FIGS. 1-3. *Fidelia villosa* Brauns. 1. Nesting site. 2. Female, just emerged from burrow entrance (hidden by front part of body), starts to flip sand with hind legs. 3. Cocoon.

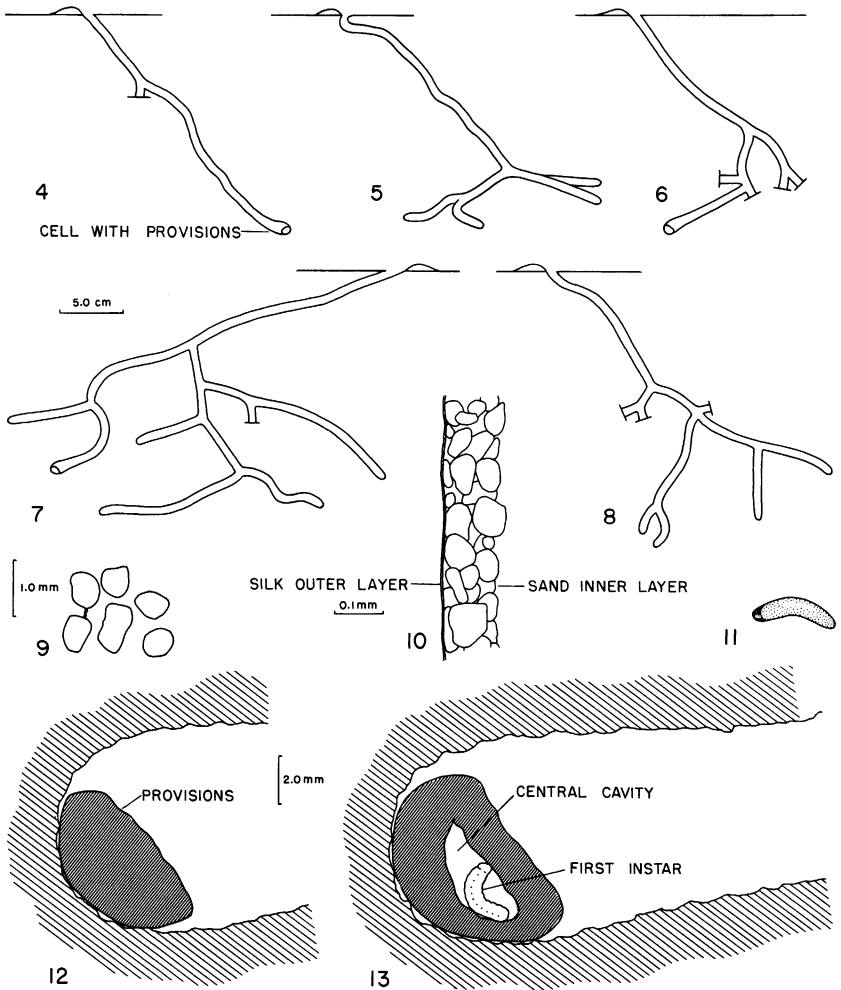
South African *Parafidelia* collects pollen from *Campanula* (Campanulaceae) according to Popov (1939). Moure and Michener (1955) reported the Chilean *Neofidelia profuga* from *Encelia tomentosa* and *oblongifolia* (Compositae) and from *Calandrinia* (Portulacaceae), and I also found males looking for females on *Encelia oblongifolia*. *Neofidelia longirostris* gathers pollen from *Alona rostrata* (Nolanaceae).

This site, restricted to *F. villosa*, was the only one discovered during two days of searching. Because this species was abundant, other sites may have existed. We did not find the nesting area of *F. paradoxa*, which was also abundant. The surface soil was loose in some places but crusty in others. In all excavations, the soil below the surface was a compact, moderately fine sand, with few small pebbles and no signs of moisture even below the cell level.

NESTING: Nests, some only 10 cm. apart, were grouped into loose, irregular aggregations. Approximately 25 to 30 nests were excavated from various parts of the site. All the main burrows (figs. 4-8) entered the ground at an angle of about 20 to 30 degrees from the horizontal, regardless of the compactness of surface soil. Most entrances appeared as small craters at one edge of dry, loose, sandy tumuli, which blew away within a few days. The majority of openings occurred on the flat or slightly sloping, barren ground and were not usually situated next to surface stones or debris. Some, however, penetrated vertical edges of hoof prints or of mammalian burrows. All entrances were plugged with loose sand. When females were away from the nests, entrance tunnels were visible for a few millimeters, but upon digging into the plugs, pollen-laden females immediately pushed up sand and obscured the tunnels.

In all cases the main tunnel, filled with loose sand, circular in cross section, and about 6.5 mm. in diameter, descended at a low angle and curved (figs. 4-8). Some bifurcated at a depth of 7 cm., but others did not until they reached a depth of 15 cm. In most cases each branch divided again and some of the secondary branches also ramified. In some places, meandering tunnels and branches were nearly horizontal, whereas in others they descended nearly vertically.

In spite of many branches, only one provisioned or partly provisioned cell was found to a nest. Multiple-celled nests may not occur, for occasional nests with more than one cell would probably have been encountered, even though it was early in the nesting season. Even in nests in which the cell was only partly provisioned, numerous branches often were found, a fact indicating that the ramified pattern of the nest is established before cell provisioning. In some cases dead-end



FIGS. 4-13. *Fidelia villosa* Brauns. 4-8. Diagrammatic representation of five nests. 9. Fecal pellets of larva. 10. Cross section of cocoon wall. 11. Egg, lateral view. 12. End of cell showing provisions before construction of central cavity. 13. Cell with completed provisions showing in cross section position of central cavity and feeding first instar. Scales refer to figures 4-8, 9, 10, and 11-13, respectively.

branches were short, only 1 cm. long, but in other cases they were as long as those leading to the cells. The ends of dead-end branches were either the same diameter as the branch or in some instances somewhat

expanded. All the tunnels were unlined and had a rough texture.

The cells (figs. 12, 13), with walls that were completely unlined, unimpregnated, and not specially worked (allotichal walls of Malyshev, 1935), were mere slight expansions of the nearly horizontal ends of the branches. Their surface was rough and, like that of the tunnels, non-waterproof. Several cells measured 7.0 to 8.5 mm. in maximum diameter. The rear ends of the cells were slightly lower than the front. Cell length could not be determined because there was no demarcation between tunnel and cell. As I used an aspirator to blow away sand filling the tunnels, sand was possibly forced into cells before I uncovered them. Hence provisional cells may or may not have been filled with sand by the bee. If a special closure existed, it was dry and unconsolidated, for it was always blown away during excavation.

PROVISIONING: Females transported dry pollen to the nest. The pollen, which was very fine (greatest diameter 50 microns), was carried primarily on the under side of the abdomen by the long non-plumose, scopal hairs. Scattered pollen grains clung to the fore, middle, and hind tarsi, to the basal parts of the midlegs and hind legs, and to much of the body which was covered with long, pale hairs. Although apidologists formerly believed that the flattened hind tarsus and its very long hairs is a specialized scopa in *Fidelia* and *Parafidelia*, the amount of pollen it carries is, for example, no greater than that found on the mid-tarsus. The broad basitarsus and elongate hairs on the upper and lower surfaces form a paddle that the females of *Fidelia* and, almost certainly, *Parafidelia*, use to flip sand from the nest entrances. In contrast, the hind basitarsi of both species of *Neofidelia*, although long, are exceedingly slender, being of the same diameter as the other tarsomeres. The dorsal surface of the basitarsus is flat, smooth, and hairless. Two rows of long, semierect hairs extend along the sides of the flattened surface and thereby form a trough. A clump of long, curved hairs arising from the dorsal apex of the femur extends over this trough. Although the function of this special structure is unknown, pollen is not transported on the hind basitarsi.

The female deposits the pollen at the rear on the cell floor after she mixes it with a liquid, presumably nectar. The mealy moist load is shaped into a somewhat irregular, grayish yellow disk. I found, on examining series of cells, that subsequent loads of pollen were added to the first to enlarge it until the provisions became a solid, roughly hemispherical form, with the flattened surface facing obliquely upward (fig. 12). The female then constructs a central hollow cavity (fig. 13) in the pollen mass, in which she deposits a single egg. The female probably

uses the hairless, yellow, metasomal tergum VI to form this cavity, as mealy moist pollen often adheres to the tips of the metasomas of females of *F. villosa*, *kobrowi*, and *paradoxa* that were collected on the flowers. The central cavity of all pollen masses containing immatures was completely sealed, so that in appearance the masses were roughly hemispherical, larger than, but otherwise similar to, the solid mass before the cavity was constructed. How the cavity was sealed after egg deposition is unknown. The grayish yellow provisions were uniformly mealy moist, slightly sweet to the taste, and essentially identical in four cases. The outer surfaces were somewhat irregular and rough, as was the surface of the central cavity. The pollen-nectar mass fitted loosely in the rear of the cell, as indicated in figure 13.

DEVELOPMENT: A single egg (fig. 11), 3.25 mm. long, was found in the lumen of the provisions. The egg was smooth, shiny, semitransparent, and whitish; the anterior end was somewhat more blunt than the posterior end. As the embryo developed, a large, clear area formed at the anterior end of the egg and contrasted with the semiopaque, white, embryonic tissues. When the amniotic fluid was absorbed, the tracheae filled with air, but the larva died before it could emerge. Two first instars were also uncovered. One was oriented, as in figure 13, whereas the other seemed to be feeding on the lower curved surface of the lumen rather than on the flat upper surface. Each apparently had its rear dorsal surface attached to the pollen mass, as the rest of the body looped (as illustrated) freely in the cavity. Each larva moved the entire anterior part of its body from the point of attachment to the provisions, so that the head could be maneuvered readily from one place to another over a broad feeding surface. Although one larva died in the second stage, the other developed quickly as it rapidly consumed the inner surface of the pollen-nectar mass. Found as an early first instar on November 1, it molted that evening and remained a second instar until November 3; by November 7 it was a last (presumably fourth) instar, although approximately half of the provisions was unconsumed. Unfortunately, by that time, the pollen mass had broken apart and the larva became partly dislodged from the cavity so that afterward the larva may have had difficulty in finding food. I believe, on the basis of these fragmentary observations, that the first three instars of this species probably feed inside the pollen mass and only the fourth leaves the mass, which by that time has become thin walled.

On November 8, just one day after reaching the last instar and while provisions remained, the larva began voiding spherical to elongate

fecal pellets (fig. 9). Unlike the moist, grayish yellow provisions, the feces were exceedingly dry and bright pale yellow. A pellet broken with forceps consisted of dry pollen grains. On about November 14, the very active larva finished feeding (although it took some pollen offered it from another cell) and within three or four days started to spin silk through its salivary opening.

The larva first encased its fecal material in a roughly spherical cocoon of soft, loose threads of brownish silk. The presence of a fecal cocoon was probably atypical, for during the spinning period, the larva was being transported in a plastic dish, first by automobile and later by airplane. Furthermore, the larva never constructed a complete cocoon such as those uncovered at the nesting site; its cocoon was only partly finished. At the end of the cocoon-spinning period, it produced, presumably through the anus, a moderate quantity of shiny black material that solidified as hard, irregular masses on the partly constructed cocoon. The larva died December 1.

Although all the nests seemed to be in the early stages of construction, three cocoons (two of which were partly damaged) were recovered from one excavation. The cocoons looked like hard tan nuts, were nipped at both ends, and were dark brown (fig. 3). The undamaged cocoon measured 12.5 mm. long and 6.3 mm. in maximum diameter. The cocoon wall was composed of two layers (fig. 10). The outer layer was a very thin, opaque, brown parchment-like silk that adhered closely to the much thicker inner layer. The inner layer, slightly more than 0.1 mm. thick and waterproof, consisted of very fine sand cemented by a dark brown, water insoluble glistening material. The inner surface of this brittle layer was even, formed a continuous curve, and provided the cocoon with its distinctive hardness. The two layers were glued only at the nipped ends and along numerous lines that extended between the ends. Where the parchment was glued along these lines, it was more closely appressed to the inner layer than it was between the lines; hence the glued lines formed faint elongate grooves on the outer surface of the cocoon. Because the adhesive soaked through the parchment-like outer layer, the bottom of the grooves appeared as dark stripes. No fecal material was deposited within the cocoons.

From the information on hand, the process of cocoon spinning can be interpreted to some extent. After defecating, the larva apparently ingests sand that will later comprise the inner layer of the cocoon, for the sand of the inner layer was distinctly more even grained than that of the substrate, and the particle size was much smaller than the average particle size of the substrate; hence the grains had obviously

been selected by the larva. One of the larvae taken from a cocoon still contained sand grains in its esophagus. The reared larva, although deprived of sand, spent considerable time searching about with its head after consuming the food; it presumably was attempting to find sand. The outer parchment-like layer is then spun. Once that layer is complete, the larva voids through the anus the mixture of fine sand and the dark shiny material which must serve as cement. The dark stripes on the cocoon are the first discharge, apparently containing little or no sand. This material is probably the same as the shiny black material deposited by the reared larva on its aborted cocoon. Many bee larvae, as they defecate, apply the feces on the cell wall of the cocoon as stripes that run parallel to the length of the cell; consequently the regularity of the stripes on the *Fidelia* cocoon is not exceptional.

Larvae of some sphecid wasps, for example certain species of *Trypoxylon*, produce a cocoon, the inner layer of which seems identical in texture and thickness to the inner layer of the *Fidelia* cocoon. The appearance of the inner layer of the wasp cocoon suggests the possibility that the wasp larva ingests sand just as does *Fidelia*. The outer layer of a cocoon of *T. archboldi* Krombein in the American Museum of Natural History collection consists of a loose, fluffy layer of sparse strands of silk that is quite unlike the parchment-like surface of the *Fidelia* cocoon. This wasp cocoon is rounded at both ends and some, if not all, of the feces are deposited inside it. This last point signifies that, even if the sand grains pass through the intestinal tract, they somehow do so before defecation and therefore that the processes of cocoon construction with sand on the part of *Trypoxylon* and *Fidelia* probably are not homologous.

Each cocoon of *Fidelia* contained a mature postdefecating larva. One moved around actively at first. It was also able to snap its body so as to make the cocoon jump with a clicking sound, much as does a Mexican jumping bean. The snapping may have been caused by the larva pressing its head against its posterior end (or vice versa) and then, as it straightened its body, forcibly striking the inner wall of the cocoon with the head (or the posterior end). The purpose of the snapping is unknown; because it took place only at first, it may have pertained to cocoon construction, perhaps to shaping and consolidating the inner layer. The larva that was reared from the first instar did not snap, however.

One of the larvae encased in the cocoon pupated May 8, 1969 and developed quickly, so that when it was preserved on May 23, the adult was nearly ready to emerge. The pupal period of another individual

was of approximately the same duration.

WATER CONSERVATION: Most bees apply a cell lining of wax, silklike material, or special materials (such as leaves or mud) brought into the nest. These linings in most cases are believed to have an important function in regulating the amount of moisture in the cell. Too much moisture can cause liquefaction of the food and too little moisture obviously leads to death of the egg or larva. *Fidelia* is unusual among bees in that it provides no cell lining of any sort. Furthermore, unlike those of most bees, the cells of *Fidelia* at 30 miles southeast of Keetmanshoop were constructed in soil with no visible signs of moisture. Because of the extreme aridity of the region, which lies between the Namib Desert on the west and the Kalahari on the east, too much moisture in the cells is an unlikely occurrence. For that matter, the distribution of all three genera of fideiines is restricted to desert parts of the world, and we can conclude therefore that liquefaction of the provisions is not a serious problem in the survival of any species, even if none of them is found to line their cells.

On the other hand, desiccation seems to be a threat. Some of the ethological and anatomical peculiarities of *Fidelia* are attributes that reduce the danger of desiccation. First, the larva is supplied with body setae which possibly cushion the waterproof epicuticle of the last instar from the abrasive cell wall and cocoon wall. Second, the egg and apparently the first three larval instars are enveloped on all sides by moist provisions, and the early instars feed within the provisions; the early stages therefore are assured a high relative humidity. As is the case with most bees, the larva consumes provisions quickly so that they have little time to dry. The fact that feces are discharged as unusually dry pellets indicates that the hind gut is especially capable of re-absorbing water. Lastly, the larva diapauses within the waterproof protection of its cocoon.

ADULT ACTIVITY: No instances of mating were observed. Males were not seen at the extensive nesting site, whereas they were moderately abundant flying swiftly from flower to flower and from bush to bush of the pollen plant. Mating may, however, take place on the flowers of the pollen plants.

Most daily activity of the adults started with the opening of flowers, which occurred between 2 P.M. and 3 P.M. However, scattered females, presumably searching for nest locations, flew over the nesting site in the morning, well before the time the flowers opened. The height of activity, both on the flowers and over the nesting site, took place from about 3 P.M. to 5 P.M. Although males and females were no longer

visible on the wide-open flowers at 6:45 P.M. one evening, a few females were still at the nesting site at that time.

Several features of the activity of females at the nesting site were of special interest. When a female disposed of sand at the opening of a burrow, she emerged, metasoma first, from the nest and shoved the sand under her body with the front legs, then snapped her hind legs forward (fig. 2), thus flinging the sand a considerable distance. As pointed out above, the dorsoventrally broadened basitarsus, with long hairs giving it an even wider surface, serves as an effective paddle for flipping the sand. The sand at the lower end of the tunnel may be loosened by the expanded bifurcate apexes of the mandibles. The females, on returning pollen-laden to their nests, invariably flew back and forth over the entrances many times, as if they had difficulty identifying their nests. In many cases the female alighted, then took off almost immediately before landing again and digging into the entrance plug. The characteristics of the nest entrances change quickly in the open windy area, but the delay, compared with nest findings by other kinds of bees, seemed unusually long.

Females slept in their burrows or, if they had no nests, apparently in any available tunnel. On one day hundreds of females were observed in the late afternoon (about 5 P.M.), searching for places to spend the night in the vicinity of the nesting area. Males, however, did not look for "sleeping" burrows in the sandy nesting area, and none was found sleeping in closed flowers. Males of this species emerged from loose sand in the late morning at Clanwilliam, Cape Province, Republic of South Africa, and, in one case, three males emerged from the same spot. At Vanrhynsdorp, Cape Province, males of *Fidelia paradoxa* looked for places to burrow into the flat sandy ground late in the afternoon.

Where the pollen plants were abundant, many females flew up almost simultaneously toward me as I walked through the plants; they made no attempt to sting or to strike. When held with fingers, females attempted to sting but their stinger was always too weak to penetrate. In a number of cases a male, picked up with thumb and forefinger, was able to pinch, although not painfully, by curving its metasoma around the finger and suddenly constricting the segments. The apical processes of metasomal tergum VII are well developed in this group of bees and apparently make the pinch more effective. Males of *Hoplitis anthodemnion* Michener from 3 miles south of Avontuur, Cape Province, pinched in a similar manner. Males of other megachilids may behave in the same way, because so many of them have dentate processes on their metasoma.

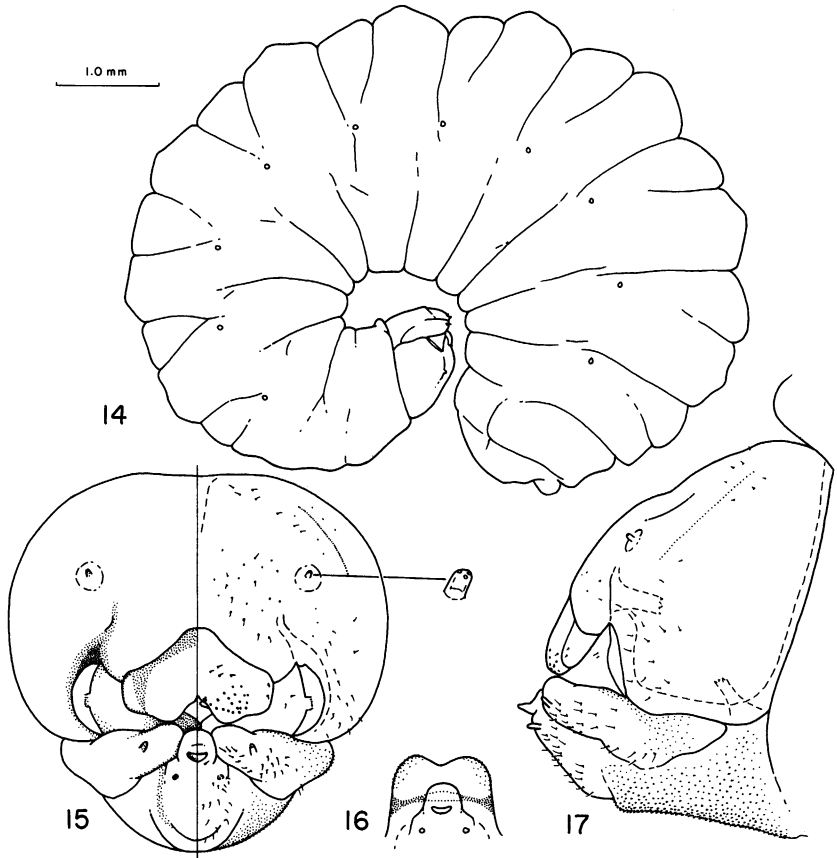
PARASITISM: No parasitic bees were associated with the nesting site. Meloid triungulins were encountered in many partly provisioned cells, and one egg (or first instar) of *Fidelia villosa* had been killed by a triungulin which subsequently molted before being discovered. Mites were also common in the cells although none was found attacking immature bees.

MATURE LARVA

Figures 14-23

HEAD (FIGS. 15, 17): Integument with numerous scattered setae; epipharynx, hypopharynx, dorsal surface and much of basal part of maxilla, and postmentum spiculate; pigmentation as indicated in figure 15. Tentorium complete and well developed; posterior pits in normal position; posterior thickening of head capsule, hypostomal ridge, and pleurostomal ridge well developed; epistomal ridge well developed below anterior tentorial pits but absent mesiad of them; longitudinal thickening of head capsule evident dorsally; parietal bands weak. Antennal papilla small but well developed, somewhat longer than diameter; each papilla not arising from basal prominence and bearing approximately three sensilla. Labrum without tubercles but deeply emarginate medially. Mandible (figs. 18-20) moderately massive and apically bidentate, with ventral tooth longer than dorsal one; obliquely transverse base of smooth apical concavity with several small teeth but apical margins not serrate. Labiomaxillary region strongly produced. Maxilla elongate, with apex bent mesiad so that palpus subapical in position; cardo and stipes somewhat sclerotic; palpus more than twice as long as diameter; galea not evident. Labium divided into prementum and postmentum and bearing salivary opening at apex; salivary opening a moderately narrow transverse slit with strongly projecting lips; palpus slightly longer than maxillary palpus. Hypopharynx (fig. 16) large and bilobed.

BODY: Form (figs. 14, 22) moderately robust with the posterior part somewhat more robust than anterior part; most body segments divided dorsally into low cephalic annulet and elevated caudal annulet; caudal annulets low medially so that larva appears to have low paired transverse tubercles on these annulets; middorsal tubercles absent; lateral tubercles (below spiracles) not pronounced. Integument of quiescent form soft; integument densely spiculate over almost all of body surface and with scattered setae (not shown in figures), which are not restricted to caudal or cephalic annulets. Spiracles (fig. 21) moderately small; atrium projecting above body wall, spinose; peritreme narrow, concave; primary tracheal opening without collar but guarded by rosette



FIGS. 14-17. *Fidelia villosa* Brauns. Mature larva. 14. Live postdefecating larva, lateral view, taken from cocoon. 15. Head, frontal view, left side showing distribution of sensilla, setae, and spicules, right side showing pattern of pigmentation. 16. Hypopharynx and anterior part of labium, frontal view. 17. Head, lateral view, showing sensilla, setae, and spicules. Scale refers to figure 14.

of long simple spines; subatrium moderately short, indistinctly annulate. Tenth abdominal segment short, with dorsal portion elevated; anus dorsal, with numerous sensilla in area immediately below it. Imaginal disc of male genitalia (fig. 23) a small median contiguous pair accompanied by cuticular invagination.

MATERIAL STUDIED: Three postdefecating, quiescent larvae taken from cocoons, 30 miles southeast of Keetmanshoop, South-West Africa,

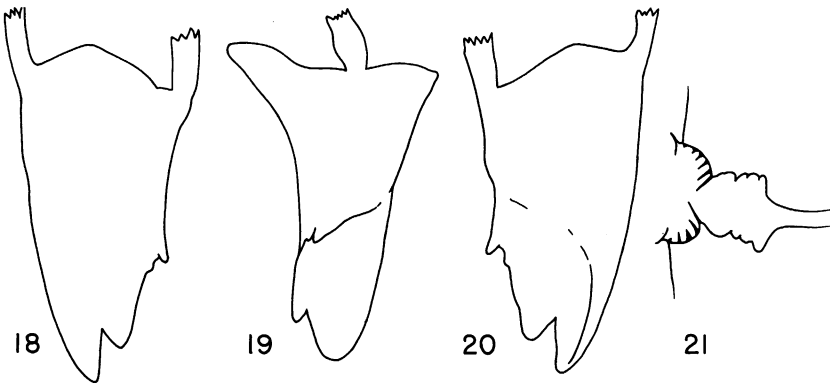
October 31, 1968 (J. G. Rozen and E. Martinez); one postdefecating larva, same data except larva reared from first stage and was not able to spin normal cocoon in rearing dish; died December 1, 1968.

FIRST INSTAR

Figures 24-27

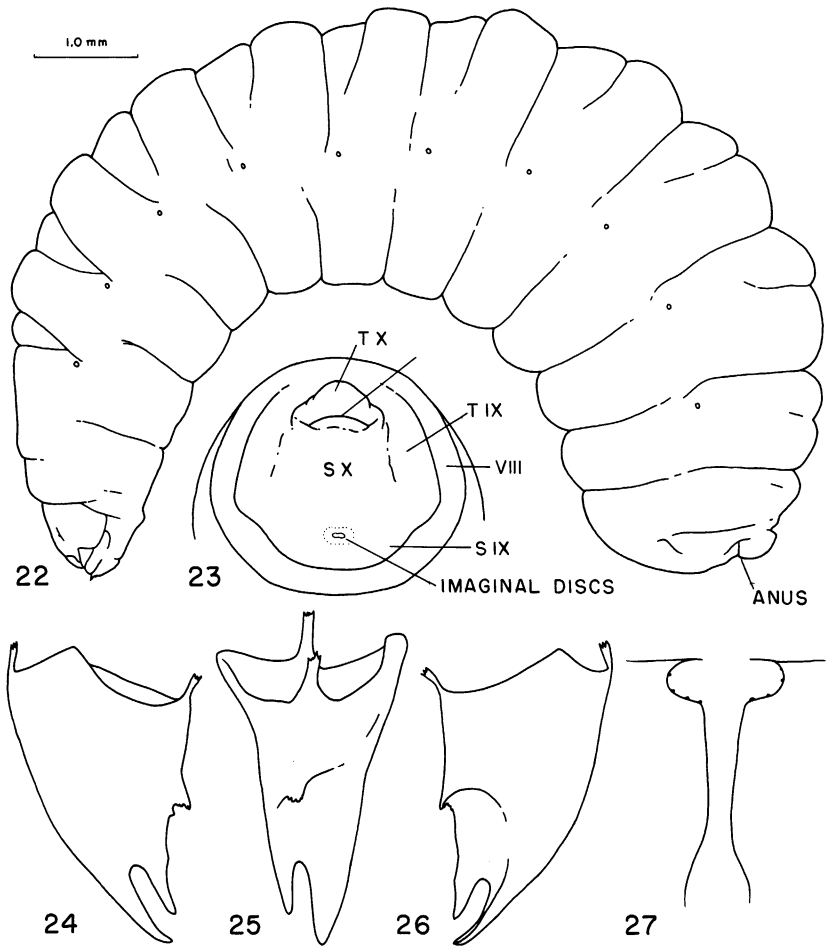
The following description, based on photographs and a cast skin, is of the first feeding instar.

HEAD: Hypognathous. Integument faintly pigmented in some areas



FIGS. 18-21. *Fidelia villosa* Brauns. 18-20. Right mandible, dorsal, inner, and ventral views. 21. Spiracle.

and with scattered sensilla and hairs. Anterior and posterior tentorial arms well developed; hence tentorium probably complete; posterior thickening of head capsule weak but evident; hypostomal ridge, pleurostomal ridge, and epistomal ridge below anterior tentorial pits well developed; epistomal ridge absent between anterior tentorial pits; longitudinal thickening of head capsule apparently absent; parietal bands not evident at least on cast skin. Antennal papilla small but distinct; height slightly less than basal diameter; apex bearing three sensilla; papillae not arising from prominences. Labrum without tubercles and with apical margin emarginate medially and with sensilla. Mandibles (figs. 24-26) short, robust, apically bidentate, with ventral tooth larger and longer; distinct apical concavity present, separated from base of mandible by obliquely transverse declivity which bears irregularly denticulate projection. Maxilla with cardo faintly sclerotic; stipes somewhat sclerotized; palpus distinct, about as long as basal diameter,



FIGS. 22-27. *Fidelia villosa* Brauns. 22. Mature larva, lateral view, not from cocoon, so that details of body segments are not distorted. 23. Mature larva, apex of abdomen, caudal view. 24-26. Right mandible of first instar, dorsal, inner, and lateral views. 27. Spiracle of first instar. Scale refers to figures 22 and 23.

subapical in position; galea apparently absent. Labium recessed so that apex not projecting as far as apices of maxillae; labium apparently divided into prementum and postmentum; palpi about the same size as maxillary palpi; salivary opening not evident on cast skin.

BODY: Form moderately slender, curved. Most abdominal segments

with dorsal intrasegmental lines; body without tubercles. Integument with fine spicules and apparently without setae. Spiracles (fig. 27) moderately large, all of approximately same size; atrium apparently not projecting above body wall, without peritreme, and almost twice as wide as deep; atrial wall beset with large denticles; primary tracheal opening with collar; subatrium long, slender, pigmented, and non-annulate.

PUPA

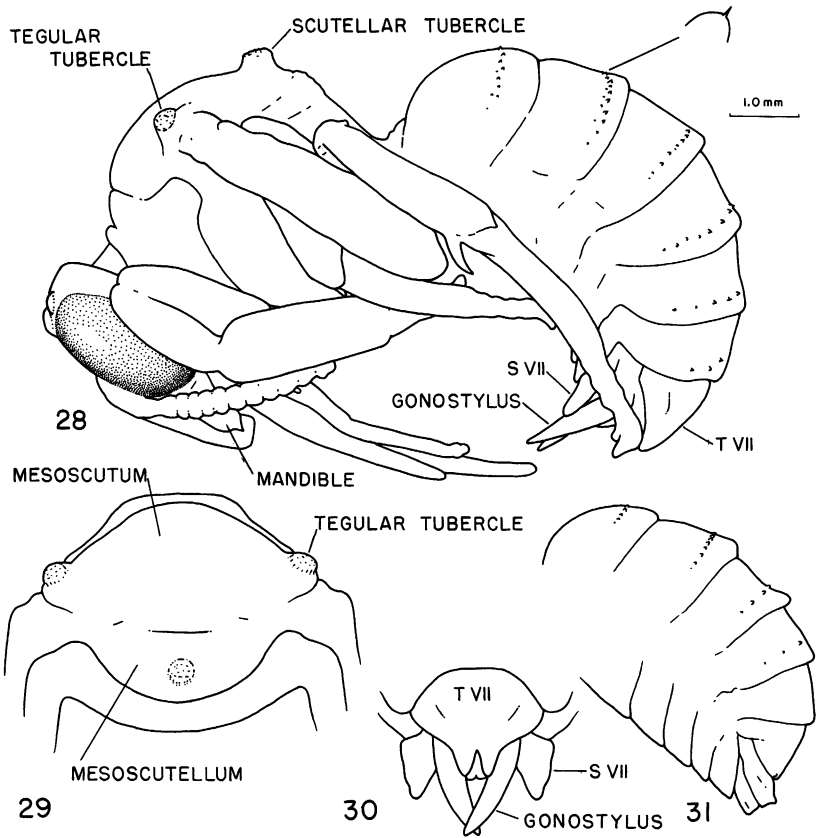
Figures 28-31

Length of male, 10.0 mm.; of female, 8.0 mm.; body curved so that tip of tongue almost touching tip of metasoma.

HEAD: Integument without setae or hairlike spicules. Scape, frons, and vertex without tubercles. Mandible of male swollen pre-apically but narrowing at apex to simple pigmented point; mandible of female strongly bidentate, corresponding to that of male, and with ventral tooth pigmented apically.

MESOSOMA: Integument without setae or hairlike spicules. Pronotum with lateral angles not produced; posterior lobes of male not produced; those of female slightly produced. Each tegula with conspicuous tubercle; mesoscutellum with conspicuous median tubercle; mesepisternum, mesoscutum, axillae, metanotum, and propodeum without tubercles, not produced. Wings without tubercles. Coxae of all legs each with moderately small tubercle on inner apical angle; trochanters with similar tubercle (fore- and mid-trochanters of male not visible); apex of hind femur with two very small tubercles; hind tibiae with small tubercle on outer apical angle; fore- and mid-tibiae without such tubercles; other leg segments without tubercles; longitudinal sulcus of protibia of male not evident in pupa; first segment of protarsus of male greatly enlarged; basitarsus of hind leg of female wider than that of male.

METASOMA: Terga I to VI of male (fig. 28) and I to IV of female (fig. 31) with apical bands of small rounded tubercles, most of which bear short, sharp-pointed spicules. (Although these sharp-pointed processes seem to be spicules, it is at times difficult to distinguish between hairlike spicules and setae on bee pupae.) Basal sterna each with longitudinal median protrusion; terminal spine absent; lateral tergal spines of adult male not expressed on pupa. Apical spines of metasomal tergum VII of adult male evident but lateral spines not evident (fig. 30); sternum VII of male produced on each side into large flat process; gonostyli elongate, tusklike processes.



FIGS. 28-31. *Fidelia villosa* Brauns. Pupa. 28. Male, lateral view. 29. Thorax, dorsal view. 30. Apex of male metasoma, caudal view. 31. Female metasoma, lateral view. Scale refers to all figures.

MATERIAL STUDIED: One live male pupa, 30 miles southeast of Keetmanshoop, South-West Africa, collected as postdefecating larva, October 31, 1968, pupated May 8 or 9, 1969, preserved May 23, 1969 (J. G. Rozen and E. Martinez); one live female pupa, same as for male except no pupation date, preserved June 20, 1969.

NEOFIDELIA

BIOLOGY

In early October, 1969, I briefly observed *Neofidelia longirostris* (de-

scription appended) and *N. profuga* Moure and Michener along the road from Vallenar to Copiapo, Atacama Province, Chile. Nesting sites were not found.

ADULT ACTIVITY: The flight behavior of the males of *N. longirostris* closely resembled that of *Fidelia villosa*, in that both flew swiftly from flower to flower, presumably in search of mates. The fact that males and females landed abruptly on flowers of the pollen plant *Alona rostrata* suggests that the bees may be incapable of a hovering flight. Although several males landed on flowers occupied by females, I observed no copulations. In each case the female apparently rejected the male by turning on her side, an act which caused the male to depart.

The daily cycle of activity of *N. longirostris* differed markedly from that of *F. villosa*. The main period of pollen-collecting activity started about 11 A.M. and did not extend beyond mid-afternoon, although information was difficult to obtain because females were scarcer than the moderately common males. Females presumably remained in their nests at night and during inclement weather. Male activity started around 10 A.M. and lasted until around mid-afternoon on clear days. The pollen flowers closed for the night and did not open on cool, cloudy days. Males of *N. longirostris*, unlike those of *F. villosa*, passed the night in the closed flowers and could be found in them early in the morning, late in the afternoon, and on overcast days.

Males of *Neofidelia* lack the lateral and apical metasomal spines characteristic of males of *Fidelia* and, unlike the males of *Fidelia*, did not attempt to pinch with their metasomas when I held them with thumb and forefinger. The greatly enlarged and modified hind legs of the males of *Neofidelia* are not used effectively for pinching or stabbing; the function of this modification is unknown.

In an area where *Encelia oblongifolia* and *Alona rostrata* grew intermixed, I observed a few males of *Neofidelia profuga* flying swiftly around the flowerheads of *Encelia oblongifolia* but not around those of *Alona*. This suggests that females of *N. profuga* probably collected pollen from *Encelia oblongifolia* at this locality and not from *Alona*. One male of *N. profuga* was found sleeping in a flower of *Alona*.

DISCUSSION AND CONCLUSIONS

There are striking similarities in biological and larval characteristics between the fideliids and the megachilids. Contrary to statements by other authors regarding the scopa on the legs of female *Fidelia* and *Parafidelia*, the modification of the hind basitarsus is clearly not for pollen carrying but for flipping sand from nest entrances. Consequently,

the fideliids bear their scopa on only the under side of the metasoma, just as do the megachilids.

Almost all bees either line their cells with plant material, mud, or stones, all carried to the nest site, or coat the cell wall with secretions (autotichal cells of Malyshev, 1935). However, the megachilid *Lithurge fuscipennis* Lepeletier (Malyshev, 1930) (but not *Trichothurgus dubius* [Sichel], Claude-Joseph, 1926) and *Fidelia* are unusual among bees in that neither provides a special lining to the cell (allotichal cell); their cells are simple, unlined excavations. Furthermore, *L. fuscipennis*, like *Fidelia*, places its egg in a chamber surrounded by pollen, a feature not found among most other bees.¹ However, *L. fuscipennis* deposits its egg when only one-quarter to one-fifth of the provisions are on hand; the remaining food, which closes the chamber, is brought in after oviposition. *Fidelia* oviposits in a chamber constructed in the completed provisions. The tunnels leading to cells of both *L. fuscipennis* and *Fidelia* are closed by fragments of the substrate (wood and sand, respectively), and the cell closures of *L. fuscipennis* and perhaps *Fidelia* have no spiral or concave construction. Possibly both fill the lumen of the provisioned cell with fragmented material. The description (Malyshev, 1930) of the feeding position and activities of the young larva of *L. fuscipennis* seems identical to that of *Fidelia*. *Fidelia*, *Lithurge*, and probably all other megachilids begin defecating before they are finished eating, but this feature is also found in some of the Xylocopinae and Anthophorinae. *Fidelia*, *Lithurge*, and a good many other bees winter as quiescent, mature, postdefecating larvae. The feeding larvae of most bees are delicate so that they can be reared only under ideal conditions. However, megachilid larvae are unusually hardy, as was the one larva of *Fidelia* which was reared even though it was being transported several days by car over rough roads. The pinching habits of the adult males of *Fidelia* (but not *Neofidelia*), *Hoplitis*, and possibly other megachilids are another similarity between the fideliids and megachilids.

The resemblance between the mature larvae of *Fidelia* and those of megachilids is pronounced; not even a single characteristic separates with certainty the larvae of the two groups. The larvae of both share such distinctive features as: Setose body integument; antennal papillae distinct; labrum without tubercles; mandibles massive, apically bidentate (except in some *Stelis*); labiomaxillary region protruding, i.e., adapted for cocoon spinning; maxillary apices strongly produced mesially so that palpi subapical; galea absent; each body segment divided into cephalic

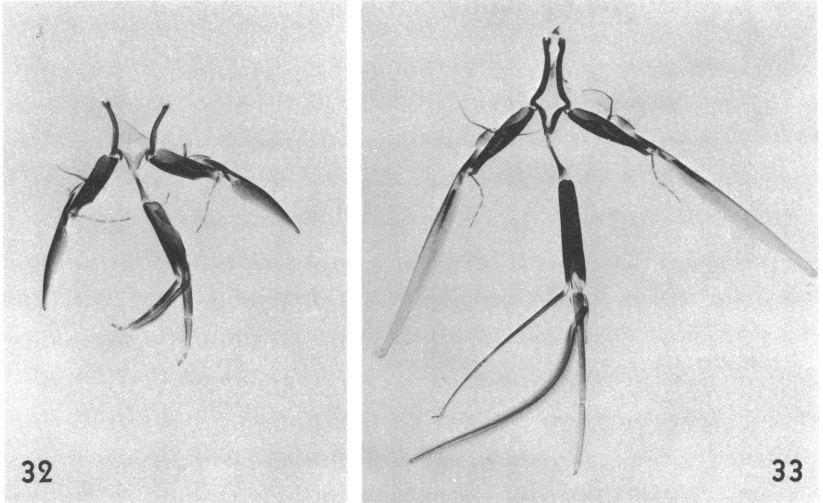
¹ Also found in some *Osmia* (Megachilinae) (Stephen, Bohart, and Torchio, 1969).

annulet and caudal annulet, with caudal annulets raised as paired low transverse tubercles. The several small teeth at the base of the apical concavity of the mandible of *Fidelia* apparently have no counterpart in the leaf-cutter bee, but it seems to be a minor feature and may not be characteristic of all fideliids.

In general aspect the pupa of *Fidelia* resembles the pupae of megachilids in body form, long labrum, and curved shape. However, unlike the pupa of *Fidelia*, megachilid pupae (*Megachile*, *Heterostelis*, *Odontostelis*, and *Osmia*) known to me have tergal or mesoscutellar tubercles. These megachilid pupae (except apparently for *Heterostelis*, Thorp, 1966) all have long setae (or hairlike spicules) on the vertex, scutum, and apex of the metasomal terga, whereas *Fidelia* has only sharp-pointed spicules—or perhaps they are short setae—and these are restricted to the apexes of the metasomal terga.

The similarities between the fideliids and megachilids are so numerous that most features must have stemmed from the ancestor of the two. The fideliids more closely resemble that ancestor because they possess the following primitive features: Bilobed seventh metasomal sternum, distinct cuspis and digitus on volsella, and pre-episternal suture above the distinct scrobal suture. The megachilids have a modified seventh metasomal sternum, a volsella without a distinct digitus and cuspis, and no pre-episternal and scrobal sutures. Because of these characteristics, it is even possible that the fideliids are most similar to the ancestor of those families of bees (Megachilidae, Anthophoridae, and Apidae), the adults of which have derived mouth parts (as defined below).

But not every question regarding the phylogenetic relationships of the fideliids to all families is resolved as yet. The crux of the problem is that, on the one hand, the fideliids (as well as megachilids) possess certain clearly specialized features: Mouth parts of adults derived (submentum and mentum differentiated and distinct, galea and other components elongate, glossa elongate, labial palpus with first two segments flattened and elongate) and larval galea absent. On the other hand, the fideliids exhibit features considered to be primitive because they are found among the sphecoid wasps or among the less highly evolved bees: For example, larval body setose, sternum VII of adult male bilobed, cells without special wall of any sort. These features represent a seemingly contradictory mixture of primitive and highly evolved characteristics that prohibit the construction of a cladogram depicting the fideliids and megachilids in relationship to other bees without postulating either the multiple origin of features or numerous reversals to primitive conditions.



FIGS. 32, 33. Mouth parts. 32. *N. profuga* Moure and Michener. 33. *N. longirostris*, new species.

APPENDIX

Neofidelia longirostris, new species

Figures 33-37

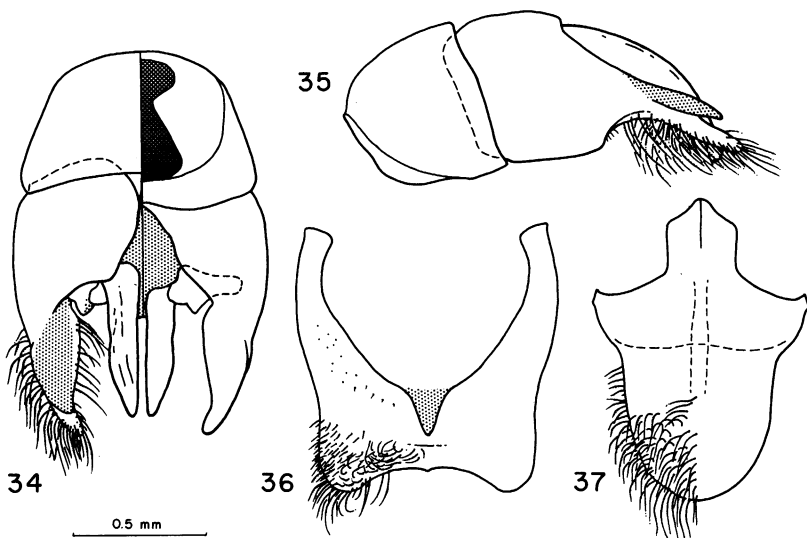
Except where noted, this species agrees with the description of the genus presented by Moure and Michener (1955).

DIAGNOSIS: Because of its elongate mouth parts, *N. longirostris* (fig. 33) can be easily distinguished from the only other known congeneric species, *N. profuga* (fig. 32). Face length, hair color, color of female pygidial plate, and male genitalia and apical sternal plates are also excellent species recognition characters.

DESCRIPTION: Male: Length 9.0 to 11.0 mm. (holotype, 10.0 mm.); forewing length 7.5 to 8.0 mm. (holotype, 8.0 mm.). Integument black, approximately as described for *N. profuga* except tarsi darker; eye color of live specimens gray in contrast to olive-green eye color of live *N. profuga*. Pubescence long, as in *N. profuga*, but tending to be grayer than brownish pubescence of *N. profuga*; pubescence dense, but on face below antennal sockets much less dense than that of *N. profuga*, so that on fresh specimens clypeus not completely hidden by hairs. Punctuation as described for *N. profuga*. Facial features as described for *N. profuga* except clypeus distinctly more protuberant and longer. Antenna identical to

that of *N. profuga* except apical flagellar segments slightly broader than long. Labrum more than 1.3 times as long as broad, with lateral margins converging only slightly toward apex; mandibles as described for *N. profuga*; proboscis (fig. 33) much elongate in contrast to that of *N. profuga* (fig. 32), so that galea measured from insertion of maxillary palpus to tip is more than 3.0 times length of maxillary palpus (that of *N. profuga* only about 1.3 times); in repose, proboscis reaching to mesothorax; galea moderately narrow near base and tapering gradually to rounded apex in contrast to galea of *N. profuga*, which is broad near base and tapers rapidly to pointed apex; two basal segments of labial palpus greatly elongate, and two apical segments minute; forewing with pterostigma, measured from base to base of vein r, variable in length from being slightly shorter than prestigma to being longer than prestigma (as is also the case with *N. profuga*); first submarginal cell along posterior margin somewhat longer than either second or third submarginal cells. Legs, including hind legs, similar to those of *N. profuga* except ventral subapical projections of hind femur slightly less pronounced and except that hind tibial spurs, particularly inner one, larger. Metasomal terga, especially of segments III to V, with depressed marginal areas wider medially than laterally (in contrast to these margins of *N. profuga*, each of which tends to be nearly uniform in width). Metasomal sternum VI with median apical spine slightly broader than that of *N. profuga*; metasomal sternum VII (fig. 36) with lateral lobes more pronounced than those of *N. profuga* and with medium projection more reduced; apex of metasomal sternum VIII (fig. 37) broader than that of *N. profuga*; genitalia (figs. 34, 35) with gonobase longer than that of *N. profuga*; posterior opening of gonobase smaller than that of *N. profuga*; gonostyli and penis valves shorter than those of *N. profuga* and penis valves of different shape (see illustrations).

Female: Length 8.0 mm.; forewing length 6.0 to 6.5 mm. Integument as described for male except median part of clypeus shiny and nearly impunctate; punctation, particularly of dorsal surface of mesosoma and metasoma, less dense than in *N. profuga*; pygidial area yellowish bordered with red in contrast to black pygidial area of *N. profuga*. Color of pubescence as described for male except hairs darker on middle and hind legs; pubescence of face much less dense than that of female of *N. profuga*; pubescence of tarsi similar to, but somewhat shorter than, that of *N. profuga*; pubescence generally less dense than that of female of *N. profuga* and that of dorsal surface of metasoma shorter and decumbent. Facial features as in male. Antenna with apical segments somewhat wider than long. Mouth parts as described for male. Wings as described



FIGS. 34-37. *Neofidelia longirostris*, new species. Adult male. 34. Genitalia, dorsal (left) and ventral (right) views. 35. Genitalia, lateral view. 36. Metasomal sternum VII, ventral view. 37. Metasomal sternum VIII, ventral view.

for male. Legs not unusually modified as is the case with males, but as in females of *N. profuga* except basitibial area of hind leg not elongate, about as long as wide; hind basitarsus as described for *N. profuga* except about as long as hind tibia. Metasoma similar to that of *N. profuga*.

TYPE MATERIAL: Holotype male, allotype, 26 male paratypes, 7 female paratypes, Chile, Atacama: 26 miles south of Copiapo, October 19, 1969, on flowers of *Alona rostrata* (J. G. Rozen and L. Peña); 10 male paratypes, same except 10-20 miles south of Copiapo, October 18, 1969; 4 male, 1 female paratypes, same except Chacritas, October 14, 1969; 18 male paratypes, same except 10-40 kilometers southeast of Caldera, October 17, 1969. Holotype and allotype in the collection of the American Museum of Natural History.

DISTRIBUTION: The species has been collected only in the desert region, from Chacritas north to near Caldera in Atacama Province, Chile. It occurs sympatrically there with *N. profuga*, but *N. profuga* ranges much farther south, reaching well into the normally more moist Coquimbo Province. It seems unlikely that *N. longirostris* will be found in Coquimbo Province because Rodolfo Wagenknecht Huss, who has collected in the Province assiduously over a period of many years, has never taken the new species.

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