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The Ethology and Systematic Relationships of Fideline Bees, Including a Description of the Mature Larva of *Parafidelia* (Hymenoptera, Apoidea)

JEROME G. ROZEN, JR.¹

ABSTRACT

Until recently bees of the Fideliidae were considered a distinct family, but new evidence dealing with biology and adult features indicates that they are a sister group of the Megachilidae. Fideliids are relegated to subfamily status (Fideliinae, new status) because of this sister-group relationship, because of the few taxa within the Fideliinae, and because such a classification will encourage further comparisons of them with other megachilids.

The following biological information is given concerning the southern African *Parafidelia pallidula* Cockerell: description of nesting area, nest structure in the ground, provisioning with pollen of *Sisyndita spartea*, development, cocoon structure, and such adult activities as mate searching,

nest excavation, and sleeping. Of special interest is the fact that females nest shallowly in desert regions and provision very large cells with food masses, each of which houses two or three eggs.

The mature larva is similar to that of *Fidelia villosa* Brauns and less similar to that of *Neofidelia profuga* Moure and Michener, but cladistic analysis of larval similarities and differences of these three taxa is not possible. Mature larvae of fideliines are nearly indistinguishable from those of other megachilids.

A comparison of the biology of *Fidelia*, *Parafidelia*, and *Neofidelia* is presented as is a tabular comparison of nesting, provisioning, and development characteristics of the Fideliinae, Lithurginae, and Megachilinae.

INTRODUCTION

The Fideliidae are a small group of moderate-to large-sized bees restricted to southern Africa and Chile. They have been considered a distinct family for the last 20 years, although before then their status varied from author to author (see Moure and Michener, 1955; Peters, 1972). The group contains only three genera: *Fidelia*, with less than 10 included species, ranges through the

arid regions of southern Africa; *Neofidelia*, containing two named species, exists only in the Atacama Desert in northern Chile; *Parafidelia* with four species is confined to southern Africa. The present paper describes for the first time the ethology and mature larva of a representation of *Parafidelia*, namely *P. pallidula* Cockerell. Now that the biology and immature

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stages of representatives of all three genera are known (Rozen, 1970, 1973), I analyze here all available data to assess the phylogenetic and taxonomic relationships of the fidelids with other bees. For the reasons I present in Discussion and Conclusions (p. 12), I now consider these bees a subfamily of the Megachilidae—the Fideiinae, new status.

Specimens of adults, immatures, and cocoons of *Parafidelia pallidula* obtained in connection with this study are in the collections of the American Museum of Natural History.

I acknowledge the able assistance of my wife, Barbara L. Rozen, for her participation in all aspects of the field work on *Parafidelia pallidula*. Drs. A. J. Hesse and Vincent Whitehead, South African Museum, Capetown; and Dr. L. Vári and Mr. Johann van Rheenen of the Transvaal Museum, Pretoria, permitted me to study the fidelids in their collections and in other ways provided helpful assistance. Dr. J. P. Rourke and others of the staff of the Compton Herbarium, Kirstenbosch Botanic Garden, Newlands, identified the pollen plant and supplied information on its range. Holotypes of *P. p. pallidula* and *P. pallidula incerta* Cockerell were kindly lent by Dr. George R. Else, British Museum (Natural History), London. Dr. Pedro Wygodzinsky kindly translated major parts of Peters's (1972) work. The research for this paper was supported by the National Science Foundation grant no. GB 32193.

The following persons kindly read parts of this paper and gave valuable advice, especially on the section comparing the biological data of fidelines with the megachilines and lithurgines: Dr. G. E. Bohart, Bee Biology and Systematic Laboratory, U. S. Department of Agriculture, Logan, Utah; Dr. George Eickwort, Cornell University, Ithaca, New York; Dr. Karl V. Krombein, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; Dr. E. Gorton Linsley, University of California, Berkeley; Dr. Charles D. Michener, University of Kansas, Lawrence; Dr. Philip Torchio, Bee Biology and Systematic Laboratory, U. S. Department of Agriculture, Logan, Utah.

RELATIONSHIPS WITHIN THE FIDEIINAE

Although *Neofidelia* is a well-defined and separate genus, the distinctiveness of *Fidelia* and

Parafidelia is questionable. *Parafidelia friesei* Brauns, the type species, is a large-bodied form that is quite different from *Fidelia paradoxa* Friese, the type of *Fidelia*, and from such other *Fidelia* as *villosa* Brauns, *braunsiana* Friese, and *kobrowi* Brauns. Marginal cells of these *Fidelia* are extremely short, and the median process of metasomal tergum VII of adult males is bifurcate, in some species strongly so. Further the pygidial plate of the female is extremely large and convex. In *Parafidelia friesei* the marginal cell is normally long, much longer than that of these *Fidelia*, the median process of tergum VII is simple and the pygidial plate of the female is moderately small and flat. Although these features suggest that *Parafidelia* and *Fidelia* are distinct, undescribed species of fidelines in the Transvaal Museum, Pretoria, possess attributes intermediate between *Parafidelia friesei* and the "typical" *Fidelia*. Further, a number of named species of *Parafidelia* and *Fidelia* described by Cockerell in the 1930s and not seen by me possess some intermediate features as judged from the descriptions.

Whatever may be the relative disposition of *Fidelia* and *Parafidelia*, the two genera taken together are a diverse spectrum of species, with forms like *F. villosa* at one end and *P. friesei* at the other. *Parafidelia pallidula* is similar in adult anatomical features to *P. friesei* (although the pygidial plate of *P. pallidula* is moderately large) and hence its biology and immature stages in all likelihood are similar to those of *P. friesei*. This means that the following account combined with the previous works by Rozen (1970, 1973a) on the other two genera probably encompasses the range of variation in the life history and anatomy of the larvae of the family. For this reason, elsewhere in the present paper I give a summary of existing knowledge of the biology of the Fideiinae (see Profile of the Biology of the Fideiinae).

Adults of *Parafidelia pallidula* collected by us at 70 km. east of Port Nolloth (the nesting area, fig. 1, 3) and at 15 km. south of Violsdrif (fig. 1, 4), both Cape Province, Republic of South Africa, were compared with the holotype, a male in the British Museum. They differ only in the color patterns of the clypeus and labrum. The apical half of the clypeus of the type is mostly yellow and the base of its labrum is dirty yellow.

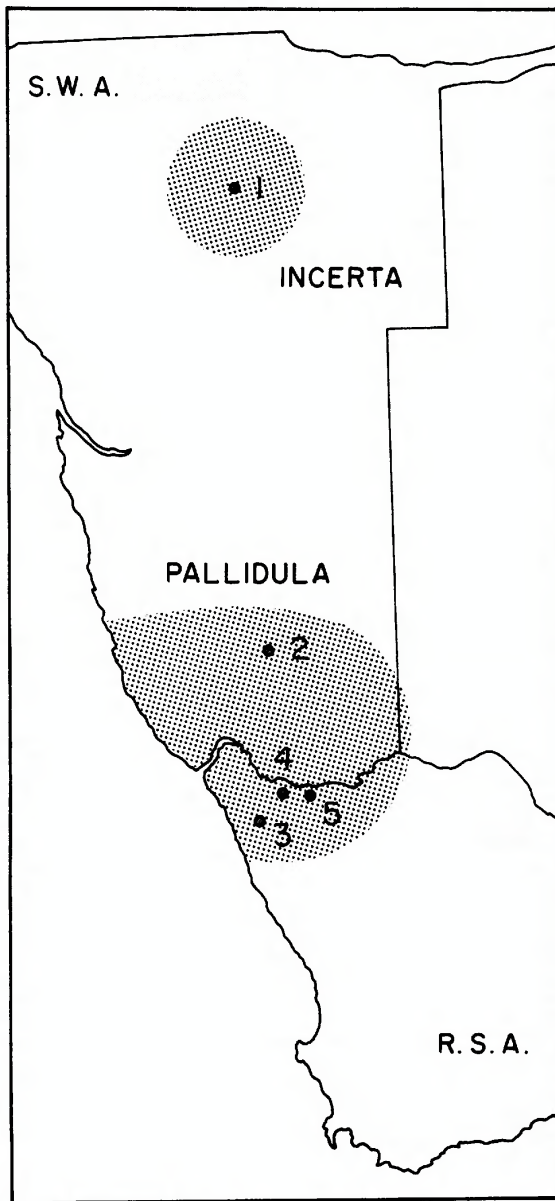


FIG. 1. Distribution of *Parafidelia pallidula pallidula* Cockerell and *Parafidelia pallidula incerta* Cockerell in southwestern Africa. Numbers refer to collection localities; for explanation, see text.

ish (the apex is covered by the mandibles). The clypeus of most males collected in the vicinity of the nesting area is totally black although the clypeus on some specimens has a small to large median subapical yellow marking or small lateral yellow spots. Most males from 15 km. south of

Violsdrif collected by us, possess yellow clypeal maculations which, furthermore, tend to be larger than those on specimens from the nest site. The degree of variability of this character leaves almost no doubt but that the specimens from both localities are conspecific with the type. All specimens collected by us have a labrum with a shiny black base in contrast to that of the type, but the color of the labral base is linked to the extent of yellow on the clypeal apex and therefore is of little importance.

Cockerell recognized two subspecies of *P. pallidula*. *Parafidelia pallidula incerta* Cockerell from Otavifontein, South West Africa (fig. 1, 1), is apparently known only from the type in the British Museum. To the characters listed by Cockerell (1936) separating this specimen from the nominate subspecies can be added the less hairy apical part of the clypeus of *P. p. incerta*. Although none of the specimens we collected exhibit as much yellow on the clypeus or have a yellow labral base as does the type *P. p. incerta*, all other characteristics of *P. p. incerta*, including body size and lack of hair on the clypeus are found on some of our specimens. Hence, the two named forms are the same species, and even if they are subspecifically different will depend on analysis of geographic variation in color pattern after the species has been collected throughout its range. The only anomalous characteristic separating *P. p. pallidula* from *P. p. incerta* is the fact that Otavifontein, a few kilometers east of Otavi, is in the northern part of South West Africa. This locality is apparently far removed from the range of *Sisyndite sparteae*, the food plant to which the species otherwise seems to be restricted. Because of large body size, somewhat less extensive yellow markings on the clypeus and labrum, and a hairy condition of the clypeus (probably due to lack of wear), the type of *P. p. pallidula* is more similar to our specimens than is *P. p. incerta*.

Because their forebasitarsi are not swollen and shiny, males of *P. pallidula* can be separated from other described species whose males are known (*P. friesei friesei* Brauns and *P. friesei colorata* Cockerell). The mandibles of female *P. pallidula* are apically simple although they possess a small subapical dorsal tooth as does *P. f. friesei*. In *P. ornata* Cockerell and *cincera* Cockerell, the other two species in the genus, the mandibles of fe-

males are apically strongly bifid. Although females of *P. f. colorata* are unknown, those of *P. f. friesei* and *P. pallidula* can be separated on a wide variety of features. The hair on the tarsi of *P. f. friesei* is dark brown, that of *pallidula* is very pale reddish tan; additionally the clypeus of *P. pallidula* is black and coarsely sculptured, whereas that of *P. f. friesei* is finely punctured and possesses a large apical yellow maculation; the facial setae of *P. pallidula* are uniformly finely plumose and flexible, and in addition to possessing a sparse vestiture of fine plumose flexible setae, *P. f. friesei* exhibits tufts of coarse, non-plumose, rigid setae between the antennae and between the ocellae. There are also conspicuous differences in the females with regard to density and color of body hair, body size, shape of claws, and shape of pygidial plate.

BIOLOGY

Description of Nesting Site. We discovered *Parafidelia pallidula* visiting flowers on the morning of November 25, 1974, at 70 km. east of Port Nolloth, Cape Province, Republic of South Africa, and within a few hours identified a nesting area. The biology of the species was studied at this locality almost daily from then through December 1, 1974. Adults were also encountered farther north at 15 km. south of Vioolsdrif, just south of the Orange River, but their nesting site could not be found. As now known, the distribution of the species (fig. 1) is limited to 100 km. south of the Orange River to about 200 km. north of there, except for the type locality of *P. pallidula incerta*.

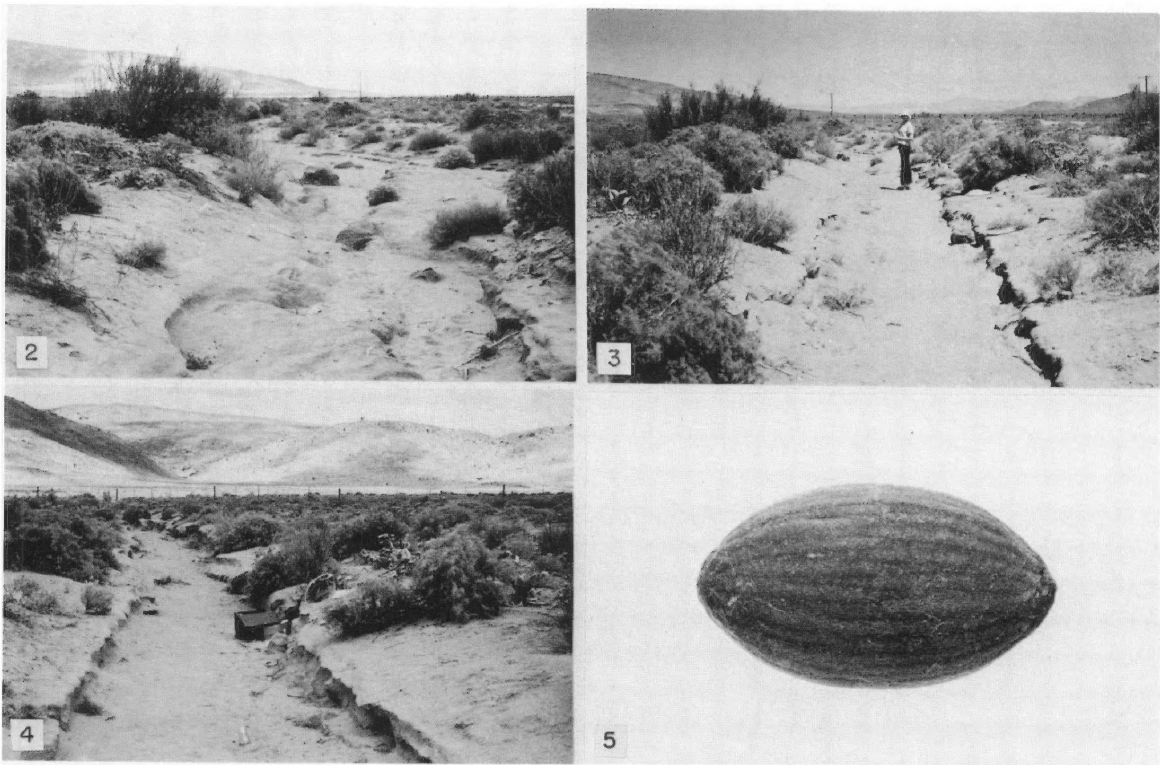
The nesting area (figs. 2-4) was a sandy, treeless region, with low hills and widely spaced desert plants, a few kilometers from a nesting site of the melittid *Capicola braunsiana* Friese, briefly described and pictured by Rozen (1974). Nests were irregularly scattered for approximately 50 meters in and alongside a shallow, low gradient wash, approximately 1 meter deep and ranging from 1 to 4 meters wide. Nests alongside the wash were both active and vacated from the previous year and occurred beneath a surface that sloped 10 to 25 degrees from the horizontal. The coarsely sandy soil tended to be compact and therefore difficult for us to excavate. Nests under construction were also situated in the wash

where the coarse sand was less compact in places than the embankment. Here, however, subsurface soil contained pockets of consolidated claylike earth intermixed with areas of very compact soil and of looser sandy material. Females avoided digging into pockets or into very compact sandy soil, for their burrows ran just above or alongside such areas and did not penetrate them. If a female could not find soft soil, she gave up tunneling, as shown by the numerous abandoned burrows near unsuitable soil. The surface of the ground in the nesting areas was dry but faint visible traces of moisture were present at the cell levels of most nests, as a result either of recent rains or a very moist winter season or both.

The pollen plant, *Sisyndite spartea* E. Meyer, a zygophyllaceous, large yellow flowering shrub that grew to 2 meters in height, occurred sporadically along the wash and was a conspicuous element in the flora of the area for 3 or 4 km. along a dirt roadway that traversed the region. None of the flowers had as yet developed large fruits at this site. The same plant, further along in fruit development, was abundant where the bee was discovered south of Vioolsdrif.

Approximately 10 active nests, each containing at least one cell, were excavated as were another 20 burrows that had apparently been abandoned because of unsuitable substrate. The nesting season had just begun as judged by the preponderance of males to females on the flowers, the few nests encountered with even one or two provisioned cells, the fresh condition of the adults, and the lack of partly grown larvae in cells.

Nesting Activity. Nest entrances whether on sloping or flat surfaces were virtually identical, being 9 to 10 mm. in diameter and having a tumulus of excavated sand to one side. In all cases the tunnels (figs. 7-9) penetrated the earth obliquely and meandered downward at approximately 30 to 45 degrees from the horizontal, although the rate of descent varied considerably. The diameter of the main tunnels and their branches varied but averaged approximately 9 to 10 mm. In more complete nests the main tunnel branched, at different depths, and in some, one of the branches again divided so that the largest number of rami for a single nest was three. As all nests seemed in the early stages of construction, completed nests may contain even more



FIGS. 2-4. Nesting site of *Parafidelia pallidula*, 70 km. east of Port Nolloth, Cape Province, South Africa. Large bush in left middle background of figures 2 and 3 is pollen plant, *Sisyndite spartea*.

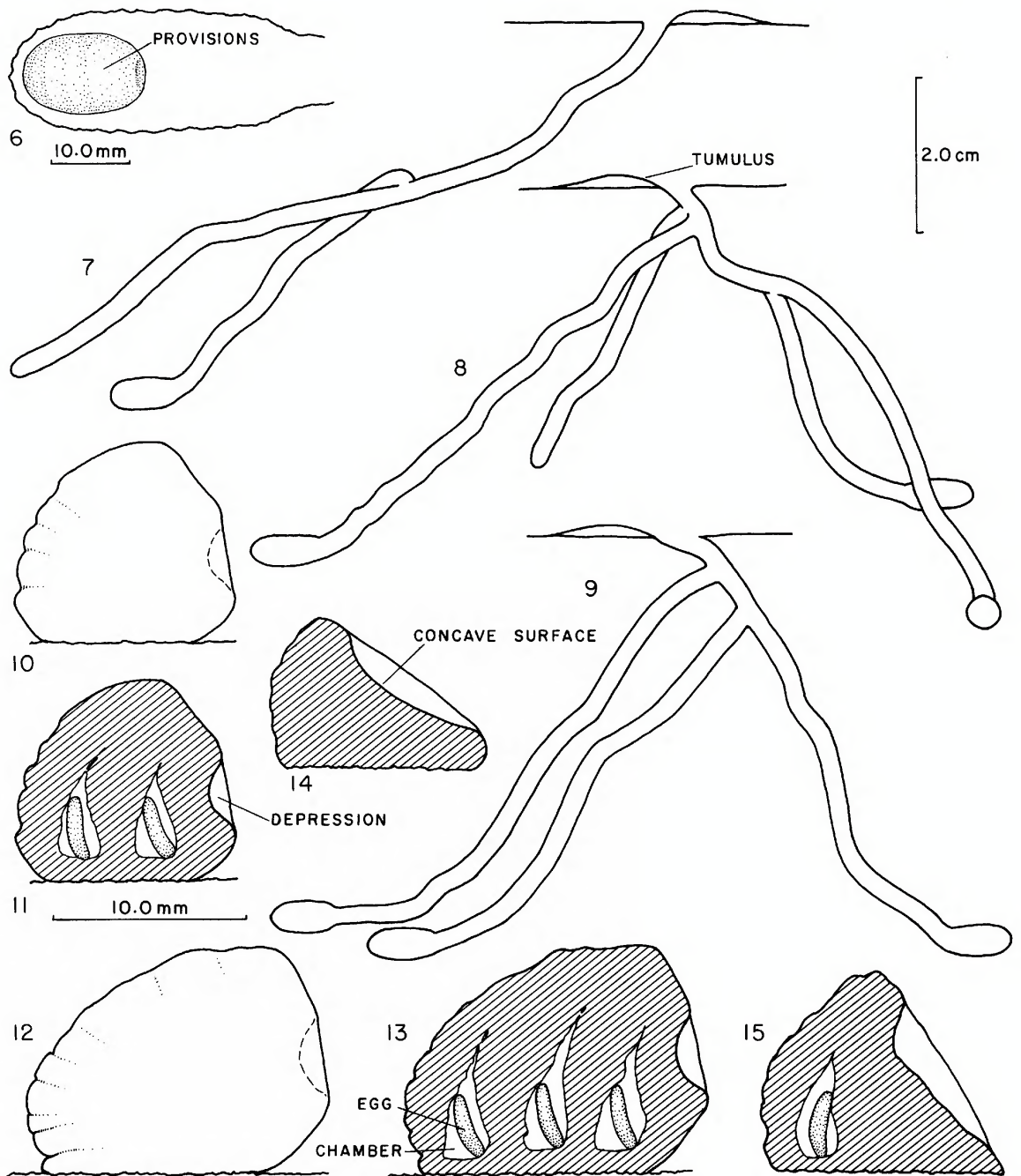
FIG. 5. Cocoon of *Parafidelia pallidula*.

branches. Some burrows ended blindly, that is, they did not terminate in cells. Blind tunnels may have been caused in some cases by the nest having been exhumed by me before the cell was constructed, but clearly some of the blind branches resulted from the female having abandoned the ramus after encountering claylike or strongly compacted soil. Indeed, we occasionally found very short rami close to the entrances where the female apparently made several unsuccessful attempts to penetrate a hard stratum just beneath the surface before she found a soft pathway through it. Several abandoned nests consisting solely of short branching burrows indicated that the nests were given up because of unsuitable soil.

Although main tunnels of active nests were open, branches leading to completed and provisioned cells were filled with soil, somewhat less compact than the surrounding substrate. These burrows could be traced most easily by blowing

away the fill with an aspirator. At least some of the blind branches were also filled.

Single cells were found at the end of branches at depths of 16 to 24 cm. (six measurements). Oriented with their long axis horizontal they were striking in appearance because of their large size compared with the size of adults. This correlates with each cell's containing two or three immatures in a single, huge pollen mass (discussed below), a situation analogous to that of *Megachile (Sayapis) pollicaris* Say (Krombein, 1967) and of some *Lithurge*. Five cells ranged from 29 to 35 mm. in length and 15 to 17 mm. in maximum diameter and were elongate spheroids (fig. 6). The cell surface was rough because of large sand grains extending into it and had no detectable lining. A droplet of water placed on the rear floor was immediately absorbed. Cells were empty except for immatures and provisions. Because of their unconsolidated nature, closures were destroyed before observations could be



FIGS. 6-15. Nest elements and provisions of *Parafidelia pallidula*. 6. Cell with provisions, top view. 7-9. Nests, side view. 10, 11. Pollen mass containing two egg chambers, full side view and cut-away view. 12, 13. Provisions containing three egg chambers, full side view and cut-away view. 14. Provisions in early stages of being gathered and shaped, cut-away side view. 15. Provisions at intermediate stage of being gathered and shaped by which time first egg chamber has been constructed, cut-away side view. Scales refer to figures 6, 7-9, and 10-15, respectively.

carried out; they may have been merely heaped sand at the cell entrances.

Each cell was constructed, provisioned, and closed before the next one was started. Evidence also indicated that a branch leading to the cell was not excavated until the bee had completed the previous cell. Material used to fill a branch probably came from the excavated material of the next branch and cell.

Provisioning. Females carried pollen only on their abdominal scopa; the large, flattened hind basitarsi with accompanying long hairs were not used for pollen transport. Having observed a number of cells in various stages of being provisioned, I conclude that a returning female shapes the first load (or early loads) into a specialized moist form (fig. 14) in the rear of the cell, rather than storing the provisions as an unworked mass. Although the somewhat concave front surface of the early mass was rough, the rear part was smooth except for low even ridges that ran transversely. This mass is obviously the completed rear of the entire load which is built up in front with successive foraging runs. One or more subsequent loads permit the mass to be enlarged as in figure 15 and the completed provisions have an elongate, somewhat ovoid shape with a circular depression in the front, as is shown in figures 10-13. Dimensions of three pollen masses ranged as follows: length, 11.0 to 15.0 mm.; height, 10.0 to 12.0 mm.; and width, 10.0 to 11.0 mm. The outer surface of the provisions was smooth except for the rounded transverse ridges most noticeable at the rear. The provisions were always at the rear of the cell (fig. 6) and attached to the floor.

The interior of the provisions was unusual in that it consisted of a number of open chambers arranged one in front of the other and each contained a single egg or larva (figs. 11, 13). The multiple inhabitants of the provision mass accounted for its extraordinary size and the size of the cell itself. Although two masses (fig. 11) had only two chambers each, three (fig. 13) consisted of three chambers, a number that will probably hold for most masses as judged by their usually large size. Chambers had somewhat roughened walls and essentially were identical to one another; they appear to be similar to the central

cavity described for the pollen mass of *Fidelia villosa* (Rozen, 1970). One incomplete mass (fig. 15) contained a single egg, a fact indicating that eggs are deposited as the mass is built up. The provisions within a mass were mealy-moist except above each egg chamber where they were quite dry. After being placed in a petri dish with a fine film of water on the cover, one mass quickly liquefied, indicating that provisions probably could not exist intact in an area where there is appreciable ground moisture because there is no lining to the cell to exclude moisture.

Development. Eggs, approximately 3.5 mm. long and 0.75 mm. in maximum diameter, were semitransparent, whitish, and possessed a smooth, rather shiny chorion. Slightly curved, they were equally pointed at both ends and widest somewhat below the middle. Females positioned them more or less perpendicular in the chamber so that one end, presumably the posterior end, touched the chamber floor while the anterior end rested against the rear wall or in one case against the front wall. Very possibly the eggs may have been free standing on their posterior ends but were disoriented during excavation or while being transported to our hotel.

First instars were not recovered *in situ*, but several, found in a liquefied food mass, were looped forward so that the head of each would have touched the pollen mass in front of the tip of the abdomen. This posture may be one assumed while they drink or feed, as is known for the first instars of *Neofidelia profuga* Moure and Michener (Rozen, 1973). One first instar, in the process of molting to the second, contained no pollen grains in its intestines. Hence the first instar apparently only drinks liquid. Feeding habits and information on development of subsequent instars are unknown.

As is the case with other fideliines, *P. pallidula* constructs a cocoon when finished feeding. Cocoons from the current generation were not recovered. However, after sifting considerable earth we found a number from previous generations, broken or vacated, and also a cocoon (fig. 5) containing a live, postdefecating, totally quiescent larva. One cell contained two cocoons, an indication that several larvae were capable of developing completely on the provisions in one cell.

Cocoons resembled those of *Fidelia villosa* (Rozen, 1970) more closely than those of *Neofidelia profuga* (Rozen, 1973), although the cocoons of all three species have distinctive features in common. The cocoon of *P. pallidula* (fig. 5) was large, ranging from 14.0 to 14.5 mm. long (four measurements) and 8.0 to 8.5 mm. wide (three measurements). The shape was essentially the same as that of *F. villosa* with a nipple at each end, but the nipples were less pronounced. The outer surface was brown, almost identical in color to but slightly duller than the cocoon of *F. villosa*. The glue lines described for *F. villosa* were quite evident in the cocoon of *P. pallidula* and were slightly embedded giving the surface a more ribbed appearance than that of *F. villosa*. As in *F. villosa*, the casing consisted of two layers, not three as in *N. profuga*. The outer parchment-like layer of silk was very thin, being only one strand thick as was also the case for the cocoon of *F. villosa*. However, it was weaker so that when broken, the two layers broke together and the outer layer could not be peeled away, as it could in *F. villosa*. The inner layer was approximately 0.15 mm. thick, brittle, and consisting of very fine sand glued by a glistening material. The only discernible difference between it and the inner layer of the cocoon of *F. villosa* was that it contained somewhat larger sand grains which, however, were covered with very fine sand and visible only in transmitted light. The outer layer seemed more tightly bonded to the inner than was the case with *F. villosa*. Neither layer was soluble in water or 80 percent ethyl alcohol and both were waterproof when tested with water droplets. Fecal material was not found inside or adhering to the outside of the cocoon. The similarities among the cocoons of *F. villosa*, *N. profuga*, and *P. pallidula* are those listed in the comparison of the cocoons of *F. villosa* and *N. profuga* (Rozen, 1973a).

Adult Activity. No matings of this species were seen at 70 km. east of Port Nolloth because females were uncommon. However, males swiftly patrolled the pollen plants and almost certainly initiated mating there. At the Vioolsdrif site where the flowers were much further advanced, males were uncommon and hence no matings were observed. Males did not patrol the nesting

area at 70 km. east of Port Nolloth, an indication that copulation is probably restricted to where females gather pollen.

Females slept in nests. Males were so infrequently encountered asleep on flowers on cool days that I assume that they do not ordinarily sleep there, although a few were observed entering burrows in the late afternoon.

Parafidelia pallidula is active during the warm part of the day. On clear, warm days they were already flying at 10:00 a.m. and continued well into the afternoon. In this respect they differ from the afternoon activity pattern of *Fidelia villosa* (Rozen, 1970).

Females, like those of *F. villosa*, disposed of excavated material at the nest entrance by backing up through the burrows while pushing excavated soil. On reaching the opening they flipped the material with their hind legs, broadcasting it from the entrances. The broad and flattened hind basitarsi with the fringe of long hair were instrumental in effectively flinging the soil.

As is the case with *F. villosa*, a female of *P. pallidula* returning from the flowers, in each case flew many times in long, swift sweeps over the nest before alighting, but on landing at the entrance, dove immediately into it. Females seeking a place either to start a nest or to spend a night flew more slowly in a searching way back and forth over the area and occasionally landed briefly as if to investigate or test a likely site.

Parasitism. No parasitic bees were encountered in the nesting area of this species. Meloid larvae were quite common in excavated food masses and probably took a heavy toll of the *P. pallidula* population. No other predators or parasites were discovered.

DESCRIPTION OF MATURE LARVAE

Figures 16-21

Diagnosis. The postdefecating larva of *Parafidelia pallidula* shares numerous characters with *Fidelia villosa* and can be distinguished from *Neofidelia profuga* by those features by which *F. villosa* differs from *N. profuga* (Rozen, 1973a). These include a somewhat narrower head, shorter clypeus, spiculate condition of the mouthparts and spiculate body integument. It differs from

the mature larvae of both *F. villosa* and *N. profuga* most notably by the somewhat differently shaped mandible (figs. 19-21), the presence of a rather distinctive dorsal ramus to the hypostomal ridge (fig. 17) and probably by the somewhat differently shaped abdominal segments IX and X, as described below. It differs further from *F. villosa* by possessing (fig. 16) a distinct although not strongly developed epistomal ridge between the anterior tentorial pits, one of the few features shared with *N. profuga* and not with *F. villosa*.

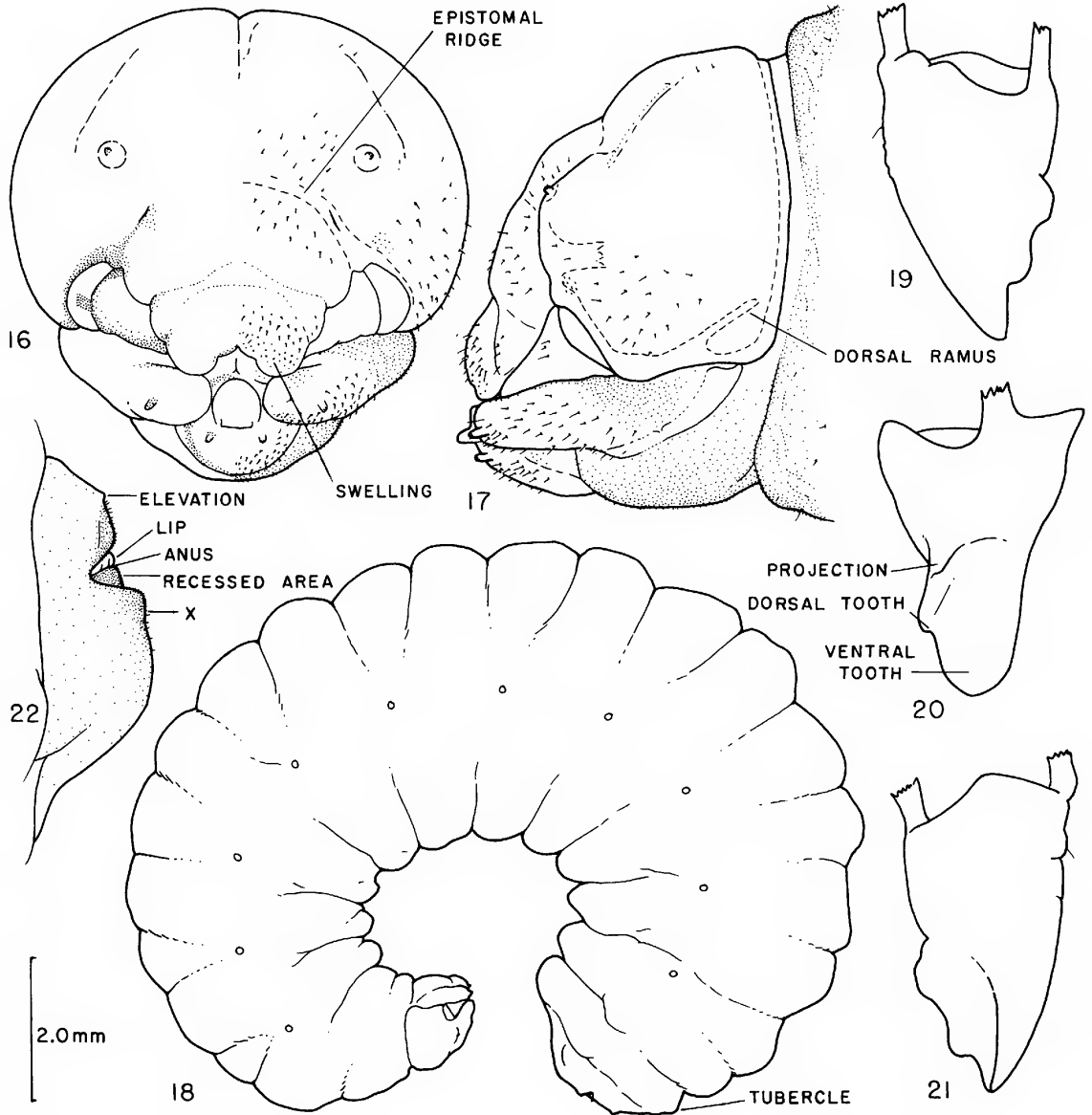
Head (figs. 16, 17). As seen from front, combined head capsule and labiomaxillary region (fig. 16) with essentially the same width-length ratio as that of *Fidelia villosa* (Rozen, 1970); hence, head capsule appearing somewhat narrower than that of *Neofidelia profuga* (Rozen, 1973a). In other respects as described for *F. villosa* (Rozen, 1970) except for following: maxilla and labium somewhat more extensively spiculate so that even basal part of prementum with some spicules; therefore spiculation of head areas even more extensive and more divergent from condition found in *N. profuga* than that of *F. villosa*. Hypostomal ridge branching posteriorly into ventral strong ramus and dorsal weak ramus, unlike condition found in *F. villosa* and *N. profuga*; between anterior tentorial pits epistomal sulcus not evident as is also case for *F. villosa*, but internal ridge evident though weak; hence this condition somewhat intermediate between *F. villosa* and *N. profuga*; clypeal length moderate as is probably also case for *F. villosa* and consequently contrasting with very short clypeus of *N. profuga*. Antennal papilla small, about as long as basal diameter or at most only slightly longer; hence papilla approximately as in *F. villosa* but conspicuously shorter than that of *N. profuga* which is approximately twice as long as basal diameter (not discussed in Rozen, 1973a). Apicolateral angles of labrum produced as low swellings (because of the position of these swellings they are not judged to be homologues of labral tubercles found on anterior surface of labrum of various groups of bees such as the Panurginae and most Nomadinae); counterparts of these swellings faintly evident in *F. villosa* and *N. profuga*. Mandibles (figs. 19-21) apically bidentate, as in *F. villosa* and *N. profuga*, but

ventral tooth much larger than dorsal one and much more rounded than ventral tooth on either of other two species; basal apical concavity near dorsal edge of mandible produced as narrow projection presumed to be homologue of large tooth at base of apical concavity in *N. profuga*, but distinct tooth or teeth not evident. Maxillary palpi and labial palpi subequal in length.

Body (figs. 18, 22). As described (Rozen, 1970) for postdefecating larva of *Fidelia villosa* except for following (predefecating larvae of neither species known): posterior part of body not quite so robust by comparison with anterior part; caudal annulets scarcely higher than cephalic ones except dorsolaterally where they tend to project considerably farther than cephalic ones (hence not visible in lateral outlines, fig. 18). Integument moderately soft and densely spiculate as is also the case for *F. villosa*, not non-spiculate as in integument of *Neofidelia profuga*; integument with scattered setae which, however, are extremely short, but little higher than spicules and hence difficult to see on most body segments; setae in anal area (fig. 22) somewhat denser and more pronounced. Spiracular subatrium consisting of approximately three chambers. Abdominal segment IX unlike that of *F. villosa*, bearing low, small, paired dorsal paramedian tubercles which are discernible in lateral view; abdominal segment X (fig. 22) without tubercles dorsally but with low median elevation above anal region; this elevation much less conspicuous than that of *F. villosa*; area surrounding anal region spiculate, faintly pigmented and produced beyond both anus and recessed area immediately below anus; anus situated dorsally on segment, with distinct dorsal lip.

Material Studied. One postdefecating larva taken from cocoon, 70 km. east of Port Nolloth, Cape Province, Republic of South Africa, December 1, 1974 (J. G. and B. L. Rozen).

Remarks. There is no question but that the mature larva of *Parafidelia pallidula* shares many more characters with *Fidelia villosa* than with *Neofidelia profuga*. Because of this and because the generic boundaries between *Fidelia* and *Parafidelia* are uncertain, one is tempted to say that *Parafidelia* and *Fidelia* not only are geographically sympatric but also closely related. However, the characteristics involved in this



FIGS. 16-22. Postdefecating larva of *Parafidelia pallidula*. 16. Head, frontal view. 17. Head, lateral view. 18. Entire larva, lateral view. 19-21. Right mandible, dorsal, inner and ventral views, respectively. 22. Tenth abdominal segment, lateral view. Scale refers to figure 18.

three-way comparison are difficult to analyze cladistically, because it cannot be determined whether the shared character states are primitive or specialized. Hence, final judgment on this matter must await further evidence.

Of special interest is the fact that the hypostomal ridge is divided posteriorly into a dorsal

and ventral ramus, a condition not known for either *Neofidelia* or *Fidelia*, but found in the Lithurginae. Indeed, because of the presence of this characteristic in the Fideliinae no single characteristic can be presented that will distinguish the larvae of the Fideliinae from the Lithurginae and Megachilinae.

PROFILE OF THE BIOLOGY OF THE FIDELIINAE

The following is a summary of the biology of fideline bees, based primarily on *Fidelia villosa* (Rozen, 1970), *Neofidelia profuga* (Rozen, 1973a), and *Parafidelia pallidula* (present paper) but incorporating other available data as well.

Nesting. Species inhabiting desert regions. Individuals, when abundant, nesting in loose aggregations in horizontal or nearly horizontal ground except for some *P. pallidula* which burrowed into surface as much as 25 degrees from the horizontal. Females constructing own nest, that is, not using old nests or burrows of other animals. Tumuli dry, loose, acentric, formed by females flipping excavated sand from nest entrances with modified hind legs. Main burrows circular in cross-section, unlined, descending obliquely in meandering fashion, plugged at entrance (*F. villosa*), below entrance (*N. profuga*), or open (*P. pallidula*); entrances without turrets; main burrow branching just below surface (*N. profuga*) or at various depths (*F. villosa*, *P. pallidula*); branches either dividing again, ending blindly (i.e., ending without cell), or ending in a cell, irrespective of species; in *F. villosa* most terminal branches ending blindly so that nest perhaps with only single cell (defined for this species as a terminus of a branch containing, when completed, provisions and an egg); in *P. pallidula* and *N. profuga* nest customarily with more than one cell; terminal branches apparently normally filled with soil whether ending in cell or blindly. Cells arranged singly, with long axis horizontal or nearly so; cells with same diameter as that of branches (*F. villosa*), somewhat wider than branches (*N. profuga*), or much wider than branches (*P. pallidula*); cell wall rough, not specially worked, not impregnated, without traces of special lining, and completely nonwaterproof; cell closure never seen or otherwise detected, hence probably piled loose sand.

Provisioning. Pollen plants various and representing variety of families:

- Fidelia* spp.—*Mesembryanthemum*, *sensu lato* (Aizoaceae)
Parafidelia sp.—*Campanula* (Popov, 1939)
(Campanulaceae)

P. pallidula—*Sisymbrium sparteum* (Zygophyllaceae)

Neofidelia profuga—*Calandrinia* (Portulacaceae), *Trichocereus* (or *Eulychnia*) (Cactaceae) and probably *Encelia* (Compositae)

N. longirostris Rozen—*Alona* (Nolanaceae)

Females somewhat selective in food preference so that some species possibly monoleges (*P. pallidula*, *N. longirostris*); other species clearly visiting a number of species for food (*N. profuga*) but nevertheless rather narrowly polylectic; all species apparently collecting from large flowers with anthers well exposed. Pollen transported on underside of metasoma and not on legs. Provisions worked into mass with species-specific (or genus-specific) shape; mass fitted into rear of cell (*F. villosa*, *N. profuga*) or toward rear of cell (*P. pallidula*); with *F. villosa* and *P. pallidula* (and probably also *N. profuga*) each pollen load placed and shaped as it is unloaded and subsequent loads added to it; that is, provisions not manipulated after all pollen transported to cell; completed mass mealy-moist and either provided with concave anterior face into which egg is partly cupped (*N. profuga*), or fitted with one (*F. villosa*) or two to three (*P. pallidula*) chambers, each of which houses egg.

Development. Eggs smooth, whitish, semi-transparent, slightly curved, inserted more or less vertically, attached possibly only at posterior end; eggs deposited one to a cell (*F. villosa*, *N. profuga*) or two to three to a cell (*P. pallidula*); oviposition taking place while provisions being stored (*P. pallidula*) or afterward (*N. profuga*). Larvae hardy (not known for *P. pallidula*), that is, can withstand some maltreatment such as being manipulated with forceps or reared in artificial cell. Defecation commencing as soon as larva reaches last stage (not known for *P. pallidula*); feces dry and brittle (not known for *P. pallidula*). Voiding of pollen-bearing feces completed before cocoon construction as no such fecal material found incorporated inside cocoon or as integral part of exterior of cocoon. Cocoon spun after completion of feeding, at least in *F. villosa* and *N. profuga*; cocoons elongate-oval, with single nipple at one end (*N. profuga*) or nipple at each end (*F. villosa* and

P. pallidula); cocoon consisting of (1) outer silken layer; (2) layer of cemented sand particles, and only in *N. profuga*; (3) inner thin layer of woven material; cemented sand layer probably resulting from ingestion and subsequent defecation of sand (for more detailed comparison of cocoons, see Biology section of present paper).

Adult Activity. Diurnal adult activity synchronized to great extent with period when flowers are blooming. Apparently only single generation per year.

Females apparently spending night in nest or in available tunnels; males sleeping in ground (*F. villosa*) or in flowers (*N. longirostris*).

Males, at least of *F. villosa*, *P. pallidula*, and *N. profuga* inclined to pinch by curling metasoma when picked up.

Mating observed for *N. profuga* at the nesting site and at the flowers; mating of both *F. villosa* and *P. pallidula* not observed at nesting sites but probably taking place in association with flowers as judged by behavior of males flying from flower to flower; mating of *N. longirostris* probably occurring in association with flowers as judged by behavior of males, but mating of this species possibly also taking place at nesting site as is case with its congener *N. profuga*.

Parasitism. No cuckoo bees associated with any fideliine; known nest associates as follows:

- F. villosa*—Acarina, Meloidae
- P. pallidula*—Meloidae
- N. profuga*—Meloidae, Mutillidae

BIOLOGICAL COMPARISONS OF THREE SUBFAMILIES OF MEGACHILIDAE

With the information presented in the previous section, it is now possible to provide a preliminary comparison of the biologies of the three subfamilies of the Megachilidae. This is done in tabular form (table 1). Although some information for the lithurgines and the megachilines is based on my own experience, I have relied heavily on the following published summary accounts: Eickwort (1975), Houston (1971), Krombein (1967), Malashev (1935), Rozen (1973b), Stephen, Bohart, and Torchio (1969). A number of persons acknowledged in the introduction also provided valuable information used here.

DISCUSSION AND CONCLUSIONS

In several papers, Rozen (1970, 1973b) brought forth evidence revealing substantial similarities between the Fideliidae and the Megachilidae, the large worldwide family of leaf-cutter bees. Recently Peters (1972), although maintaining them as a separate family, pointed out that fideliids are a sister group of the other megachilids on the basis of cladistic analysis. I concur in his conclusions but now relegate them to subfamilial status for the following reasons: (1) They are a sister group of the other megachilids, sharing at least a number of apomorphic characters; (2) they are a minute group (compared with most other families of bees) consisting of approximately 16 described species in three genera; and (3) their being placed as a subfamily of the Megachilidae demonstrates their close similarity to, and their relationship with, the other megachilids and encourages comparisons between them and the others. Point 1 in particular is discussed below.

Peters (1972) provided a detailed account of the cladistic relationships of the fideliines with the other megachilids. He identified four synapomorphies shared by the two groups. Character numbers used below refer to his paper. I agree that a labrum considerably longer than wide (6), reduced basitibial plates (7), and scopa restricted to the metasomal sterna (8) are apomorphies shared by the fideliines and the pollen-carrying megachilids. Although synapomorphies 6 and 7 appear elsewhere in long-tongued bees, they are of limited occurrence and are parallelisms where they do appear, judging from correlation with numerous other characters. The most consistent synapomorphy is the presence of a well-defined metasomal scopa without scopal hairs also on other areas of the body (8). Recently Pasteels and Pasteels (1975) showed that the scopa of the fideliines and the other megachilids were essentially identical on the basis of microscopic anatomical structure as revealed by scanning electron microscopic examination; this is supportive evidence that the specialized metasomal scopa evolved only once, in the ancestor of the Megachilidae as here redefined.

However, I question Peters's interpretation of a nondenticulate cusp on the larval mandible

TABLE 1
Comparisons of Nesting, Provisioning, and Development Characteristics of the
Three Subfamilies of Megachilidae, Excluding Parasitic Forms

Characteristics	Fideliinae	Lithurginae	Megachilinae
Nest substrate	soil	wood and other plant material	extremely variable (in soil, wood, stems); exposed nests on and under rocks, attached to branches
Nest type	secreted, burrows branched	secreted, burrows branched and linear	exposed; secreted, burrows branched and linear
Hind legs of female modified and used for dispersing excavated substrate (soil) from nest entrance	yes	no	no
Nest construction	freshly constructed by female	freshly constructed by female; nests of past generations used	freshly constructed by female; nests of past generations used; other burrows and cavities used; in open
Special cell lining	none	none	none; made from foreign material (resins, plant hairs, petals, leaves, soil, pebbles, etc.)
Cell arrangement	single	single; linear series	various (single, clustered, linear series, branched series)
Cell closure	apparently loose soil only – no special closure	apparently loose plant fiber only – no special closure	special closure made of foreign material; rarely none
Pollen transported only on underside of metasoma	yes	yes	yes, except apparently for <i>Aspidosmia</i> (Peters, 1972)
Provisions	distinctive shape, not occupying entire cell	shape corresponding to cell, which they completely occupy	often not distinctive shape, occupying end of cell; sometimes a mound of distinctive shape where free from cell wall; rarely occupying entire cell
Eggs deposited	before (<i>F. villosa</i> , <i>P. pallidula</i>) and after (<i>N. profuga</i>) provisions are complete	before provisions are complete	usually after provisions are complete, but sometimes (in some <i>Osmia</i> , Stephen, Bohart and Torchio, 1969; <i>Megachile pollicaris</i> , Krombein, 1967) during provisioning
Number of eggs to a cell	1; 2-3	1; 2	usually 1; rarely (<i>M. pollicaris</i>) up to 3
Initiation of defecation	start of last larval instar	start of last larval instar	usually at start of last larval instar but sometimes in earlier instar
Cocoons present	yes	yes	yes
Cocoon with sand layer	yes	no	no

(9) as being a derived feature. Nondenticulate cusps appear to be the rule in the Apidae and in such groups of Anthophoridae as Nomadinae, Centridini, Anthophorini, Melectini (at least most), Rathymini, Ctenioschelini, and Xylocopinae. Hence, there seems little basis for determining the evolutionary polarity of the dentate-nondentate cusp of the larval mandible.

Peters (1972) further identified six synapomorphies (10-15) of the Megachilinae (*sensu* Michener, 1944) and Lithurginae as distinct from the Fideliinae. I concur with his judgment with one possible exception, namely character 15, the apomorphic condition being "denticles on inner surface of larval mandible completely reduced" and the plesiomorphic condition being "denticles present in rudimentary state." These presumed denticles are questionably homologues of the denticles found on the mandibles of other larval bees, as judged on the basis of their position on the edge of a sharp basal declivity of the apical concavity in the fideliines. Furthermore, they are essentially absent in *Parafidelia pallidula*, and in addition those of both *Fidelia* and *Neofidelia* seem to be homologues of the adoral basal tooth of the mandibular concavity of the Lithurginae (Rozen, 1973b).

Peters recognized two synapomorphies by which fideliines differ from the other megachilids. The present study confirms the importance of the modifications of the hind basitarsus ("scopa" of Peters) used to disperse soil from the nest entrance (16), because this feature is now known also for *Parafidelia pallidula*.¹ Synapomorphy 17, i.e., "presence of only short

setae on the pupa," should be modified to "setae reduced (*Neofidelia*) or absent (*Fidelia*)" (pupa of *Parafidelia* still unknown).

Peters's (1972) discovery of a scopa on the hind leg of *Aspidosmia* (Megachilinae, *sensu* Michener, 1944) is most interesting and difficult to explain. He believed it a relic, but if true then we would have to assume (1) that the loss of scopa on the hind leg has occurred at least twice, once in the Fideliinae and again in the Megachilinae-Lithurginae lineage, and (2) either that the absence of a leg scopa in the Lithurginae is another parallelism, or that the Lithurginae evolved from a Megachilinae-like ancestor. The alternative hypothesis is that the leg scopa of *Aspidosmia* is an evolutionary reversal or convergence. These hypotheses are awkward and suggest that we need to know more about *Aspidosmia*, particularly with respect to its immature stages and biology.

Peters (1972), Moure and Michener (1955) and other authors have discussed the polarity of several character states exhibited in metasomal sternum VII of the male. They have considered the deeply divided, bilobed, and ornamented sternum VII to be a primitive condition as opposed to a simple, platelike structure, because the bilobed condition occurs in a wide selection of families including the Colletidae and Andrenidae, as well as in *Fidelia*. However, an examination of this sternum among the fideliines and some of the other megachilids suggests the polarity might be the opposite, namely the simple platelike structure might be primitive. A comparison of male metasomal sternum VII and VIII in *Neofidelia*, *Parafidelia*, and *Fidelia* shows that sternum VII of *Parafidelia* is intermediate between the deeply bilobed condition of the sternum in *Fidelia* and the platelike structure in *Neofidelia*. Most importantly, the condition found in *Fidelia* seems to be a special adaptation to permit sternum VII to function in connection with an elongate median process of sternum VIII. Sternum VIII of the other two genera is not elongate and produced as a median process. Hence, the suggestion is that the deeply bilobed condition may actually have arisen many times in the bees, in each case in connection with its functioning in relation to a highly modified sternum VIII.

In summary, although certain of the charac-

¹Peters regards the long hairs on the basitarsus of *Fidelia* and *Parafidelia* to be a scopa that has lost its pollen-carrying function. However, this is open to serious question because (1) the femur in both genera does not possess elongate hairs as is found on a true pollen-bearing scopa on legs, and (2) the gross morphology of the basitibial hair brush and of the basitibia itself in the fideliines bears little resemblance to that found on pollen-carrying anthophorids. Hence, there is no reason to assume that the modification of the hind leg of these two genera evolved from a scopa-bearing hind leg; this structure appears to be a simple modification of the hind basitarsus to a flattened, paddle-like surface to flip excavated soil laterally just as the troughlike modification of the hind basitarsus of *Neofidelia* is a specialization to flip sand backward.

ters used by Peters to demonstrate the sister-group relationships of the fideliines and other megachilids may be open to question, his analysis still holds and in some ways is even strengthened by the information added here. Larvae of fideliines are strikingly similar to those of the Lithurginae and Megachilinae. However, because either most of the shared characteristics appear to be plesiomorphic or their evolutionary condition cannot be determined, larvae are of little use in ascertaining the relationships of the fideliines to the other megachilids. Although fideliines and other megachilids share many biological features, only mode of pollen transport can be identified as being synapomorphic at the present time.

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