Distribution, biology and flower relationships of fideliid bees of southern Africa (Hymenoptera, Apoidea, Fideliidae)

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Fideliids are ground-nesting bees, covered in a dense pale straw to brown pile, with pollen being carried on an abdominal scopa. *Fidelia paradoxa, F. villosa* and *F. kobrowi* are restricted to flowers of the Mesembryanthemaceae, and *Parafidelia major* and two new *Parafidelia* species to *Grielum* and *Neuradopsis* (Roseaceae). *Parafidelia ornata* collects pollen mainly from *Tribulus* and *Tribulocarpus* and *P. pallidula* only from *Sisyndite* (Zygophyllaceae). *Parafidelia friesei* visits flowers of *Sesamum* (Pedaliaceae) and *Fidelia braunsiana* is confined to *Berkheya* (Asteraceae). The rainfall pattern divides the species into early summer bees (7 species) of the winter rainfall and autumn bees (4 species) of the summer rainfall areas. Two of the above species have populations in both regions. The winter rainfall bees have a south-western distribution with Graaff-Reinet the eastern limit but the summer rainfall species occur further north, with the eastern Botswana border their eastern limit and Keimoes on the Orange River their southern limit.

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Die Fideliidae is grondnestende bye wat met 'n digte dons bedek is wat wissel van strooikleurig tot bruin. Stuifmeel word op die buik versamel. *Fidelia paradoxa, F. villosa* en *F. kobrowi* versamel stuifmeel net op blomme van die Mesembryanthemaceae, en *Parafidelia major* en twee nuwe *Parafidelia*-spesies is beperk tot *Grielum*- en *Neuradopsis*-blomme (Roseaceae). *Parafidelia ornata* versamel stuifmeel hoofsaaklik van *Tribulus* en *Tribulocarpus* en *P. pallidula* van *Sisyndite* (Zygophyllaceae). *Parafidelia friesei* versamel stuifmeel alleenlik van *Sesamum* (Pedaliaceae) en *Fidelia braunsiana* is beperk tot *Berkheya*-blomme. Die reënvalpatroon verdeel die spesies in vroeë somersoorte (7 spesies) van die winterreëngebied en najaarspesies (4) van die somerreëngebied. Twee van die bogemelde spesies kom in albei gebiede voor. Bye wat in die winterreëngebied voorkom, het 'n suidwestelike verspreiding met Graaff-Reinet as die oostelike grens. Die najaarspesies het 'n meer noordelike verspreiding en Keimoes op die Oranjerivier is die suidelikste terwyl Serowe in Oos-Botswana die oostelikste versamelingsplek is.

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The genus *Fidelia* was established by Friese (1899) for the new species *F. paradoxa* from the Cape. Within a short period more new species were added (Brauns 1905; Friese 1905, 1911) as well as the new genus *Parafidelia* (Brauns 1926). Cockerell (1935) added several new species and Moure & Michener (1955) described a new genus from South America. A further new species, from Morocco, was added by Warncke (1980).

Because of the long mouthparts and scopa-like setae on the hind legs Friese (1899) placed his new genus near the Anthophoridae. Popov (1939) was the first to look at the genitalia and because of their structure considered these bees better placed near the Colletidae, but Moure & Michener (1955) found many megachilid-like characters which, with the evidence from larvae provided by Rozen (1977), indicated that they had definite affinities with the Megachilidae. Winston (1974) and Michener & Fraser (1978) place this group as the family Fideliidae between the Anthophoridae and the Megachilidae.

Biology

Research on the taxonomic revision of the bee family Fideliidae has entailed a considerable amount of field work which, although undertaken primarily to supplement the South African Museum collections, yielded valuable information on distribution, biology and flower relationships. These aspects of bee biology are not only interesting in themselves but have possible value in indicating taxonomic relationships.

Fideliid bees are medium to large (1 – 2 cm) with a dark integument which in most species is obscured by a dense cream to brown pile, sometimes also giving a banded appearance. They are extremely fast flying and do not hover at flowers but drop briefly into them to collect pollen or nectar. Pollen is not transported on the legs but on a dense mat of specially modified hairs on the underside of the abdomen. The leaf-cutter bees and their relatives (Megachilidae) also have this abdominal scopa but can be distinguished from the fideliids by several morphological and biological characters, the wing venation and their ability to hover at flowers being the most obvious.

The fideliids are all solitary, ground-nesting bees with pilose hind legs adapted for dispersing loose sand from the entrance of the burrow. Using the mandibles and legs, tunnels are dug into the sand to depths varying from 16 cm (Rozen 1977) to 2 m, depending on the species. Single cells are made at the end of the tunnels and are provisioned with a ball of pollen and nectar into which an egg is laid (Rozen 1977). The larva develops by feeding inside the brood ball and goes into a resting stage on reaching maturity. Pupation and emergence takes

place in spring, early summer or mid-summer depending on the species.

Males are the first to emerge in the season and patrol selected patches of pollen plants where they eventually mate in the flowers. Males are also the first to start the daily activity, arriving at the flowers at about 11h00. The patrolling is interspersed with brief feeding visits to flowers, mainly at the beginning and the end of the day. Other periods of rest are spent either basking on the sand or perched on a prominent point within the area patrolled.

From about 15h00 males return to the overnight nesting places. The overnight sites of only some of the species are known. Rozen (1977) found that *Parafidelia pallidula* females and also an occasional male slept in burrows in the soil. Some males of this species were found to overnight in the host flowers. I have regularly found both females and males of this species as well as *P. friesei* sleeping in flowers. Females of *Fidelia kobrowi*, like those of *P. pallidula* sleep in their burrows. Males of *Fidelia paradoxa, F. major* and *Parafidelia ornata* have all been seen to dig themselves into the soft sand at the end of the day.

Bee activity at the flowers is obviously affected by the daily rhythm of the hosts, some of which close at night and only open late in the day (*Grielum* spp. and Mesembryanthemaceae). Under normal early summer conditions flowers open at about noon with female bees arriving as the flowers open. However, on one occasion when the temperature had risen to 37 °C by 09h00, bees were active by 09h30. *Parafidelia friesei* and *P. pallidula* have *Sesamum* and *Sisyndite* respectively as hosts, the flowers of which do not close at night. In these species females were found to be active by 09h00.

The seasonal occurrence of the species depends on the time of rainfall. In the winter rainfall region where plants grow during the cool wet period to flower in spring and early summer, some bees (*Parafidelia major*) complete their seasonal activity by the first week of October and others (*Fidelia paradoxa, F. villosa, F. kobrowi*) start in October and complete their activity by the middle of January.

In the summer rainfall area bees start flying in December and continue into May (*Parafidelia friesei, P. ornata, Parafidelia* sp. C). There are two species, however, (*Parafidelia pallidula, Parafidelia* sp. A) whose host plants occur in both winter and summer rainfall areas. These bees have early summer populations in one area and autumn populations in the other.

Host plants

Fidelia paradoxa, F. villosa and *F. kobrowi* collect pollen and nectar exclusively from flowers of some (but not all) of the genera of the Mesembryanthemaceae. *Fidelia paradoxa* has the widest host range, 117 males and 221 females being collected on the following genera: *Aridaria, Brownanthus, Carpobrotus, Delasperma, Mesembryanthemum, Opophytum, Psilocaulon, Prenia* and *Spalmanthus. Fidelia kobrowi*, 20 males and 78 females, have been collected on the flowers of *Aridaria, Mesembryanthemum, Opophytum, Psilocaulon* and *Spalmanthus. Fidelia villosa* appears to have a narrower range of host flowers and has only been collected on *Mesembryanthemum, Prenia, Psilocaulon* and *Spalmanthus*. These genera have white, pale cream or pale pink flowers which, when open, form a shallow cup. The female bees simply drop into the flower to collect pollen and nectar. The plant genus *Grielum* and the closely related *Neuradopsis* (Roseaceae) provide pollen for two undescribed *Parafidelia* species and *P. major*. Two species of *Grielum* provide pollen for *Parafidelia major*, 57 females and 22 males being taken on this genus. However, 28 specimens, both males and females, were collected on flowers of *Hermannia, Arctotis, Mesembryanthemum* and *Lapeironsia* presumably taking nectar, as the females had no pollen on the scopa. *Neuradopsis* is the only plant on which *Parafidelia* sp. B (6 males, 9 females) has been collected. *Parafidelia* sp. A is found on both *Grielum* and *Neuradopsis* (82 males, 152 females) but two males have been collected on *Tribulus*.

Parafidelia ornata has been found to collect pollen from *Tribulus* (Zygophyllaceae) (11 females) but also from *Tribulocarpus* (Aizoaceae) (15 females). In the field it was noticed that from 09h00 to 11h00 females were seen only on *Tribulus* and when these flowers started to wilt, after mid-day, females moved on to *Tribulocarpus*. In the afternoon both males and females were found on many other flowers including *Salvia* and *Cleome* but none of the females was found to be carrying pollen. Another zygophilous plant *Sisyndite spartea* is the only plant visited by *P. pallidula*, on which 45 males and 24 females have been collected. *Parafidelia friesei*, the largest of the fideliids, has many morphological similarities to *P. pallidula* but collects pollen only from flowers of the genus *Sesamum* (Pedaliacae). Twenty-six males and 39 females were collected on this host but two females, without pollen were found on *Crotalaria*.

Fidelia braunsiana does not fit with any of the bee – plant groupings as it visits only the flowers of yellow thistles of the genus *Berkheya* (Asteraceae).

When arranged according to host plants, the fideliids fall into several groups (Table 1). Three of the fideliid species, *F. paradoxa, F. villosa* and *F. kobrowi* are all found on flowers of the Mesembryanthemaceae, many on the same species. Morphologically (shape of mandible, antennae, wing venation, male tergites), these three species are very similar so that grouping morphologically and according to host plant coincides. *Fidelia braunsiana* on the other hand, placed in *Fidelia* because

Table 1 Pollen plants of fideliid bees

Bee species	Family	Genus
Fidelia paradoxa	Mesembry-	*Aridaria*
F. villosa	anthemaceae	*Brownanthus*
F. kobrowi		*Carpobrotus*
		Mesembryanthemum
		Opophytum
		Prenia
		Spalmanthus
		Psilocaulon
F. braunsiana	Asteraceae	*Berkheya*
Parafidelia major	Rosaceae	*Grielum*
Parafidelia sp. A	Rosaceae	*Grielum*
		Neuradopsis
Parafidelia sp. B	Rosaceae	*Neuradopsis*
Parafidelia sp. C	?	?
Parafidelia ornata	Aizoaceae	*Tribulocarpus*
	Zygophyllaceae	*Tribulus*
Parafidelia pallidula	Zygophyllaceae	*Sisyndite*
Parafidelia friesei	Pedaliaceae	*Sesamum*

of wing venation and shape of the male tergites, has a very different host plant. Closer inspection showed that there were many characters (mandibles, marginal cell of forewing, antennae) which differed from the three *Fidelia* species on mesembryanthemums and substantiated the difference indicated by the host-plant grouping.

Parafidelia major and the two new species, *Parafidelia* sp. A and *Parafidelia* sp. B share the same or closely related host plants. They are also similar morphologically. *Parafidelia* sp. C and *P. ornata* are morphologically also similar to this group, but *P. ornata* has an unrelated host plant, whilst that of *Parafidelia* sp. C is unknown

The remaining species, *Parafidelia pallidula* and *P. friesei,* have similar mandibles and male tergites which are slightly different from the other *Parafidelia* species. Host plants, however, are not related.

From the foregoing it is apparent that similar species may have similar host plants but the many anomalies indicate that caution is required when extrapolating from morphological similarity to host-plant preference.

Distribution

Two species of Fideliidae are found in the desert areas of western Chile (Moure & Michener 1955; Rozen 1970), one species in southern Morocco (Warncke 1980) and 11 species in southern Africa. Our southern African species have a definite western coastal distribution with some spreading eastwards into the Karoo in the south and the Kalahari in the north. Because of their host specificity they are obviously restricted by the distribution of their host plants but in most cases are more limited, probably because their nesting requirements confine them to sandy substrates.

Three *Fidelia* species, *F. paradoxa, F. villosa* and *F. kobrowi,* are the three most numerous and widespread, occurring from Swakopmund in the north, down the west coast to Hermanus. Eastwards they are found in the Karoo as far as Beaufort West and Graaff-Reinet (Figure 1).

Parafidelia ornata, Parafidelia sp. B and *P. major* all have a limited western distribution (Figure 2). *Parafidelia ornata* has so far only been found from Khorixas to Usakos in the north and at Asab in the south, with one specimen from Gobabeb. *P. major* is distributed along the coast from the Klinghardt mountains to Clanwilliam. The new *Parafidelia* sp. B is found further inland on the red dunes at Seeis and along the eastern border of South-West Africa down to Noenieput in the north-ern Cape. Both *P. major* and *Parafidelia* sp. B excavate burrows to a depth of 2 m or more and have only been found where there are large dunes.

From Figure 3 it will be seen that *Parafidelia* sp. A has a coastal distribution similar to that of *P. major* and a south-western Kalahari distribution similar to that of *Parafidelia* sp. B. This is no coincidence as it shares the same hosts with the above two species, the coastal one in early summer and the western Kalahari host in autumn.

The distribution of *Fidelia braunsiana* (Figure 3) is mainly south-western and although the host plant (*Berkheya*) does occur up the east coast, the bee has as yet not been found in that area. The isolated record from the north-eastern Transvaal is the type locality. No further collections have yet been made there.

The largest bee in this family, *Parafidelia friesei,* has a trans-Kalahari distribution from Sesfontein in the north-west to the eastern border of Botswana. The most southern collection in South-West Africa was made at Gibeon, and in the Cape at

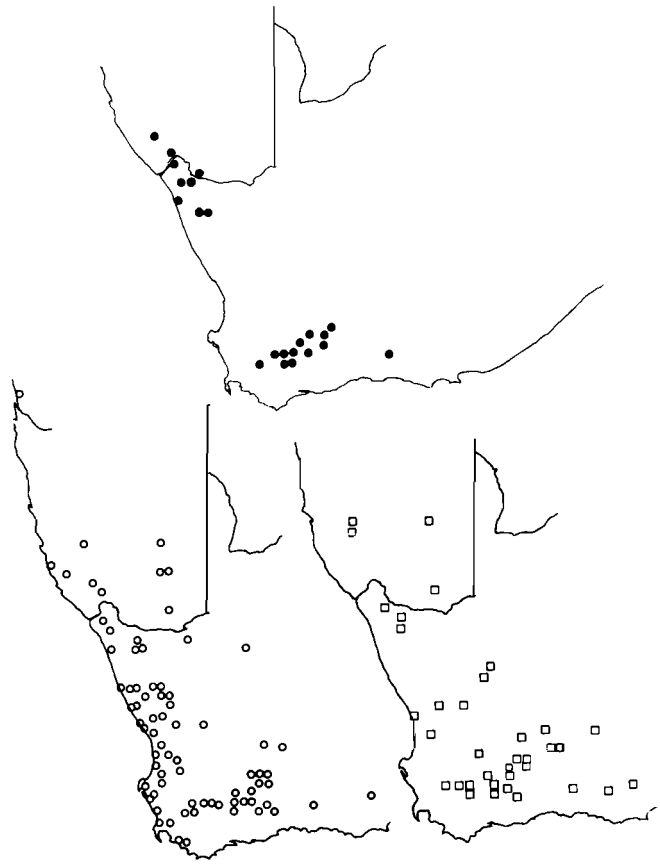

Figure 1 Distribution of *Fidelia paradoxa* ○, *F. villosa* □, and *F. kobrowi* ●.

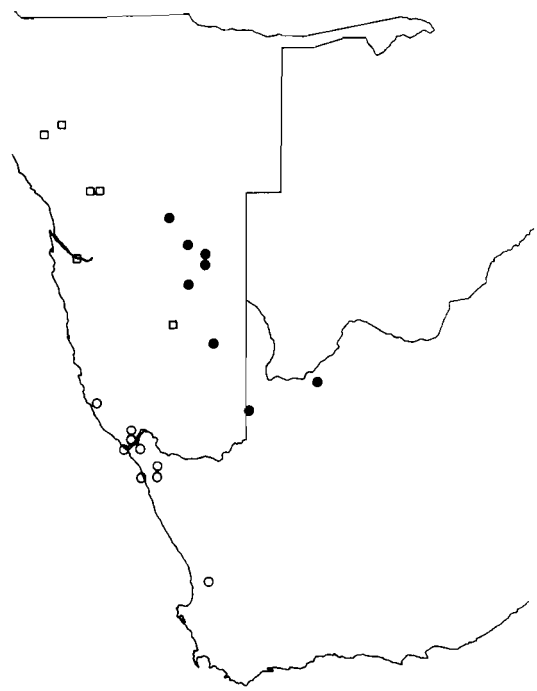

Figure 2 Distribution of *Parafidelia ornata* □, *Parafidelia* sp. B ●, and *Parafidelia major* ○.

Danielskuil (Figure 4). Also in Figure 4 is shown the restricted distribution of *P. pallidula* within the area bounded by Keetmanshoop, Augrabies, Springbok and the coastal dunes.

Parafidelia sp. C is known only from one male and two females collected 16 km north of Vioolsdrift on the Orange River. The host plant is not known and after five years of collecting in that area, no further specimens have been found.

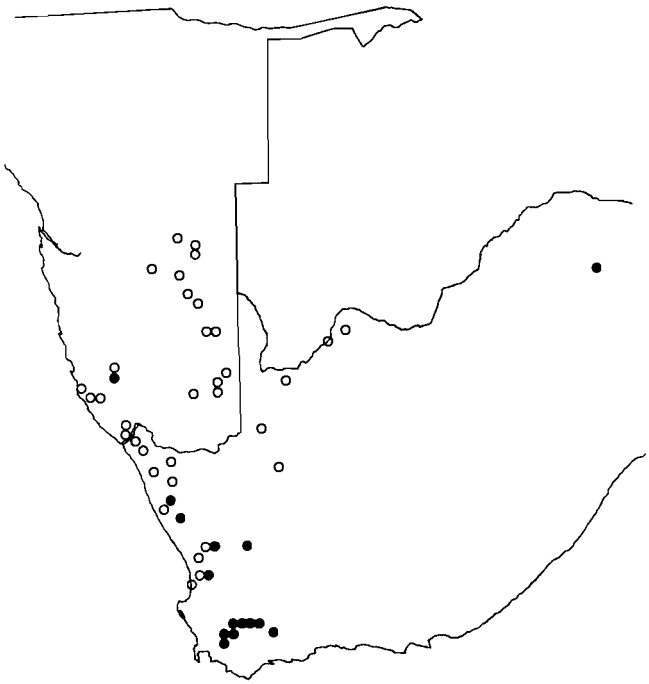

Figure 3 Distribution of *Parafidelia* sp. A ○ and *Fidelia braunsiana* ●.

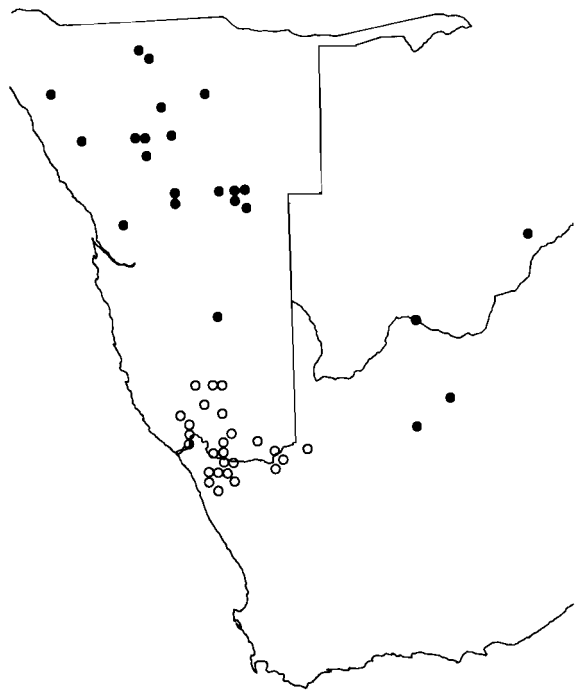

Figure 4 Distribution of *Parafidelia friesei* ● and *P. pallidula* ○.

Discussion

The fideliids of southern Africa have a relatively restricted distribution in the western part of the region, but *Fidelia braunsiana*, whose host plant has an Africa-wide distribution, has been collected outside this area.

When grouped according to host plants, two clusters of species appear, three of the *Fidelia* species (*F. paradoxa, F. villosa, F. kobrowi*) on Mesembryanthemaceae and three *Parafidelia* (*P. major, Parafidelia* sp. A, *Parafidelia* sp. B) on Roseaceae. *Fidelia braunsiana* does not fit with the other species of this genus from the host plant point of view and morphologically has characters which fall between the two genera. Host-plant association also adds little to the grouping of *Parafidelia friesei* and *P. pallidula* nor does it give any pointers to the relationships of *Parafidelia ornata* or *Parafidelia* sp. C.

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