

THE DIASCIA FLOWER AND ITS BEE – AN OIL-BASED SYMBIOSIS IN SOUTHERN AFRICA

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Key words: *Diascia* – Scrophulariaceae – *Rediviva* – Melittidae – Oil-flowers

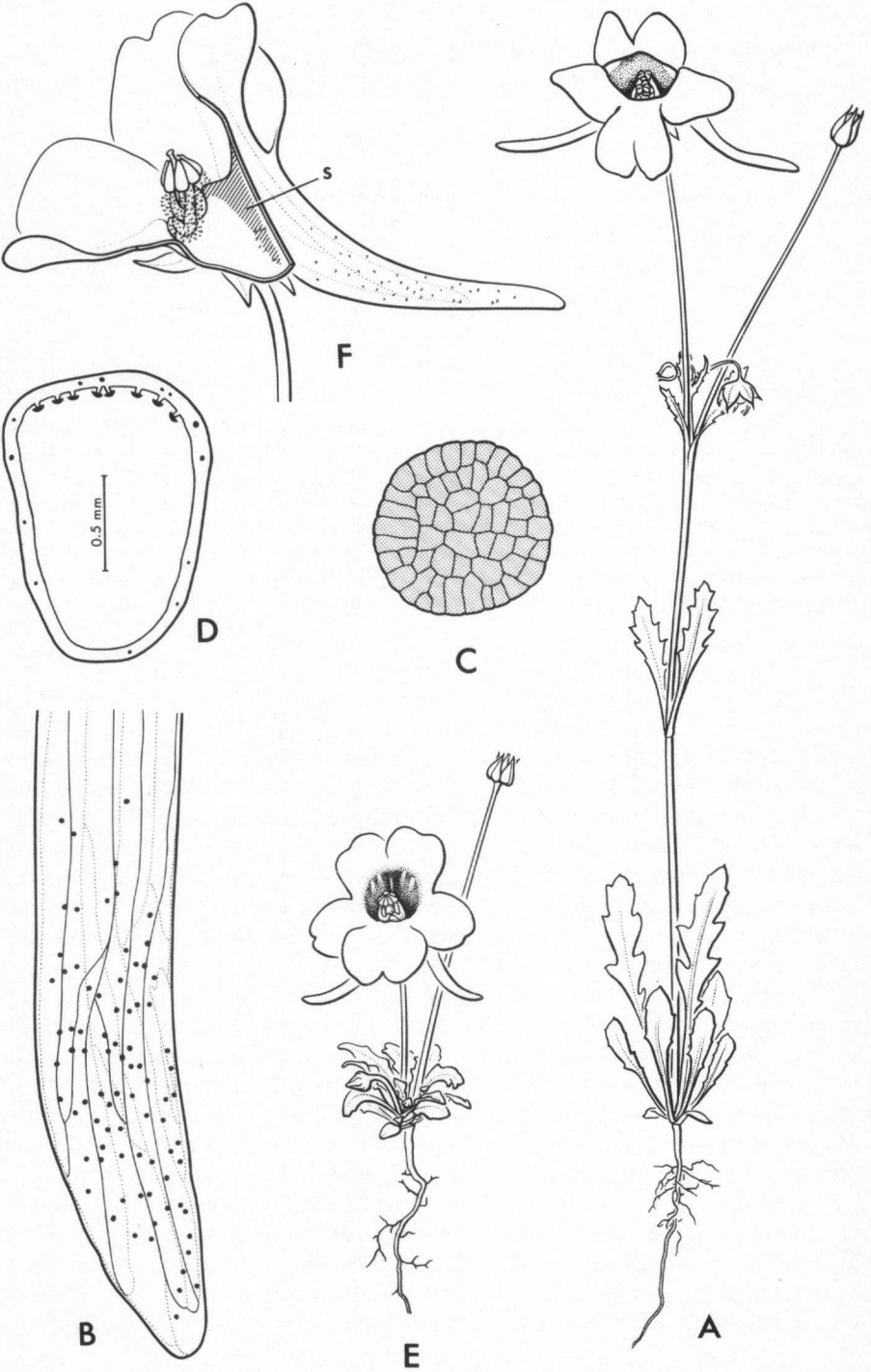
SUMMARY

As has been formerly shown, the double-spurred flowers of the South African genus *Diascia* (Scrophulariaceae) produce fatty oil as a primary attractant. Their oil-collecting pollinators have so far remained unknown. It is concluded from the morphology and from direct evidence of flower visitation that the recently established Melittid genus *Rediviva* represents the co-evolved pollinator group of these plants, at the same time demonstrating the presence of “manual” oil collectors in Southern Africa. The bees must introduce their especially equipped forelegs into the paired spurs of *Diascia* for harvesting the oil, thereby pollinating the flower. In the described case, a new species, *Rediviva emdeorum*, has extremely elongate front legs which perfectly fit the spurs of *Diascia longicornis*.

1. INTRODUCTION

Beginning with Darwin’s famous prediction that a hawkmoth will be found with a tongue long enough to manage the 30 cm nectar spur of Madagascan *Angraecum sesquipedale*, a prediction which later came true, anthecologists repeatedly have been fortunate in experiencing the discovery of a certain special pollinator they previously had inferred from the shape or syndrome of a flower. Sometimes, however, such a deduction, though logical to some extent, sounds too fantastic to be worth postulating seriously. This seemed to me to be the case when I formerly considered the adaptation of certain *Diascia* flowers.

The delicate double-spurred flower of *Diascia*, a genus belonging to the tribe Hemimerideae of Scrophulariaceae and comprising around fifty species of southern Africa, were believed to produce nectar in the usual fashion by J. D. HOOKER (1871) and GOEBEL (1928: 386). Initially sharing this error (VOGEL 1954) I later found the spurs of *Diascia* to contain, in lieu of nectar, small amounts of fatty oil (VOGEL 1974: 34). The secretion of floral oils in special glands (elaiophors) as a primary attractant to pollinators was first discovered in *Angelonia*, a South American relative, the corollas of which bear a similar pair of pouches or spurs, and in *Calceolaria* (tribe Calceolarieae). Both genera, along with “oil flowers” of various other families, were found to be pollinated by solitary bees belonging to three endemic subfamilies of the Anthophoridae whose females are specialized to collect oil and pollen as a mixed provision for their offspring.



As the collecting procedure of these bees consists in the scraping or brushing the oil with their especially equipped fore- or also middle legs, the development of paired lateral oil sources (elaiophors) as is found in the Malpighiaceae, the Krameriaceae, and some Orchidaceae, was an understandable coadaptive consequence. As a rule, the elaiophors are freely exposed; in a few instances they were for their protection sunk into pouch-like depressions, just as nectaries may be hidden in tubes or spurs. While the nectaria of zygomorphous flowers usually have a median position, corresponding to insects' tongues, "oil spurs" accessible for legs had to be double, as encountered in *Angelonia*. Although field observations on this genus are scarce and fragmentary till now, it is certain that its visitors, bees of the genus *Centris*, pollinate the flower in a median position of their bodies while gathering oil by inserting their forelegs into the pouches simultaneously (VOGEL 1974: 159).

Records on the natural pollination of *Diascia* were not available. Once this genus was recognized to have oil flowers, it seemed consequent to predict a similar way of exploitation as in *Angelonia*.

However, there were two handicaps that made this supposition improbable: firstly, the absence of oil-collecting Anthophorids, or seeming absence of other "manual" oil collectors in the home country of *Diascia*. And secondly, the narrow, elongate flower spurs of some species which appeared incompatible with any potential oil collector. Of the two bee genera later recognized to be oil collecting pollinators in the eastern hemisphere, *Macropis* (Melittidae, also in North America), and *Ctenoplectra* (Ctenoplectridae), the latter only occurs as far south as South Africa, accompanying *Momordica* (Cucurbitaceae), one of its two known oil host genera. *Ctenoplectra* mops the floral oil from the large elaiophors of these plants, using its specialized abdomen instead of its legs (VOGEL 1981). Technically, *Ctenoplectra* could also be a pollinator (still to be verified) of *Bowkeria*, another South African plant group producing oil as a floral attractant, which is a member of the Scrophulariaceae but not closely related to *Diascia*; yet it would be unable to enter narrow spurs such as those of *Diascia*.

At least, the existence of another unknown insect capable of "manual" oil collecting in Southern Africa could have been postulated, having in view those *Diascia* species with spurs of moderate sizes, accessible for visitors of normal proportions. But as mentioned above, it was difficult to imagine bees with collecting organs so exceedingly elongate as to fit some western species of *Diascia* which possess spurs up to 25 mm in length. Such organs "...setzen ja grotesk verlängerte Sammelbeine voraus!" (VOGEL 1974: 162). As this seemed unlikely, we suggested some unknown insect able to extract oil from these deep spurs successively with its tongue or proboscis for direct consumption. Nevertheless the bees with the elongate forelegs do exist, and actually prove to be visitors

Fig. 1. A. *Diascia longicornis* (1.3 × nat. size), B. distal part of the spur, cleared, showing the oil-producing glands on the opposite inner wall, C. a single glandular head seen from top, enlarged, D. *D. barberae*, cross section of the spur with unilateral elaiophor. E. *D. nana* (1.3 × nat. size), F. its flower in a median section; s = septum between the spur orifices.

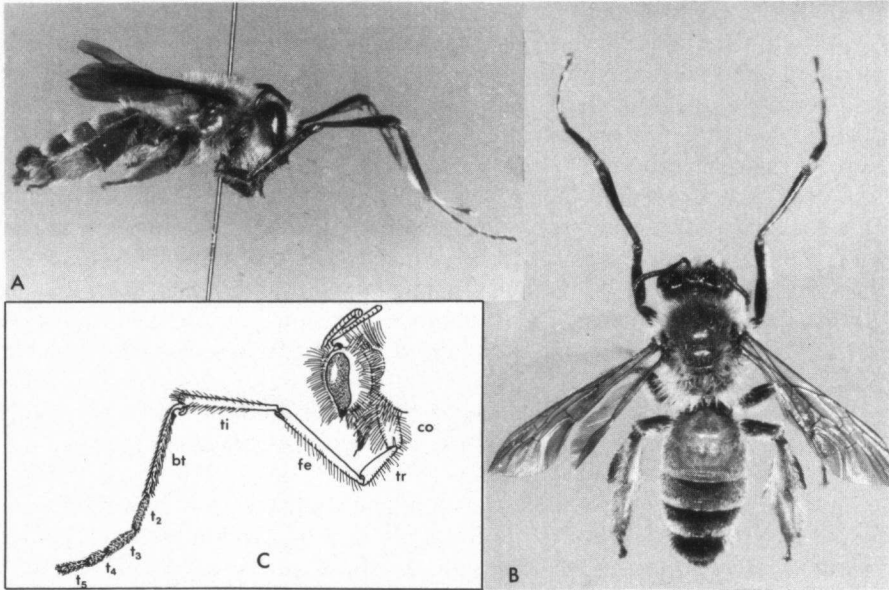


Fig. 2. A and B. *Rediviva emdeorum*, female, dorsal and lateral view. C. head and left front leg. t2-5 = tarsi, bt = basitarsus, ti = tibia, fe = femur, tr = trochanter, co = coxa.

of a long-spurred *Diascia*. Informations on these strange Hymenoptera was now gained from two independent sources.

In his classification of the bee family Melittidae, MICHENER (1981) re-established a genus *Rediviva* Friese (= *Notomelitta* Cockerell) comprising some eight species*. The group had been originally misplaced as a subgenus of *Andrena* (Andrenidae) because of the superficial resemblance of the type species to certain true members of this genus found at the Cape. While some species of *Rediviva* have normal proportions, the ♀♀ of various other ones including the type of the new genus, *R. peringueyi* Friese (collected near Paarl, Cape Province) exhibit front legs slightly to distinctly longer than normal. Professor Michener who on close examination recognized the group in question as belonging to the Melittidae, subfamily Melittinae, assigned to it two new species; one of them, *R. longimanus* Michener (= long-handed) had been collected in September 1961 near Nieuwoudtville in the Calvinia district, a semi-desert region of the western Cape. According to the description and drawing (MICHENER 1981: 46, 123) based on a single female which is deposited in the South African Museum (males are not known), the bee possesses front legs of about 19 mm length, exceeding by far her body length (14 mm). The remaining extremities have normal proportions. On the basis of the other new species, *R. colorata* Michener, with males and females known (the latter only with – moderately – elongate front legs), it could

* Described by FRIESE 1911: 671; and COCKERELL 1931: 401; 1934: 449.

be concluded that the character is restricted to the female sex. A second specimen near *R. longimanus* in the South African Museum collection without data differs somewhat in coloration, possibly a conspecific morph.

MICHENER (1981) further established a surprising resemblance of *Rediviva* to *Macropis*. The oil-collecting property of this Holarctic genus belonging to the same subfamily was described by VOGEL (1976) and CANE et al. (1983). From his finding of specialized hair vestiture on the legs similar to that of *Macropis*, Michener already inferred a possible connection with oil collecting, and attributed the elongate shape of the forelegs of some species to the respective manipulation of "some specific kind of flower...", although at that time nothing was known about the habit or host plants of *Rediviva* "...Whatever the function of the fore tarsal pubescence of females, it must be exaggerated in females of certain species which have these tarsi and indeed the whole front leg greatly elongated..."

MICHENER's (1981) description of *Rediviva longimanus* presented exactly what could be the pollinator of a long-spurred *Diascia*. Indeed, I found two of such species belonging to sect. Axillares recorded in the Flora Capensis (THISLTON-DYER 1904: 151) from the Calvinia region where the longimanous bee had been collected: *D. nana* Diels (spurs 10–12 mm; fig. 1E), a local endemic, and *D. longicornis* (Thunb.) Druce (= *D. thunbergiana* Spreng., = *D. tanyceras* E. Meyer; spurs 13–25 mm), with a distribution extending from Malmesbury to the Little Namaqualand, where also *D. namaquensis* Hiern. occurs, with spurs 17 mm long.

2. MATERIAL

Recently I had the pleasure of receiving a well preserved individual of another long-armed bee which I recognized as a species of *Rediviva*, confirmed to be new by Prof. Michener. It was presented to me by my colleague Professor D. Müller-Doblies from the Technische Universität of West Berlin, and his wife, well-known experts of the Liliiflorae of the Cape. During one of their field trips they had remembered our unsolved problem, and also inspired their son Uwe, then eleven years old, to have a look for *Diascia*. Uwe was lucky enough to capture the animal near Grootvlei, W of Kamieskroon in the Little Namaqualand on August 15, 1979.

The bee, again a female, had been visiting patches of a long-spurred annual species of *Diascia* growing in the arid plains on deep sand. Samples of this population, kindly forwarded to me by the finders, were identified as *D. longicornis*.

3. OBSERVATIONS

No details about the flower visitation could be observed. However, we found the bulk of yellow pollen adhering to the dried bee to be identical with that of *Diascia longicornis*; the grains are quite distinctive*. Mixed with hardened

* Small, isopolar, $p = 16-17 \mu\text{m}$, $e = 20-21 \mu\text{m}$, suboblate, zoni-7(8)-colpate, granulate including polar areas.

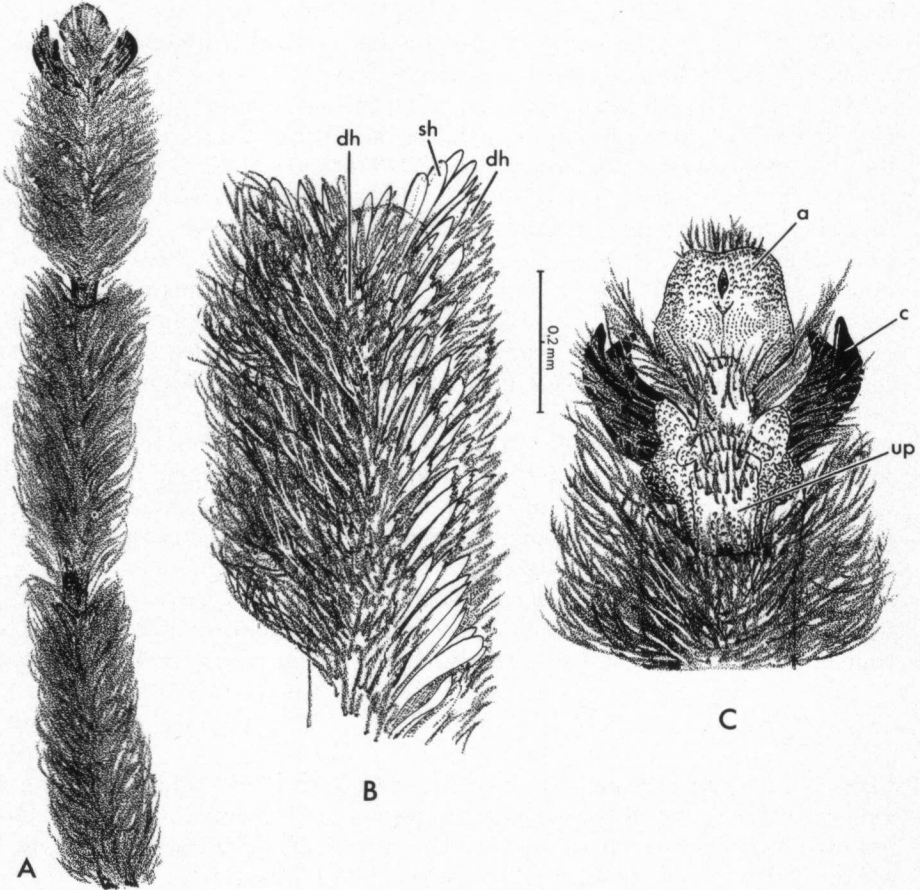


Fig. 3. *Rediviva emdeorum*, front leg of female with oil-collecting structures. A. three distal tarsi, seen from above, B. part of fourth tarsus, seen from below, showing rows of spatulate (sh) and dentate (dh) trichomes, C. end of fifth tarsus, seen from below, with claws (c), arolium (a) and unguitractor plate (up).

remnants of oil, this type also prevailed in the scopal loads. No doubt is left that *Diascia longicornis* is the oil host (and possibly the only one) of this bee, as is also obvious, on the part of the latter, by its morphological adaptation so tightly fitting the spurs of the flower.

The samples as shown in Fig. 1A are small plantlets, 10 or 12 cm high, bearing 1–3 flowers open at the same time in a terminal, leafy raceme. From photographs in LE ROUX & SCHELPE (1981: 116) and ELIOVSON (1972, pl. 27) it follows that this species (“Bokhorinkies”) may be taller and many-flowered upon moister conditions. As far as can be assessed from our dried material and the pertinent literature, the flower of *D. longicornis* is basically similar in shape to that of the often cultivated *D. barberae* Hook. which has spurs only 9 mm long. The

throat is produced, below the anterior lip, into the two lateral divergent spurs (of 20 mm length and 1.5 mm width in our samples), which are curved towards the front of the flower. Their entrances lie on either side of the 4-staminate isantherous androecium and style which project forward close to the floor of the corolla's mouth. According to THISELTON-DYER (1904: 152) the colour is red on the segments and deep purple inside, with two bright yellow markings, each above the orifice of a spur.

Fig. 1F shows in greater detail the flower of *D. nana*, drawn from alcohol material which I also owe to my colleague D. Müller-Doblies (collected near Soetwater, Calvinia division, October 11, 1978). This stemless, dwarfish species (fig. 1E), a near relative of *D. longicornis*, has somewhat shorter spurs, a glandular-pilose androecium, and four yellow spots. Remarkably, the corolla bears on each of the five intersegmental angles a couple of (secreting?) glands equivalent to those inside the spurs.

From the position of the androecium and the main area of pollen deposited on the insect – a median prothoracic portion including the middle coxae – a symmetrical posture of the bee and sternotribic pollination can be deduced. I assume that the bee must lower her stretched forelegs simultaneously down the spurs already before landing on the lip. She will only contact the pollination organs when her feet have reached the bottom of the spurs.

The elaiophors of *D. longicornis*, not seen in the living state, are similar anatomically to those of *D. barberae* which have been described in detail (VOGEL 1974: 34) and consist of big, hemispherical, blackish secretory hairs which comprise about 56 glandular cells each (figs. 1B–D). It is interesting to note that the glands' number is much smaller (± 90 per spur) than in *D. barberae* (± 200), although the spurs of the former are one and a half times longer. Its scattered glands are confined to the distal third of the concave interior (adaxial) spur wall. Presumably the secretion does not fill the spur lumen in the manner of nectar but merely forms a liquid patch, or film adhering to the surface of the glandular area, as also happens with *D. barberae*. Thus the bee cannot fully submerge her feet into the fluid but only absorb it by "dabbing" a moist layer.

The newly discovered *Rediviva emdeorum* Vogel et Michener* with a body length of 15 mm still surpasses *R. longimanus* in the dimensions of its front legs (26 mm). All of the slender limbs including coxa and trochanter take part in the elongation (figs. 3A–C). As compared to the sizes of "normal" legs such as the middle leg of the same individual, or e.g., the forelegs of *R. rufocincta* Cockerell (see MICHENER 1981: 46), it has extended more than threefold. Following our measurements and taking the latter species as a basis, the respective elongation is allometric, the increase rate of the five tarsal segments (4.7) being greatest among all segments, which average 2.9. Its evolutionary growth rate rose exponentially, because the corresponding values of *R. longimanus* are 3.3 : 2.3. The strigilus is so remote that the bee probably does not use it in cleaning her antennae. Possibly these legs do not even take part in stepping and sitting.

*The epitheton signifies the initials: M and D = Müller-Doblies, a dedication to the finder and his family.

Their bidentate claws, almost hidden among plumose hairs, have a weak and reduced appearance while the arolium is unusually big. (*fig. 3C*).

Originally the tarsi had been pasted up with hardened remnants of oil. The sample was cleaned by exposing it to a sonocation vibrator following NEFF & SIMPSON (1981).

As Michener already noticed in his species, the tarsi of the front and middle extremities bear dorsally a dense velvety hair vestiture, which he related to possible oil-harvesting. More precisely, at least in *R. emdeorum*, the specialized pubescence is only pronounced on the dorsal side but also covers the ventral part where it is shorter and somewhat flattened. In the tarsalia, except the distal (fifth) one, this ventral cover, which is probably the only part directly involved in the "dabbing", bears on its outer flanks longitudinal rows of trichomes different from the pinnate remaining hairs: shorter, lamellar pluridentate, and longer, blunt spatulate trichomes (*fig. 3A, B*). There is again resemblance to *Macropis* in these points (VOGEL 1976).

As was tested with castor oil, the hair cover develops strong capillary forces. When applied to the foot tip, the lipid readily flows up to the tibia – just as in a wick; when in touch with the "sole", it will quickly be taken up by the spongy pubescence above. These observations allow us to reconstruct the way in which *Rediviva* collects the oil: Having introduced her forelegs, she presses, in an embracing attitude, her tarsal soles, in particular their spatulate crests, upon or across the elaiophor, thereby mopping the liquid which then preliminarily accumulates in the dorsal cover. In a second manipulation which perhaps takes place on the wing, the soaked feet will be squeezed out by pulling them lengthwise through the flexed middle legs of the same side (which are equally furnished with storage vestiture but lacking the collecting hairs); finally, the middle legs transmit the oil by an analogous procedure to the scopae. A corresponding behaviour was observed in *Macropis* (VOGEL, in preparation). As MICHENER (1981) already pointed out, the scopae of *Rediviva*, covered with a plumose "understory" interspersed with long bristles on the tibia and basitarsus, also resemble those of *Macropis*.

Because *Diascia* has no nectar and only little pollen, it follows that the bee certainly directs her entire activity to the oil; but she may subsequently comb and collect pollen from her body during flight. Our individual bore considerable scopal loads. A glucose test of the loads was negative. As already mentioned, the main constituent was *Diascia* pollen embedded in an insoluble translucent mass, no doubt solidified oil of the same plant. Three to four other pollen types were found each in low numbers, indicating that the bee had also visited plants of other kinds, probably for nectar or pollen. Since *Rediviva* has a very short tongue (1,5 mm) its nectar hosts should be allophilic, like those of *Macropis*.

4. PHYLOGENETIC CONSIDERATIONS

The oil-based symbiosis of *Diascia* has biohistoric and evolutionary implications of considerable interest.

Its near relative in the Neotropics, *Angelonia*, has unrelated pollinators but a similar morphology and a similar ecology. Did these taxa acquire their floral syndrome independently?

The occurrence in the southern hemisphere of a Melittid group morphologically and biologically so akin to the Holarctic genus *Macropis* raises the same question: had they a common ancestry or distant origin within the subfamily Melittinae? Following Michener, the crossing of structural characters renders this question difficult to answer. The acceptance of a monophyletic origin of oil-collecting, as a synapomorphism of the Melittinae, has the consequence that the rest of this subfamily including *Melitta* must have secondarily lost this property. An independent evolution, on the other hand, would represent a remarkable case of parallelism. MICHENER (1981) preliminarily proposes two alternative cladograms. It is in favour of convergent evolution that the oil hosts of *Macropis* and *Rediviva* are taxonomically not related and in their distribution as separated as their bees. Notabene, of *Lysimachia* (the genus comprising the oil hosts of *Macropis*) only nectar-producing groups have reached tropical and southern Africa.

Future observations will have to show how directly the array of different spur lengths of *Diascia*, ranging from the rotundate, spurless corolla of *D. engleri* Diels to the long-horned flower of *D. longicornis* (DIELS 1887; VOGEL 1974: fig. 13, p. 35), parallels the gradation of front leg lengths exhibited by *Rediviva*. Judging from the great diversity in flower modelling, form and curvature of spurs and pouches, stamen positions etc. within the genus, as pointed out by HILLIARD & BURTT in their forthcoming revision of Sect. *Racemosae* of *Diascia* (*Journ. S. Afr. Bot.*, in press), the anthecological interrelations are probably more complicated.

In my earlier work (VOGEL 1974: 37) I have presented some evidence that spurs and glandular covers were initially independent, and that the elaiophors were incorporated only subsequently into the spurs. On the other hand, spurs and the yellow guides ("windows") which form shallow pits, seem to be homologous, both having developed from a ring-like or pentamerous basal depression still found in more primitive species.

Rediviva may well have co-evolved with *Diascia* from the beginning. The term "co-evolution" certainly applies here in its literal sense, but of course, it does not yet provide by itself the full explanation, especially if we consider the phenomenon of parallelism in the sister genus *Angelonia*.

With the help of direct observations we must also try to shed light on how both organs, flowers' spurs and bees' legs, influenced each other to become longer and longer... Whatever the explanation will be, our *Diascia/Rediviva*-symbiosis is another impressive example of a certain "hypertelic" tendency of evolution, i.e. a tendency to allow a functional system to drift, by its inherent dynamics, far beyond what would seem to us an "economic", let alone a "parsimonious", relationship.

ACKNOWLEDGEMENTS

I am most thankful to Uwe Müller-Doblies (Berlin) for leaving to me the sample of *Rediviva emdeorum*, and to his parents, Dr. Ute and Professor Dr. Dietrich Müller-Doblies for the material of *Diascia*. Professor Ch. Michener (Kansas) kindly has provided the description of the bee (to be published separately). I also owe thanks to Dr. B. L. Burt (Edinburgh) who enabled me to see drafts of his manuscript, and to Professor Dr. D. Hartl, Dr. U. Hecker and Ch. Westerkamp (Mainz) for literature hints. *Fig. 1* has been drawn by E. Goepfert (Mainz).

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