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THE ECOLOGY OF OIL FLOWERS AND THEIR BEES[1]

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INTRODUCTION

Nectar and/or pollen are the only floral rewards traditionally investigated. Such myopia has impeded full understanding of flower-visiting organisms. Flowers in fact offer a great diversity of products, all in the name of accomplishing their gene flow, including: nectar, pollen resin, volatiles, lipids, and waxes. Narrow views that focus only on nectar and pollen as "the" floral rewards date from the earliest investigators and often continue today.

A new area of research in pollination ecology arose in 1969 when Stefan Vogel (75) described a hitherto unrecognized "floral syndrome." Plants in many genera of five families (Iridaceae, Krameriaceae, Malpighiaceae, Orchidaceae, Scrophulariaceae) were confirmed as having highly specialized oil-secreting organs, he called these elaiophores. To these floral groups have been added genera containing oil flowers in the families Cucurbitaceae, Melastomataceae (tribe Memecyleae only), Solanaceae, Primulaceae, and Gesneriaceae. Oil flowers are found most abundantly, but not exclusively, in neotropical savannas and forests. Flowers offering fatty oils instead of, or in addition to, nectar and/or pollen are found in 8 orders, 10 families, 79 genera, and 2402 species of flowering plants worldwide (Table 1).

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Table 1 Angiosperm (Division Magnoliophyta) taxa, with oil-producing elaiophores. Classification follows that of Cronquist (1981). Numbers following families and genera (numerator values are elaiophore-bearing taxa, while denominator gives total genera or species in taxon).

Class Liliopsida (monocots):		
Subclass		
Liliidae	Liliales	
		Family Iridaceae 60/800 (*Alophia* 10/10, *Cypella* 15/15, *Ennealophus* 7/7, *Sisyrinchium* 40/100, *Sphenostigma* 17/17, *Tigridia* 1/12, *Trimezia* 5/5)
	Orchidales	
		Orchidaceae 735/20,000 (*Anochilus* 1/1, *Ceratandra* 6/6, *Corycium* 15/15, *Disperis* 75/75, *Huttonaea* 5/5, *Maxillaria* 20/300, *Oncidium* 50/350, *Ornithocephalus* 50/50, *Pterygodium* 18/18, *Sigmatostalix* 16/16, *Zygostates* 4/4
Class Magnoliopsida (dicots):		
Subclass		
Dilleniidae	Violales	
		Cucurbitaceae 2/110 (*Momordica* 45/45, *Thladiantha* 15/15)
	Primulales	
		Primulaceae 1/20 (*Lysimachia* 78/200)

Subclass
  Rosidae
Myrtales
  Melastomataceae 6/240 (*Memecylon* 285/300, *Mouriri* 71/75, *Spathandra* 6/6, *Votomita* 6/6, *Warneckea* 31/31)
Polygalales
  Krameriaceae 1/1 (*Krameria* 25/25)
  Malpighiaceae:
    Acmanthera 6/6
    Aspicarpa 10/10
    Banisteriopsis 83/92
    Barnebya 2/2
    Blepharanda 6/6
    Burdachia 65/65
    Byrsonima 150/150
    Callaeum 10/10
    Camarea 7/7
    Clonodia 2/2
    Cordobia 1/1
    Diacidia 12/12
    Dicella 6/6
    Dinemandra 3/3
    Diplopterys 4/4
    Galphimia 4/10
    Gaudichaudia 20/20
    Glandonia 3/3
    Heladena 3/3
    Henleophytum 1/1
    Heteropterys 120/125
    Hiptage 30/30
    Hiraea 55/55
    Janusia 20/20
    Jubelina 6/6
    Lophanthera 5/5
    Lophopterys 8/8
    Malpighia 45/45
    Mascagnia 55/55
    Mcvaughia 1/1
    Mezia 6/6
    Peixotoa 28/28
    Peregrina 1/1
    Pterandra 11/11
    Spachea 6/6
    Stigmaphyllon 100/100
    Tetrapterys 87/90
    Tricomaria 1/1
    Triopterys 3/3
    Tristellateia 9/18
    Verrucularia 2/2

Subclass
  Asteridae
Scrophulariales
  Scrophulariaceae 220/3000 (*Angelonia* 30/30, *Alonsoa* 6/16, *Anastrabe* 1/1, *Basistemon* 7/7, *Bowkeria* 3/3, *Calceolaria* 388/400, *Colpias* 1/1, *Diascia* 38/45, *Hemimeris* 4/4).
  Gesneriaceae 120/2000 (*Drymonia* 5/35)
Solanales
  Solanaceae 1/90 (*Nierembergia* 5/35)

Total Worldwide: 8 Orders, 10 Families, 79 Genera and approximately 2402 oil-producing species.

Table 2 Families and genera of bees that have structural modifications for harvesting and transporting floral lipids, and those that occasionally harvest oils but are not morphologically modified (e.g. Apidae). Oil host plants are also indicated by genus when known.

Oil-Collecting Bees	Oil Host Plants
Family Melittidae	
S. F. Melittinae - *Macropis* (18)	*Lysimachia*, Primulaceae
- *Rediviva* (9–19)[1]	*Alonsoa, Anastrabe, Anochilus, Bowkeria, Ceratandra, Colpias, Corycium, Diascia, Disperis, Hemimeris, Huttonaea, Pteygodium*, Scrophulariaceae, Orchidaceae
Family Ctenoplectridae	
- *Ctenoplectra* (26)	*Momordica, Thladiantha*, Cucurbitaceae
Family Anthophoridae	
S. F. Anthophorinae	
Tribe Centridini	
Centris (200+)	*Krameria, Calceolaria, Nierembergia*, Krameriaceae, Scrophulariaceae, Solanaceae, many Malpighiaceae
Ptilotopus (24)	Malpighiaceae
Epicharis (30)	*Drymonia*, Gesneriaceae, many Malpighiaceae
Caenonomada (5)[2]	unknown, Malpighiaceae?
Tribe Exomalopsini	
Chalepogenus (1)	*Cypella*, Iridaceae
Lanthanomelissa (4)	Iridaceae?
Monoeca (6–10)	*Malpighia*, Malpighiaceae
Paratetrapedia (35–55)	*Mouriri*, many Malpighiaceae, Melastomataceae.
Tapinotaspis (10–12)	*Calceolaria, Nierembergia, Sisyrinchium*, Scrophulariaceae, Solanaceae, Iridaceae
Tribe Tetrapediini	
Tetrapedia (13)	Malpighiaceae, Orchidaceae?
Family Apidae	
S.F. Meliponinae	
Tribe Meliponini	
Trigona (3)	*Mouriri, Drymonia, Stigmaphyllon*, Melastomataceae, Gesneriaceae, Malpighiaceae
Melipona (1)	*Mouriri*, Melastomataceae

[1] When ranges given, first number denotes named species within genus and second, the sum of described plus undescribed species (C. Michener, R. Snelling personal communication).

[2] *Caenonomada* (formerly placed in Exomalopsini) may be an oil-harvesting centridine. It lacks basitarsal oil-scraping setae but has long pile similar to *Rediviva*.

Oil flowers are visited and pollinated by highly specialized bees (Hymenoptera: Apoidea) found in four families (Melittidae, Ctenoplectridae, Anthophoridae, Apidae) and 15 genera comprising 1.9% of the approximately 800 bee genera and 1.4% of the more than 30,000 bee species (Table 2). Oil bees use energy-rich floral oils in diverse ways: Some bees use the lipid secretions with or in place of nectar in their pollen provisions for larval development. Others use the oils not only as larval foodstuffs but also for water-resistant cell linings, and possibly even for adult nutrition.

OIL SECRETION BY ANGIOSPERMS

Botanists have known for over 100 years that some flowers, such as *Krameria* or Malpighiaceae, have unusual secretory glands. These unexplained structures were believed by early workers to be full or vestigial nectaries. Surprisingly, these received no detailed attention until late in the twentieth century, even though pollination ecology has a long rich history dating from Dobbs (14) and Sprengel (68). The number of plant taxa (classification of Cronquist, 13) containing at least some species with elaiophores represents 9.6% of the angiosperm orders, 2.6% of the families, and about 1.0% of the species. The polyphyletic evolution of oil glands has been a highly successful evolutionary strategy. Moreover, once elaiophores evolved in a group they were infrequently lost (Table 1). The pollination ecology of the Krameriaceae has recently been reviewed by Simpson and coworkers (62–66) and will not be reviewed further.

Vogel (79) recognized two very different morphological types of elaiophores. Epithelial elaiophores are small areas of secretory epidermal cells in which the secreted lipids accumulate in great quantity below a thin protective cuticle (Figure 1B). Examples of epithelial elaiophores are found in the Krameriaceae, Malpighiaceae, Melastomataceae (Memecyleae), and some Orchidaceae. These are the numerically dominant type of lipid-secreting organs. The second type is trichome elaiophores. They consist of fields of many hundreds to thousands of glandular trichomes that actively secrete lipids (Figure 1A). Flowers with this type of organ are found in the families Iridaceae, Cucurbitaceae, Primulaceae, Scrophulariaceae and Solanaceae (Table 1). Each flower or gland usually secretes far less lipid than epithelial elaiophores. A film of oil is produced, which forms an oil reserve. Secretions from trichomatous elaiophores are not covered by a protective cuticle and are thus sometimes exposed to air and floral visitors of all types. Nonetheless, partial protection may be afforded inside complicated flowers *(Calceolaria)* or within deep spurs that to the uninitiated resemble nectar spurs *(Diascia).*

CHEMISTRY OF ELAIOPHORE OILS

Floral lipid collection for chemical analysis is laborious when elaiophores are of the trichomal type but is relatively easy from flowers possessing larger epithelial glands. Oil secretions from trichome glands (*Calceolaria, Angelonia, Bowkeria, Lysimachia,* etc) can be collected by pressing the gland

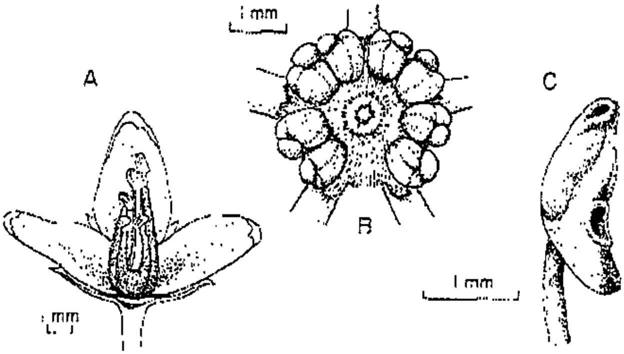

Figure 1 The three major types of oil secretory glands (elaiophores) found in flowering plants. (A) Trichome elaiophore of glandular hairs on androecium and petal bases of *Lysimachia quadrifolia* (Primulaceae). (B) Abaxial surface of *Callaeum macropterum* flower, with pedicel and petals removed (Malpighiaceae). Eight calycine epithelial elaiophores are present with oil pressure bulging up the cuticle to form lipid blisters. (C) Another form of epithelial elaiophore as a deeply concave gland on an anther of *Mouriri myrtilloides* typical of the Memecyleae (Melastomataceae). The secreted free fatty acids do not push the cuticle up. The *Lysimachia* is redrawn from Vogel (1986) and the *Mouriri* from Buchmann & Buchmann (1981).

field against glass and washing with solvent, scraping with a spatula, or applying a very rapid rinse of the excised glands or gland fields with solvent, followed by concentration (79; S. Buchmann, unpublished). Other floral lipids can be suctioned directly into capillary pipettes (as in *Mouriri*; 7) or in malpighiaceae can be suctioned by puncturing the cuticle with a pin and pressing a capillary pipette against the hole. This allows collection of pure oil without contamination. Some large flowers (e.g. *Callaeum lilacina*, Malpighiaceae) yield as much as 2.2 μl oil per flower (10).

The first floral oils to be analyzed were those from *Calceolaria* spp. (Scrophulariaceae) (79). Vogel noted both the physical and chemical properties of *Calceolaria* oils. Floral lipids are often colorless or yellow—*Diascia*, *Malpighia* (79); *Mouriri* spp. and *Byrsonima* (7); and S. Buchmann, unpublished—and are odorless, with a viscosity similar to olive oil. Vogel (1974) noted that for at least *Calceolaria*, the pure oil has a "repulsive *Ricinus*-like taste" and is neither sticky nor stringy. Other results from Vogel's (79) examination of *Calceolaria pavonii* lipids showed them to have a mean refractive index of 1.445 and a specific gravity of 0.96; the related *C. arachnoides* yielded an elemental analysis of 0% nitrogen and sulfur, 1.4% phosphorus, 9% hydrogen, 60% carbon, and 31% oxygen. Vogel also noted that the oils did not mix readily with water but that there was pronounced "smectic swelling" with production of myelin figures in alkaline media or neutral or slightly basic aqueous media. For *Calceolaria* the pure oil exhibited a slight bluish fluorescence under longwave (366 nm) ultraviolet illumination.

A greenish fluorescence is observed in oil from *Mouriri* (7). When left as the crude oil at ambient temperature for one year, the oil formed an insoluble residue. A similar phenomenon is sometimes observed on oil-saturated scopae on pinned bee specimens.

Vogel (79) found 3 dominant and 11 detectable components (by thin layer chromatography-TLC) in the secretion of *C. pavonii.* At least 7 other *Calceolaria* spp. were examined in less detail. A 300-mg sample of crude oil derived from 530 flowers of *Calceolaria pavonii* yielded the major lipid β-acetoxy palmitic acid. Vogel mentioned the rarity of 3-hydroxy fatty acids in plants and stated that he knew of no reports of β-acetoxy fatty acids in plant tissues. He did not, however, mention that *Calceolaria* oils contain diglycerides of β-acetoxystearic acid, as was later reported by Seigler et al (53) (Figure 2).

In addition to the lipid components of the elaiophore oil, nonvolatile isoprenoid compounds (e.g. sterol ester) were suspected as being responsible for the yellow color of some *Calceolaria* and *Malpighia* oils (79). In other oils carotenoids were postulated as the sources of the yellowish coloration. An earlier report of sugars in a malpighiaceous exudate *(Stigmaphyllon ciliatum)* prompted Vogel (79) to examine floral oils (of *Calceolaria, Heteropterys, Cypella)* for carbohydrates. None were found except possibly some trisaccharides in *Calceolaria.* Sugars were also absent in floral oils from *Krameria* (58), but Buchmann & Buchmann (7) report traces of glucose as revealed by paper chromatography performed by I. Baker.

The chemistry of four species of rhattanys *(Krameria cuspidata, K. cytissodes, K. revoluta, K. parvifolia)* was investigated using a combination of TLC, GC, IR, NMR, and mass spectroscopy (53, 55, 56, 60). The main lipids were 3-acetoxyhexadecanoic acid, 3-acetoxyoctadecanoic acid, and 3-acetoxyeicosanoic acid (53). These compounds range in carbon chain length from C_{16} to C_{20}, and all have the substituted acetate (acetoxy) moiety in the number 3 carbon position (Figure 2). The authors did not, however, indicate what proportion of the total lipoidal secretion consisted of each of the three identified components. Simpson et al (56) presented chemical results from lipids of seven additional South American *Krameria* spp. that also contained free 3-acetoxy fatty acids. *K. grayi* and *K. parvifolia* contain a complex mixture of lipids; some have chain lengths as short as C_{10} (S. Buchmann, unpublished).

Oil from *Mouriri myrtilloides* from Panama and *M. nervosa* from Brazil is viscous and yellow in color, not clear as are many floral oils. This coloration precluded accurate amino acid content reading on a ninhydrin scale (3). Nevertheless, amino acids (proline, alanine, glycine) that apparently were not due to contamination from pollen grains were present in low amounts, that is less than 100 nanomoles/ml. Colorimetric tests (dichlor-phenol-indophenol,

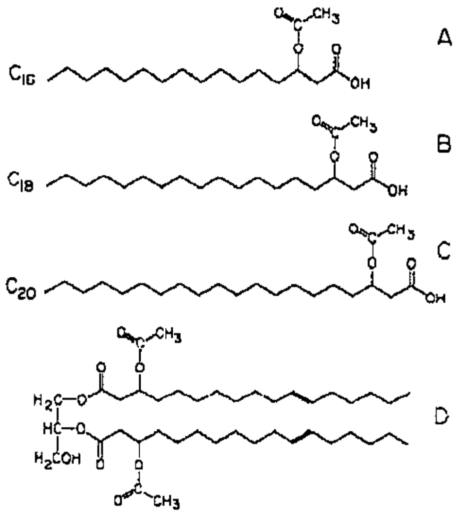

Figure 2 Chemical structures for typical elaiophore-derived lipids. A, B, and D are C_{16}-$C_{20}\beta$-acetoxy substituted free fatty acids (3-acetoxyhexadecanoic acid, 3-acetoxyoctadecanoic acid and 3-acetoxyeicosanoic acid) typically found in *Krameria* and *Calceolaria* (Krameriaceae and Scrophulariaceae, respectively). (D) Is one of the major floral lipids from *Calceolaria* and *Lysimachia*. It is 1,2-di-(3-acetoxy-E-11-octadecenoy)-*s n*-glycerol.

p-nitroaniline) indicated that the lipoidal secretion of *Mouriri* was acidic and contained phenolic compounds. Phenolics were also indicated by the greenish fluorescence (under longwave ultraviolet light) of the oil. When oil was vortexed strong bubbles formed and persisted, evidence suggestive of the possible presence of saponin(s). Trace amounts of glucose were found; these have not been detected in other floral oils (58; K. Steiner, personal communication). Despite the presence of diverse minor, unidentified components, the *Mouriri myrtilloides* gland exudate is dominated by lipids (> 95% of total components). These major lipoidal constituents were derivatized with boron trifluoride and their methyl esters examined by combined GC/mass spectroscopy. Some 13 free fatty acids were found with chain lengths from C_{12} to C_{24}. Stearic acid was identified and 12-methyltetradecanoate was tentatively identified (7). Further examination of *Mouriri myrtilloides* and *M. nervosa* secretions have confirmed the presence of mixtures of β-acetoxy free fatty acids like ones described by Simpson et al (53, 55, 56) for *Krameria* and Vogel (1974, 1986) for *Calceolaria* and *Lysimachia* (S. Buchmann, R. Carlson, S. Renner, unpublished). Carbon chain lengths are from C_{14} to C_{20} for these free fatty acids now being identified in *Mouriri* secretions and from other taxa including *Aspicarpa, Byrsonima, Callaeum, Janusia, Mascagnia, Malpighia, Oncidium, Ornithocephalus,* and *Sigmatostalix.*

Simpson & Neff (59) examined oils from the loosestrife, *Lysimachia ciliata*

(Primulaceae) and reported the presence of acetoxy fatty acids plus other unidentified components. Another study by Cane et al (11) explored the foraging, grooming, and mate-seeking behavior of a melittid bee *(Macropis nuda)* on *Lysimachia ciliata.* They conducted comparative analysis on the scopal oil loads of *Macropis* and pollen/oil provision masses destined for bee larvae. Both hand-collected *L. ciliata* oils and provisioned food masses shared major lipoidal constituents. These included palmitic acid, aldehydes (C_{14}, C_{16}), acetates (C_{18}, C_{20}, C_{22}), alkanes (C_{23}, C_{25}, C_{27}, C_{29}), alkenes (C_{25}, C_{27}), and three hexanyl esters (tetra-, hexa-, and octacosanoate). An acetate moiety was found in fatty acids from *L. ciliata.* Cell linings of nests of *M. nuda* revealed the same acetates and aldehydes (the aldehydes in greater amounts in the lining than in either oil or pollen) as from *L. ciliata,* and the cell linings additionally contained ketones (C_{13}, C_{15}, C_{17}) of unknown origin. It is significant that the loosestrife oils were incorporated into the larval food by the bees, and the oils were also used, presumably after some modification by the bees, as waterproof cell linings (11). The Dufour's gland, which normally produces compounds used for lining cells, is very small (less than one mm) and could not account for the mass of material put into cell linings. This was the first record of an oil-collecting bee using floral oils to construct nest cell linings.

Vogel (88) explored in great detail the relationship between the genus *Macropis* and its loosestrife *(Lysimachia)* oil hosts. Floral oils of *Lysimachia vulgaris* and *L. punctata,* two European species, were studied by TLC, GC, and mass spectroscopy (including fast atom bombardment mass spectroscopy). In *L. vulgaris* 88% of the total secretion is diglycerides of 3-acetoxy-trans-11,-12-octadecanoic acid (1,2-di-(3-acetoxy-E-11-octadecenoyl)-*sn*-glycerol), or, respectively, 3-acetoxy-octadecanoic acid (2:1 by volume), and acetic acid. The remainder of the secretion consisted of five related glycerides of 3-hydroxy-fatty acids. These results demonstrated that the *Lysimachia* floral oils, like those of *Calceolaria,* are identical in their dominant lipid components. *Lysimachia* oils remained in a liquid state for a long time, but when they contacted pollen or bees, they solidified more rapidly as an insoluble "crystalline mass." Certain neotropical bees (*Centris* and *Epicharis*) also collect, modify, and use floral oils (from *Byrsonima* and perhaps others) to line their cells (S. Buchmann, D. W. Roubik, unpublished; S. Vogel, unpublished; S. Buchmann, S. B. Vinson, G. W. Frankie, unpublished). Some bees (e.g. *Centris analis, C. bicornuta, C. vittata*) deposit oily outer plugs of unknown function (probably derived from Malpighiaceae) to finish their nest (D. W. Roubik, personal communication).

The oil chemistries of *Diascia, Hemimeris* and *Alonsoa* are quite similar, containing only mono and diglycerides (K. E. Steiner, personal communication; see also 50).

ENERGETIC VALUE OF FLORAL LIPIDS

Energy derived by consumption, digestion, and metabolism of fats is higher per gram than for equivalent amounts of carbohydrates (sugars or starches) or other foodstuffs. On average, the metabolism of one gram of lipid yields 37.6 joules, while one gram of carbohydrate produces only 16.7 joules of energy. Although the oil contains more energy per unit volume than sugar, it is also more expensive for plants to produce. Values for stearic acid cannot be used to approximate the energy equivalent of hydroxy acids (e.g. acetoxy substituted acids) or of more complicated natural mixes of fatty acids present in natural elaiophore secretions. Buchmann (10) found, for example, that values for stearic acid heat of combustion averaged 39,948 plus or minus 134 (SD) j/g, while elaiophore lipids (from *Aspicarpa, Krameria, Malpighia* and *Callaeum*) averaged only 33071 ± 186 (SD) j/g. Lipids of non elaiophore but floral origin were also subjected to calorimetry for comparison. Pollenkitt (the surface oily mixture of lipids and carotenoids) from zoophilous taxa *(Agave, Cercidium, Cucurbita, Helianthus, Prosopis)* averaged more energy, 40,172 ± 388 (SD) j/g, while those of extracted pollenkitt lipids (technique after H. E. M. Dobson—15; see also Dobson—16) from anemophiles *(Carya, Hymenoclea, Pistacia, Simmondsia, Typha)* had a mean value of 41,084 ± 146 (SD) j/gram. These various results warn that the energy of each oil must be determined empirically.

Determining energetic values for floral lipids is a useful beginning step toward determining the relationship between oil flowers and bees in nature. In addition to the energy content of floral lipids, we also need knowledge of the amount of oil per flower and per plant/day over an entire season. This information is available after the volumes of oil/elaiophore and numbers of flowers/unit area are determined. For total analysis, all oil-producing species in a given community, their density on a per hectare basis, the number of bee species competing for the oil reserves, and their densities and population parameters from good to bad years should be known. *Callaeum macropterum* serves as an example for such calculations. Each flower has 8 functional calycine elaiophores, and each produced 0.14 μl oil, or each flower offers 1.12 ± 0.24 μl. The heat of combustion of *C. macropterum* is 23.2 ± 0.9 j/μl, i.e. 26 ± 6 j/flower is available to oil-collecting bees (Buchmann 1987, in preparation). The oil is collected by *Centris*, a bee that is not (as is bomb calorimetry) 100% efficient at energy extraction. From the number of flowers produced daily and seasonally per hectare, and the amount of oil (plus pollen and/or nectar) necessary to produce one oil-bee of each species, we can approximate the carrying capacity of oil-flower plant communities.

OIL-COLLECTING BEES AND THEIR TOOLKITS

Bees comprise 11 families (Andrenidae, Anthophoridae, Apidae, Ctenoplectridae, Colletidae, Fideliidae, Halictidae, Megachilidae, Melittidae, Oxaeidae, and Stenotritidae) within the hymenopterous superfamily Apoidea (33). Bees are extraordinarily diverse in their biologies, especially in regard to food harvesting techniques, morphological adaptations for collecting and storing food for themselves and their young, and food preferences. The taxonomy of the bees is still in an active phase of description with probably 30,000–40,000 extant bee species worldwide (R. R. Snelling, personal communication). These species are divided into 800 genera (C. D. Michener, D. W. Roubik, personal communication). Most bees are solitary, and the females (no male bees are known to participate in food collection for their larvae) provision nests containing cells into which are placed mixtures of pollen and nectar with various ratios of nectar to pollen.

Bees that harvest and use floral oils occur both in the New and Old World but are most diverse in tropical and subtropical areas of North and South America. They are found primarily in three families, Melittidae, Ctenoplectridae, Anthophoridae, and to a minor extent the Apidae. The large family Anthophoridae contains by far the majority of genera (9 of 15) and species presently known or suspected of harvesting lipids from flowers, and many (especially *Centris*) are important pollinators of neotropical trees (17).

Melittidae

This is a relatively small family (16 genera) but a crucial one for students of bee evolution since it exhibits many primitive features; it is perhaps the sister group of the Ctenoplectridae and the long-tongued bees. If McGinley (28) is correct that the bifid glossa of most colletids (cellophane or plasterer bees) is a derived rather than a plesiomorphic wasp-like feature, then the melittids could prove to be as old as the colletids or it may even be the "ancestral" family of bees (32). The melittids are found primarily in the African and Holarctic regions. Only *Macropis* (with 18 described species) and *Rediviva* (with 9 named taxa) are known to harvest floral oils and, at least in the case of *Macropis*, to use them in their larval provisions and cell linings. We do know that *Macropis* is a floral specialist (for oil but not pollen or nectar) on *Lysimachia* in the Primulaceae. A South African group, *Rediviva* is a likely example of diffuse coevolution with the oil-producing *Diascia* (Scrophulariaceae). All bees can be likened to living "Swiss Army knives" since their bodies contain numerous tools consisting of modified and highly specific cuticular and setal structures designed for grooming and for harvesting, for transporting and storing of floral and other plant and animal materials (73).

Melittids are no exception to this generality. These bees are equipped with pro- and mesothoracic legs (tarsi covered by a tomentum of spatulate setae, combined with recipient "hair felt") with which they dab at elaiophores. Oil is collected mostly by capillary action of the legs appressed against trichomal elaiophores of *Lysimachia* (88). The other oil-collecting melittid, *Rediviva*, is a specialist on the flowers of *Diascia*, and other Scrophulariaceae, which usually bear trichomal elaiophores hidden from view within paired floral spurs. (Figure 3).

Ctenoplectridae

This is a very small Asiatic and African family consisting of only the genus *Ctenoplectra*, with 26 named species, and the presumably cleptoparasitic *Ctenoplectrina* (51). *Ctenoplectra* has only been observed collecting oil from cucurbit flowers (in the genera *Momordica* and *Thladiantha*) using a highly unusual form of abdominal wagging to harvest oils (from trichomal petal elaiophores) without using modified leg appendages as all other oil bees do.

Anthophoridae

This is the largest family within the Apoidea and shows a diversity of oil-collecting genera in three tribes (Centridini, Exomalopsini, Tetrapediini). Centridines are known to collect and use floral oils from the Malpighiaceae and also those from *Krameria* and *Calceolaria* (Table 2). They use these oils mostly in lieu of or in addition to admixed nectar in their cell provisions (58),

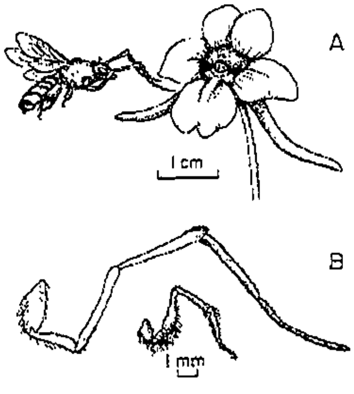

Figure 3 A twin-spurred flower of *Diascia longicornis* from South Africa with an approaching pollinator, a female bee, *Rediviva longimanus*. (A) The bee is about to land, then insert its elongate prothoracic legs into the floral spurs containing trichomatous elaiophores. (B) The extreme elongation of a *R. longimanus* foreleg showing elongation of all segments and the dense velvet-like oil-mopping setae on the tarsus. Below is the foreleg of a honey bee worker, *Apis mellifera*, drawn to the same scale for comparison. This drawing is modified after that in Whitehead et al (84).

or the oils may be modified, probably enzymatically, into tough, resistant biopolymer cell linings (S. Buchmann, D. W. Roubik, unpublished). Only New World taxa seem to be involved in oil collecting. Nine genera are confirmed oil collectors *(Centris, Ptilotopus, Epicharis, Chalepogenus, Lanthanomelissa, Monoeca, Paratetrapedia, Tapinotaspis, Tetrapedia)* while one genus formerly placed in the Exomalopsini *(Caenonomada)* is likely a centridine (R. W. Brooks, personal communication) and may be a tarsal "oil-dabber" (Table 2). The biggest group of oil-collecting bees is the centridines, represented by three genera (*Centris, Ptilotopus, Epicharis*). Almost all these bees possess, in the females, greatly modified blade-like setae on their fore and mid tarsi, which act to rupture lipid-filled elaiophores, especially in the Malpighiaceae. Collected oils are transported to nests on the modified, coarse, mostly nonplumose, setae comprising the scopae of the hind legs. An exceptionally good treatment of the various setal structures developed by centridines and other anthophorid bees was recently published by Neff & Simpson (37).

Most *Centris,* Ptilotopus and *Epicharis* use a "four legged" (pro- and mesothoracic legs) approach to oil collection. Male centridines (except some *Epicharis*) lack basitarsal combs for oil collection. *Centris, Epicharis,* and *Ptilotopus* have distinctive oil-harvesting comb formed of a single row of giant, flattened and apically curved, overlapping setae, along with two to five giant spatulate setae on the ventral surfaces of the anterior and middle basitarsi in opposition to the primary anterior comb (37, 79). Vogel (79) referred to these giant setae as the "hood organ" (Kaputzorgane); its function in oil collection or for grooming oil is poorly understood. All of the *Centris* with this typical comb pattern (85% of the more than 200 species) are known or suspected to harvest oils from Malpighiaceae flowers (37, 42). Some *Centris (Paracentris, Wagenknechtia)* have reduced combs and collect oils from *Calceolaria* (37). The loss of the oil collecting habit and associated modified setae has occurred independently in at least two lineages of *Centris* in North and South American deserts. These are the subgenera *Xerocentris* (8 spp.) and *Wagenknechtia* (4 spp.; 67, and Snelling, personal communication) and these bees do not harvest floral oils.

Caenonomada lacks basitarsal combs but does have unusually modified fine felt-like setae on the forelegs, somewhat similar to *Rediviva;* it may be an oil-dabbing bee. Neff & Simpson (37) report that *Caenonomada* is possibly a non-oil-collecting bee derived from an oil-collecting ancestor, but they state that this bee has strongly flattened hind basitarsi and coarse scopal setae typical of many oil collectors.

The tribe Exomalopsini contains 5 genera (*Chalepogenus, Lanthanomelissa sensu stricto, Monoeca, Paratetrapedia*—not all, *Tapinotaspis*) that routinely harvest floral oils from many plants (Table 2). Vogel reported that

Chalepogenus has setal combs similar to those of *Paratetrapedia* and that it collects oils from *Cypella* (Iridaceae; 79). *Monoeca* (with 6 described spp.) has basitarsal oil combs almost identical to those of *Centris* and *Epicharis*, but the combs are formed by several irregular rows of appressed, tapered simple setae; this is the comb type found generally in species of *Tetrapedia* (tribe Tetrapedini) and in *Paratetrapedia* and *Chalepogenus* (Exomalopsini). It is interesting that males of some *Monoeca* possess basitarsal combs (29), and males of *M. mexicana* (reported as *Tetrapedia saussurei*) visit flowers of *Malpighia*. Combs of some level of development occur in most male oil-collecting "exomalopsines" and *Epicharis*. Roberts & Vallespir (47) suggest that these are oil-collecting bees associated with the Malpighiaceae. Renner (personal communication) has observed *Monoeca* collecting oils from Malpighiaceae. Most *Paratetrapedia* have fully developed combs of the type usually associated with harvesting oils from flowers with epithelial elaiophores (as in Malpighiaceae and some orchids). There are few field observations of the bees harvesting oils even though they are not so rare as non-oil flowers nor are they rare in museum collections. *Paratetrapedia* visits numerous Malpighiaceae and possibly some orchids (since they are the right size for flowers of many oil-producing orchids), and they have been observed to collect oils from *Mouriri* (7, 44–46). Steiner (personal communication) has collected *Paratetrapedia* spp. on 9 species of malpighs in Panama. Some *Lanthanomelissa* possesses fine combs and is probably associated with the Iridaceae (37). *Tapinotaspis* (with 10–12 species) has been associated with flowers having trichome elaiophores such as *Calceolaria*, *Nierembergia* (Solanaceae) or *Sisyrinchium* (37, 79). Little is known of the oil-collecting biology of *Tetrapedia*, although Steiner (personal communication) has collected *Tetrapedia* on 3 Panamanian malpigh species. On the basis of the morphology of the *Tetrapedia* tarsal combs,. Vogel (79) predicted that it is an oil collector. Neff & Simpson (37) reported on an unidentified *Tetrapedia* collecting floral oils in an inverted position from *Banisteriopsis* flowers in Brazil. Oil collection is at present unknown for other Anthophorinae.

The bee groups reported above routinely use, or are quite likely to use, floral oils as a part of their nesting requirements. They are also all solitary bees. There are scattered reports of social bees in the tribe Meliponini of the family Apidae (3 *Trigona* and 1 *Melipona*) that harvest oils. Buchmann & Buchmann (7) found *Trigona pallens* visiting anther epithelial elaiophores of *Mouriri myrtilloides* in Panama, although it is not known what the collected oils were used for (see later discussion). Steiner (69) reported *Trigona* collecting oils from *Drymonia* (Gesneriaceae) and *Stigmaphyllon* (Malpighiaceae). Renner in a study of several Brasilian *Mouriri* found a *Melipona* to collect oils (44–46). None of these stingless bees has any special structural modifications of the legs or scopae as do the true oil-collecting bees.

ABDOMINAL OIL-MOPPING

Michener made observations in 1967 in Kenya of a ctenoplectrid bee *(Ctenoplectra albolimbata)* on cucurbit flowers *(Momordica trifoliata)* (31). He noticed that the female bees were only interested in the basal portions of the floral petals and in a darker colored area which had blunt sticky floral trichomes. The *Ctenoplectra* females walked over these different perianth areas while swinging their abdomens from side to side in vigorous downward rubbing motions. At this same time cucurbit pollen from the flowers collected on the dorsal surface of the bees. These early observations, made before Vogel's 1969 and 1974 papers, indicated that Michener's bees were doing something unusual. In a latter paper, Michener & Greenberg (31) mentioned the Kenyan notes and interpreted them as a new example of an oil flower and an oil-collecting bee. Vogel predicted that *Momordica* and *Thladiantha* were oil flowers based on morphological evidence (81–83, 112); he then made field observations in North Borneo (83) that confirmed his earlier speculations. The ranges of these cucurbits and their specialized ctenoplectrid bees are nearly congruent. In relation to pollination and oil harvesting, Ctenoplectrids are unique in possessing several morphological attributes either not found or not as developed in other bee taxa. Females have a crescent-shaped inner hind tibial spur (comblike with close-set teeth, used for squeezing oil out of the metasomal brushes prior to scopal packing on the hind legs). They also have long dense setal fringes on metasomal sterna 2 to 5, used as capillary brushes to adsorb oils from their cucurbit hosts.

Ctenoplectra differs from melittids (*Macropis* and *Rediviva*) by its reliance on abdominal wagging with specialized "mop" setae to absorb oils, rather than modified leg structures for collection as in all other known oil bees. The second and more distal metasomal sterna of these females bear paired setal fringes that form a "bipartite brush" (see Figure 1c in (83). The setae that make up these unique brushes are not thread-like but are composed of two series of thin leaf-like blades which develop a strong capillary attraction for lipids. The bee walks across the elaiophores, swinging its abdomen laterally to mop up the secretion. At each swing, the soaked brush is immediately cleaned of lipids by alternate combing movements of left and right hind legs, using the inner tibial spur as described above. The fluid then collects in a shaggy underlayer of the tibio-metatarsal scopa. It is transported pure, or, if it moistens the scopal pollen loads, as a soft paste (83). Pollen is gathered in a separate behavioral act. These bees apparently nest in burrows left by other insects, usually in wood, and the fate of the cucurbit elaiophore lipids, whether for brood nutrition and/or cell lining material, is not known (31, 83).

ECOLOGY OF *LYSIMACHIA* FLOWERS AND *MACROPIS* BEES

Lysimachia is a large genus containing about 200 species (43, 88, 92). Vogel (88) surveyed herbarium material to determine the extent of oil production in the genus. He found that the genus is apparently almost entirely melittophilous (bee pollinated) with the exception of a few suspected bird-pollinated forms. Oil flowers occur in 78 (39%) of the *Lysimachia* species (88), all members of the subgenus *Lysimachia*. These flowers are yellow and possess trichomatic elaiophores of glandular setae on the basal corolla or filament tube (see Figure 1). About 32% of *Lysimachia* are typical nectar flowers, while 23% or 46 species have pollen flowers of the "*Solanum* type" (88). These flowers have highly modified androecia, and access to pollen is restricted to small apical anther pores. Pollen must be released by floral sonication by buzzing bees (9). Few *Lysimachia* appear to be obligately autogamous (59, 88).

The oil-producing *Lysimachia* are visited by a narrow guild of bees, except in the United States. The most dependable and likely the most efficient pollinators are *Macropis* (Melittidae). The known range of the 18 *Macropis* species coincides almost exactly with the distribution of the 78 oil-producing *Lysimachia* species (except for a few *Lysimachia* in Sri Lanka and Australia). Both *Macropis* and the oil-producing *Lysimachia* are most species-diverse in southern China (32, 33, 40, 41, 93). Vogel (88) believes that their coevolutionary mutualism likely began in SE-Laurasia soon after the origin of *Lysimachia* during the early Tertiary. Descendants maintained the relationship and subsequently reached North America and Europe; the extant system occurs in a circumboreal zone between 63° and 25° north lat.

Simpson & Neff (59) present a table of 19 species of *Lysimachia* in 3 subgenera *(Seleucia, Lysimachia, Naumbergia)* that occur in the United States and Canada. They include the known or possible associations with *Macropis* pollinators. They stated, as did Popov (40), that the relationship is not an obligate one on the part of the plants, since the range extends beyond that of the bees. They failed, however, to consider that 55% of the species are without elaiophores. Cane et al (11) presented data from their field observations of *Macropis nuda* on flowers of *L. ciliata* in New York, finding that female bees collect both oil and pollen from fringed loosestrife, while both sexes took nectar from other plants. They also performed chemical studies of the loosestrife floral oils, the provision masses of the bees, and leg loads of pollen and oil. They, thus, were able to demonstrate for the first time a floral oil used not only as a foodstuff but as a component of modified cell wall linings. This work as well as the later extensive studies of Vogel (88) demonstrates that oil-producing *Lysimachia* in the New World are dependent on *Macropis* for pollination (59). In North America, however, oil-producing *Lysimachia* are abundant and widespread, but the *Macropis* bees are much rarer than their floral hosts (59).

Vogel (88) observed *Macropis labiata* and *M. fulvipes* collecting oil (and pollen by ingestion) from flowers of *L. vulgaris* and *L. punctata* in central Europe. His bees collected oil by clinging to filaments, while curled around anthers, and absorbed oils from the glandular trichomes by "dabbing and mopping it with their front and mid legs alternately (ipsalaterally) within each pair." As in other bees, the mouthparts were not involved in oil collection. The bees became dusted with pollen, sternotribically and passively, thus transferring pollen to subsequent protruding stigmas. He noted that they were also occasionally fertilized by pollen-collecting generalists (especially halictid bees and syrphid flies, which have no oil harvesting tools). Vogel (88) described the nest architecture and provision chemistry of cells of *M. fulvipes* (finding some admixed sugar). As noted above, *Lysimachia* floral oils serve to waterproof bee cells, as cell linings (11, 88), and Vogel (88) suggested that the linings are "not, as usual, bee-produced but a solidified derivative of the *Lysimachia* lipids (possibly altered by some secretion of the bee)." He further described unusual setae on the scopae (penicillus) which, when moistened with oils, might be involved in the cell-lining process.

MOURIRI AND THE MEMECYLEAE (MELASTOMATACEAE) AS OIL FLOWERS

Buchmann & Buchmann (7) discovered that these decidedly atypical melastome flowers *(Mouriri myrtilloides)* bore anthers with unusual glands (Figure 1c). In what Buchmann (9) has termed buzz or vibratile pollination, female bees grasp individual or grouped stamens and shiver their flight muscles in rapid short bursts. This causes the small, non-oily pollen grains to blast out of the apical anther pores and allows these bees *via* floral sonication to harvest efficiently more pollen per unit time than do non-buzzing bees (8; S. Buchmann, unpublished). *Mouriri* is not, however, a typical vibratile plant. Its anthers are not yellow, are small and on long filaments, and do not "mimic" copious pollen as do those of other poricidal taxa such as the genus *Solanum* (7–9, 82). Elaiophores were found on each of the 5 short and 5 long stamens in this species. The secretory nature of these unique androecial glands was confirmed by absorbing the oily viscous liquid onto filter paper strips or into glass capillaries where it gave positive reactions for lipids using standard chemical tests (Sudan IV, neutral red, osmium tetroxide). In Vogel's classification (79) these elaiophores are of the epidermal type but do not have a protective cuticle to protect the oils from degradation or spoilage until oil-harvesting bees arrive (as in the cuticles over *Krameria* and *Malpighia* elaiophores). The secretory layer in *Mouriri* anther glands is 4–6 cells thick and the uppermost epidermal layer is especially modified. There is a thick (2–3 μ) porous cuticle, but it never bulges into a "blister" over the secreted oil. Each gland is about 0.7 mm long and 0.3 mm wide and is estimated to contain 0.02 μl (or 0.02 mg oil/flower with 10 glands). This is about one fifth of the total oil production from a *Krameria* flower (58). To explain exactly why some bees collect *Mouriri* oils is complicated by Renner's observations (44, 46) of 12 species of bees visiting *M. nervosa* and *M. guianensis* in Brazil. She found that 9 bees (6 *Euglossa* spp., 3 *Xylocopa* spp.) vibrated the poricidal flowers to harvest pollen, while only three species (*Trigona williana, Melipona fulva* and *M. marginata*) scraped at the connective glands and collected oil. Both Buchmann and Renner presume that the euglossines are the major *Mouriri* pollinators. Renner (44, 46) observed *Melipona* and *Trigona* to mix the oil with *Mouriri* pollen in scopal loads (which suggests a nutritive use by these social apids) and confirms observations of *T. pallens* collecting oils from *M. myrtilloides*. *Mouriri* secretions are oily and viscous but not sticky in the usual sense. Renner (44) states "the 'oil' produced by the staminal glands of this genus cannot be compared to that of true floral oils; it is most likely used as propolis (in nest construction) by the meliponines, or as an optional pollen-wetting" agent. Apart from ignorance of exactly how the collected oils are used by bees (*Paratetrapedia* and *Trigona* in Panama), there can be no argument that rich lipoidal secretions of substituted free fatty acids are produced by unique anther epithelial elaiophores from at least two *Mouriri* species. Roubik (personal communication) suspects that *T. pallens* may use *Mouriri* oils as important components in nest construction along with resins collected elsewhere. Recently, Roubik (personal communication) has reported that *Trigona (Tetragona) dorsalis* commonly visits Malpighiaceae in Panama and harvests floral oils that are probably used in nest entrance construction. If used for constructing nest entrances, they might have a repellent effect on ants. That *Mouriri*, and probably the rest of the Memecyleae, are true oil-producing flowers is clear; we have not studied enough species in detail to know how the oils are used by anthophorids or meliponines, and how this may increase both plant and bee fitness.

The tribe Memecyleae within the tropical Melastomataceae contains 6 genera—*Lijndenia, Memecylon, Mouriri, Spathandra, Votomita,* and *Warneckea*—with 4, 300, 75, 6, 6 and 31 species respectively (5, 6, 34, 35). The tribe includes the paleotropical genera *Memecylon* and *Lijndenia*, the neotropical *Mouriri* and *Votomita*, and the African *Spathandra* and *Warneckea*. Thus, the tribe Memecyleae contains 422 species; 322 have oil-producing flowers. White flowers or eglandular anthers occur in some species of *Mouriri, Memecylon* and *Lijndenia* (5, 35). Most *Memecylon* and *Spathandra* have variously blue flowers and anthers with prominent concave glands

(71). Apparently only the small genus *Lijndenia* is totally eglandular within this tribe.

Unfortunately, there are no field observations of pollination and the behavior of anthophiles for Memecyleae (excluding *Mouriri*). On the basis of floral conservatism (2) within this tribe, i.e. the presence of morphologically similar glands, Buchmann & Buchmann (7) predicted that almost all of the Memecyleae (excluding the eglandular or vestigial-glandular taxa) would be confirmed as having true anther elaiophores that would be visited by oil-collecting bees.

DIASCIA FLOWERS AND REDIVIVA BEES—A CASE OF COEVOLUTION?

The twin-spurred flowers of the South African genus *Diascia* (Scrophulariaceae), a genus of about 50 species in the tribe Hemimerideae known only from southern Africa, produce lipids from trichomal elaiophores at the apices of spurs or sacs previously thought to secrete nectar (18, 24, 38). Part of the genus was recently taxonomically revised by Hilliard & Burtt (22). That these were not ordinary nectar-producing flowers was first postulated by Vogel (34, 79). He predicted that if the oil were used in species with long spurs, this would require a bee with extraordinarily long legs.

Diascia was an enigma because it appeared to be a flower with elaiophores, yet it occurred in a country with no known oil-harvesting bees. The only previously known oil-collecting bees in South Africa are in the genus *Ctenoplectra* (Ctenoplectridae), and the only analogous case of oil-producing floral spurs is that of *Angelonia* (tribe Calceolarieae of the Scrophulariaceae). *Angelonia* has shorter spurs containing oil glands and is known to be visited by *Centris* species that insert their legs into these floral pouches to extract the oil film (79). Another oil-secreting genus within the Scrophalariaceae, *Bowkeria*, occurs in South Africa and has only recently been found to be visited by *Rediviva* bees (27).

Unique bees with very long legs do exist in South Africa. Michener (32) revised the bee family Melittidae and reestablished the genus *Rediviva* containing eight species. Females of some *Rediviva* species have forelegs of normal proportions, but most, such as *R. longimanus*, have long legs and are known from the western Cape region. This bee has front legs 19 mm long which far exceed her body length (14 mm); the other two leg pairs are proportioned normally. Males of these long-legged species have normal legs. Vogel was presented (86) a similarly long-legged female, *R. emdeorum*, captured on *D. longicornis* in Namaqualand and found that most of the pollen on this specimen belonged to *Diascia*. Hardened oil was mixed with the pollen in the scopal loads. The postulated bee had been found. It has been named *R. emdeorum;* it has a body length of 15 mm but prothoracic legs 26 mm long (87)! It would be interesting to see if such efficient oil probe legs ("dipsticks") have been acted upon by opposing selection pressures related to grooming, navigation, and flight, as well as to negotiating narrow nest burrows or evading predators.

Female *Rediviva* bees may approach *Diascia* flowers with outstretched prothoracic legs which are then inserted to the bases of the floral spurs to collect lipids (see Figure 2). In this position it is likely that pollen is deposited and later sternotribic stigmatic contact is made. The elaiophores in *Diascia* (e.g. *D. barberae*) consist of large hemispherical dark secretory trichomes consisting of 56 cells each and with 200 hairs per floral spur. These are scattered and confined to the distal third of the adaxial spur wall (79). It is unlikely that much oil accumulates, and it certainly would not fill up any part of the spur. Rather, the lipids collect as a thin film over the glandular area.

Vogel (86) has speculated that *Rediviva,* with legs inserted fully into *Diascia* spurs, then presses the ventral surfaces of her tarsomeres (1–4) against the elaiphore field and perhaps rubs across it. The velvety pubescent vestiture on both the dorsal and ventral surfaces of the tarsi would allow for rapid oil pickup by passive capillary "wicking." The oil would then accumulate on the dorsal areas of these tarsi and then would be secondarily manipulated (probably in flight as in other oil bees) by pulling the oil-laden tarsi lengthwise through the flexed middle legs of the same side (which also have velvety setae). Whitehead et al (90, 91) were the first to discuss the fact that the middle legs transmit the oil by analogous movements to the scopae on the hind legs for transport to the nest.

The lipid-based association of *Diascia* and *Rediviva* has both historic (biogeographic) and evolutionary implications beyond pollination ecology. *Angelonia* is Neotropical and reputedly a relative of *Diascia*. Did these two genera evolve their oil-spurs independently? The southern hemisphere occurrence of a melittid genus so similar both biologically and morphologically to *Macropis* raises the same question relative to oil-collecting by *Macropis* and *Rediviva.* Oil-collecting in this group may have been monophyletic, a synapomorphy in the Melittinae. Alternatively, independent evolution of such traits would represent quite a parallelism. Indeed, Michener (32) proposed two alternate cladograms for the Melittinae.

Vogel (86, 87) postulates that *Rediviva* may have coevolved with its *Diascia*-oil hosts. If the parallelism in the Neotropic sister genus *Angelonia* is considered, coevolution may not apply in the specific sense. Unfortunately, no unique definition exists for coevolution (25, 52). A 1:1 reciprocal coevolution probably has not taken place in this system, but coevolutionary changes in both seem likely. This form of "coevolution" has been described as "diffuse coevolution" for euglossine bees and orchids (49).

Manning & Brothers (27) described floral visits of *Rediviva politissima (R. neliana)* to four *Diascia* species, and they provided the first observations of oil collection from *Bowkeria.* They further document visits by *R. colorata* to many nectar plants. Steiner & Whitehead (70) provided new observations on many bees and *Diascia* flowers from diverse locations, and they summarized current knowledge. They found amongst the 12 *Diascia* spp. much variability in flower size and spur length, some of which exceeded the corresponding variability in foreleg length and overall size known for *Rediviva.* According to their observations, species specificity among the bees was low; in areas of sympatry between two or more *Diascia,* an individual bee could visit more than one *Diascia* species on a single foraging bout (one bee carried pollen from 3 *Diascia*). In these cases, however, Steiner & Whitehead state that interspecific pollen flow (therefore potential hybridization) is reduced by differential stamen and stigma placement, and by pollen deposition on different bee body areas (head, sternum or dorsal abdominal terga). Steiner & Whitehead (70) also provide information on a yellow translucent area at the base of the upper corolla lobes known as the window (22); they suggest it functions as an orientation cue for bees. Behavior of the *Rediviva* pollinators on *Diascia* spp. is stereotypic. Bees insert their forelegs into the two spurs simultaneously as they alight on the flowers and place their mandibles into or on the window area. Once inside the spurs, the forelegs rub the elaiophores for 1–20 sec with an average of 4 sec (70). The departing bee hovers in mid air to transfer the oil to the scopae on the hind legs, stored alone or with pollen for later use in nest cells. *Diascia* produces no nectar, so *Rediviva* must visit other shallow flowers for nectar, as is the case of *Macropis.* No sugars were found admixed with *Diascia* oil on *Rediviva* legs (86, and K. Steiner, personal communication). Thus, we do not know if *Rediviva* mixes floral oils with pollen alone, or with nectar and pollen, or possibly even transforms the oils enzymatically into insoluble polymers. Steiner has excavated cells of *Rediviva* but has not yet examined them for an oil/pollen mixture or for oil-derived cell linings (K. E. Steiner, personal communication). Steiner is currently conducting further studies on *Diascia* and reports that *Alonsoa, Anastrabe, Colpias, Hemimeris* and 6 orchid genera (table 2) are all oil flowers visited by *Rediviva* bees.

A discussion of species specificity by Steiner & Whitehead (70) and other recent papers by these workers (89–91) suggest that little evidence exists to argue that floral variation is the result of selection by *Rediviva* species. Despite the lack of specificity between 4 *Rediviva* and 12 *Diascia* species, all the *Diascia* they tested were self-incompatible—a fact they interpreted to mean that the flowers are largely dependent on oil-collecting bees for sexual reproduction (halictid bees may effect some pollination according to K. Steiner). With this weak "constancy," they suggest that there is evidence for competition among *Diascia* spp. for pollination and that differences in pollen placement on bees may be attributed to such interspecific competition for pollen transfer. Recently, Steiner (70) has reported that *Rediviva* bees harvest floral oils from 38 species in 6 genera of S. African orchids, bringing oil production in this family to the Old World.

HOW MUCH OIL IS OUT THERE?

The answer to the question of how much oil exists is crucial if we are to understand the evolution and maintenance of plant communities consisting of oil plants and their specialized bee pollinators. Most of these communities occur in tropical, subtropical or desert regions. The estimation of floral rewards (nectar, pollen, oils or resin) on a community basis requires a formidable team effort and has rarely been attempted. Only for a high arctic tundra community (23), for sites in two warm convergent deserts—Argentina and Arizona (54), and for saguaro cacti in Arizona (52a) do we have productivity data for nectar and pollen per hectare. Such estimates of community floral resource productivity must not, however, be confused with standing crop values actually available to bees and other floral visitors.

Fortunately, representative data for a desert community in Arizona on vegetative change and plant demographics are available (19). The use of plant density information for common, often sympatric, oil plants of the Sonoran Desert (e.g. *Krameria grayi, K. parvifolia,* and *Janusia gracilis;* in 19, and microfiche data appendix) allows preliminary calculations of oil amounts and oil bee carrying capacity of a desert community. Based on plant densities of Goldberg or Turner, I calculated densities for *K. grayi* and *J. gracilis* to be 255/ha and 763/ha respectively. Amounts of oil reward per gland and per flower (10) of 1.0 μl/flower for *K. grayi* and 0.1 μl/flower for *J. gracilis* (S. Buchmann, unpublished) were also calculated. Estimates of flowers produced by an average plant per season—1000 for *K. grayi* and 1500 for *J. gracilis*—are rough approximations based on my ongoing phenological research with these plants. From these data, it appears *K. grayi* would contribute 260 ml/ha, or 26 liters/km^2 of floral oil, while *J. gracilis* would produce 110 ml/ha or 11 liters/km^2. Estimates for *K. parvifolia* are not given since it occurred in the plots but apparently at unusually low levels (6 individuals/ha). Since both *K. grayi* and *J. gracilis* occur over wide areas in sympatry, we may conclude that together they would offer 0.4 liter/ha or 37 liters/km^2 to the local oil-harvesting bee community of about 5 *Centris* species. These rough estimates will need to be refined to account for plants of different sizes and floral production between wet and dry years.

Finding nests of oil-collecting Arizona species is serendipitous at best, and no empirical estimates for amounts of oil mixed with pollen in cell provisions (or used for cell linings) are available (1). From the amount of olive oil it takes to mix with, and thoroughly wet, enough pollen to fill one third of the provisions of *C. atripes* (an abundant oil bee), I estimate 100 μl oil (or 100 flowers) of *Krameria grayi* oil is needed for each provisioned cell. This bee constructs nests of one to three cells and the nests are widely scattered (see account in 1). At 100 μl oil per *C. atripes* cell, our *Krameria*/*Janusia* landscape would provide enough lipid to produce 4000 bees/ha or 370,000 centridine bees/km^2. Nor do we know if floral oils are ever in limited supply for local bee populations. Unfortunately, in addition to our ignorance about floral production, we know even less about population density of any *Centris* or the way these populations fluctuate seasonally, or year to year, in response to floral biomass and other density dependent and independent factors. If this relatively depauperate oil flower community offers this much oil, how much oil can the rich malpighiaceous neotropical savanna assemblages offer to their bees?

ORIGIN OF OIL FLOWERS—AN ANCIENT MUTUALISM?

Did oil flowers originate in an ancient mutualism? An answer to this question is confounded by lack of oil-bee and oil-flower fossils (20, 72, 94). There are no known fossils of bees that exhibit modified basitarsal "scraper" setae. In fact, very few bee fossils have been found, and with the exception of those in amber, most of the few known are not preserved in enough detail to reveal specialized oil-bee toolkits. The oldest bee fossils are from the Eocene (94) and include presumably eusocial apids. Thus, the origin of more primitive bees from their sphecoid wasp ancestors undoubtedly took place much earlier, perhaps as early as the lower Cretaceous.

As with the oil bees the fossil history of oil plants is not extensive. For the Malpighiaceae, both the megafossil (leaves and fruits) and pollen records are sparse and open to diverse interpretation (72). Taylor & Crepet (72) recently reported a new Malpighiaceae taxon, *Eoglandulosa warmanenis*, from the middle Eocene Claiborne formation of Tennessee. These fossils are beautifully preserved flowers that have paired abaxial elaiophores, 5 free, clawed and reflexed petals and 20 stamens. They are in almost every respect like extant Malpighiaceae that produce floral oils. Taylor & Crepet (72) from their fossil floral evidence suggest that oil production and pollination, likely by anthophorid bees, existed at least by the middle Eocene. Iridaceae, Krameriaceae, and Orchidaceae are all either unknown or the determinations to family are suspect (20). Relatively good dates of first appearance (for fossil pollen) are available only for the Malpighiaceae, Cucurbitaceae, and Primulaceae, among oil-producing families (36). However, for the Cucurbitaceae and the Primulaceae, we may assume that these fossils are not from the relatively limited number of species bearing elaiophores within these families. Vogel (83) further suggested that the cucurbits (the paleotropical oil forms) and their *Ctenoplectra* pollinators are both ancient lineages. At least two well-preserved species of *Ctenoplectrella* (a supposed relative of *Ctenoplectra*) are preserved in Eocene Baltic amber (94).

Neff & Simpson (37) speculated that the oil-bee and oil-flower system first evolved in flowers with trichome type elaiophores (such as the Iridaceae, Scrophulariaceae, or Primulaceae). Neff & Simpson (37) also propose an early (mid-Eocene) origin for proto-Centridini and the Malpighiaceae in the New World and present a hypothetical phylogenetic tree for the oil-collecting Anthophorinae based on oil-collecting organs (see their Figure 44).

Most flowers possess vast arrays of trichome types, from the simple forms like osmophores (74), to complex glue-producing anther hairs ("Klebstoffhaare") in *Cyclanthera* (Cucurbitaceae) which may facilitate pollen adhesion to bees (21, 84). Many trichomes secrete sugary solutions, some of them containing trace or moderate quantities of lipids. Lipid layers are produced on the surfaces of many floral nectars, especially in neotropical species (4). It would seem an easy progression for the metabolic switch to pure acetoxy fatty acids, which are rare final products in plants but are common intermediary metabolites. The epithelial elaiophores of the Malpighiaceae could be derived from preexisting trichomes or other tissues. Similarly, for bees, unspecialized scopal setae on the legs or abdomen can be used for harvesting oil, and more elaborate setal modifications could have arisen after the initial relationship was underway.

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NOTE ADDED IN PROOF

It is now known that foraging female *Rediviva* bees do not fly with outstretched prothoracic legs as depicted in Figure 3—K.E. Steiner, personal communication.

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