FLORAL REWARDS: ALTERNATIVES TO POLLEN AND NECTAR[1]

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ABSTRACT

In angiosperms selection has led to the utilization of numerous substances other than pollen and nectar that help to insure repeated visitation by pollinating animals. Here, we group the various substances into nonnutritive and nutritive rewards and discuss within each group the specific kinds that occur. In our discussion of nutritive rewards, we emphasize floral oils, lipids produced by one of two types of specialized secretory organs called elaiophores and which serve as nutritive rewards for certain New World anthophorine bees. Although discovered only within the last 15 years, the syndrome of oil production now appears to be one of the most widespread kinds of floral rewards. We report here for the first time the occurrence of oil production in the Solanaceae (*Nierembergia*). It is apparent that oil production has evolved independently many times, but plants which produce oils that are collected by female anthophorine bees show similarities in the chemistry of the oils and the types of structures that produce them. It is not clear whether other groups of plants reported to produce oils but which are not pollinated by anthophorine bees possess an analogous system or not.

Floral rewards can be considered any component of a flower or inflorescence that is used by animals and, because of this use, insures repeated visitation that will lead to pollination. Without doubt, pollen and nectar are the primary rewards offered by flowers to visiting animals in order to buy their services as pollinating agents. Of the two, nectar is sought by a wider array of animals than pollen. On the other hand, pollen is the primary reward for which bees, probably the single most important group of pollinators, visit flowers. The role of pollen and nectar in the attraction of potential pollinators has been appreciated for hundreds of years, but we have only recently begun to realize the complex nature of these two rewards. Nectar, for example, formerly considered to be a simple sugar solution, has been shown to consist of a variety of chemicals dissolved, or suspended, in an aqueous solution. These range from mixtures of one to three common sugars (glucose, sucrose and fructose) to more complex sugar solutions (Percival, 1961) or combinations of sugars, free amino acids, "vitamins," lipids, and other compounds (Baker & Baker, 1975; Baker, 1978). The complex chemical nature of pollen has been realized for a century (refs. in Barbier, 1971), but only in the last twenty years have researchers begun to explore the varied nature of specific enzymes contained in the pollen walls and their possible roles in incompatibility reactions (Stanley & Linskens, 1974). These same enzymes may play a role in pollen recognition by specific pollinators. The chemistry of pollen is in fact so complex that it has been impossible to provide a precise description of pollen chemistry that is all-inclusive. The continued elucidations of the intricate nature of these common rewards has spurred studies of pollination biology and provided an impetus for the investigation or reinvestigation of other floral rewards.

TABLE 1.   Floral rewards other than nuptual nectar and functional pollen.

Nonnutritive rewards
  Incidental by-products of floral structure
    Floral trichomes used in nest construction
    Sleeping places
    Heat sources
    Mating sites
  Products actively secreted as rewards for potential pollinators
    Nest materials (resins, waxes, or chemical mixtures)
    Sexual attractants
Nutritive rewards
  Brood places (larval nutrition)
  Adult nutrition
    Food tissues (food scales, food bodies, sweet tissues, pseudopollen)
    Nonfertile "food" pollen
    Stigmatic secretions
    Fatty oils (lipids)

Here we will concentrate on floral rewards other than nectar and pollen in the traditional senses of pollen as functional gametes and nectar as a primarily sugar-dominated water solution secreted from one of the numerous kinds of floral nectaries (Fahn, 1952, 1979; Kartashova, 1965). Most of the rewards we discuss have been derived from totally different portions of the flowers or inflorescences, but we will include rewards that have been derived from pollen or nectar but which are now functionally or chemically distinct.

In our discussion, we have divided alternative rewards into two groups. The first group includes those used by pollinators for purposes other than nutrition and the second, those which serve primarily as food sources for adults, larvae, or both. Table 1 lists the kinds of rewards within each of these categories. Of the rewards in the latter group, we will emphasize lipids most heavily, primarily those of the Krameriaceae and Malpighiaceae, groups with which we have been working for several years.

Nonnutritive Floral Rewards

STRUCTURES WHICH SECONDARILY SERVE AS FLORAL REWARDS

Nest Construction.—In several cases animals, primarily insects, visit flowers for something which appears to be unrelated to pollination per se. In other words, the structures used appear to have an adaptive function not directly related to the attraction of pollen vectors. The relationships between the flower and the visitor in these instances is often so casual and/or the probability of pollen transfer so low, that there has been no selection for the enhancement of the association, and consequently no further modification of the structures used. An example of this type of association is the collection of floral trichomes for use in nest construction by some bees. We have observed bees of the genus *Anthidium* visiting *Krameria* and *Larrea* flowers in order to clip trichomes from the surface of the ovaries. The position of the bees indicates that they can effect some pollination while engaging in this activity. Generally, however, these bees use vegetative trichomes, and there appears to be no selection for an increase in the abundance

of ovarian trichomes as a reward to encourage such visitation. Similarly, during the collection of petals or pieces of petals of some flowers, leaf cutter bees occasionally may effect pollination, but the relationship is always a very casual one.

Sleeping Places and Heat Sources.—Flowers, as a result of their shapes and behavior, can be used by either male or female (but primarily by male) bees as sleeping places. In some instances the selection of a particular flower species in which to spend the night is quite rigid; in other cases, any funnel, tube, or dish-shaped flower that closes for the night apparently will do. The use of flowers as sleeping places is quite common, but rarely reported even though the movement into and out of flowers undoubtedly leads to occasional pollination (Linsley et al., 1956; personal observations). Nevertheless, there appears to be no selection for the reinforcement of this relationship, presumably because the females of the species which sleep in the flowers usually collect nectar and/or pollen from open flowers during the day and serve, much more efficiently, as pollinators.

Resembling the use of flowers as sleeping places is their use as "heaters." Particularly in the Arctic and at high elevations where ambient air temperatures are quite low, dish-shaped flowers can collect heat within the bowl and provide energy necessary for insect activity (Hocking & Sharplin, 1965; Kevan, 1972; Smith, 1975). Several researchers have postulated that selection has increased the ability of some flowers to absorb or concentrate heat (Hocking & Sharplin, 1965; Kevan, 1972; Smith, 1975) because they attract insects that can serve as pollinating agents.

SUBSTANCES PRODUCED SPECIFICALLY TO SERVE AS FLORAL REWARDS

Nest Construction.—The production of chemical substances by plants that are gathered by bees for use in nest construction is well known (Krombein, 1967; Grigarick & Stange, 1968; Iwata, 1976). The substances are generally resins exuded from the stems of plants, including conifers, legumes, mangroves, and species of the Euphorbiaceae. These exudates are believed to serve a primary function within the plant as deterrents to predation (Berryman, 1972). A novel case of resin production as a "floral" reward has been recently investigated by Armbruster & Webster (1979) in *Dalechampia* (Euphorbiaceae). Terpenes secreted by glands on the pseudanthium, a highly reduced inflorescence, of several species of the genus (Armbruster, in correspondence), attract female euglossine, anthidiine, and trigonine bees that visit the inflorescences to gather the resin and, while doing so, deposit and pick up pollen. In actuality the secretory gland is a vegetative structure, but the nature of the inflorescence is such that the entire structure with its subtending bracts functions as a flower.

Some species of *Clusia* (Guttiferae) have been reported also to have flowers that secrete a sticky substance collected by bees, presumably for use in nest construction (Armbruster & Webster, 1979; Armbruster, in correspondence). Florally produced waxes of *Maxillaria divaricata*, *M. veriferum* and *M. flavoviride* (Orchidaceae) collected by female bees as nest-construction material can apparently also serve as pollinator rewards (Porsch, 1905; van der Pijl & Dodson, 1966).

Other cases that may eventually be shown to involve the production of non-

nutritive rewards include Ericaceae that produce concentrations of waxes on the back of the stamens (Dorr, 1980), oily exudates of *Eria vulpina* (Orchidaceae) flowers (Kirchner, 1925), and the secretions of the anthers of *Mouriri* (Melastomataceae, Buchmann, 1978, but see lipids below).

Sexual Attractants.—Deceit, or the trickery of flowers to lure pollinating insects to themselves by mimicking food, brood places, or female insects is not considered here to be an actual reward. In *Ophrys* (Orchidaceae, cf. Bergstrom, 1978), flowers have been shown to produce scents that attract male bees, but they do not appear to provide any actual reward for the individuals which land on, and attempt to copulate with, the flowers. Other plant species, however, produce sexual attractants that are collected in appreciable quantities by pollinating male bees. In these cases the chemicals can be considered true rewards. The most publicized examples of the production of sexual attractants and their collection involve members of the Orchidaceae and euglossine bees (Dodson & Frymire, 1961a, 1961b; Vogel, 1963, 1966a; van der Pijl & Dodson, 1966; Dodson et al., 1969). The oils, now known to be primarily monoterpenes, are collected only by males which land on flowers and brush patches of secretory tissue with hairs on the tarsi of the front legs. The oils are absorbed onto the plumose hairs and then transferred to the hind legs where they diffuse into highly vascularized regions inside the tibia (Vogel, 1963, 1966a). Despite years of investigation, the use of the collected oils has not yet been conclusively proved (cf. Williams, in press, for a thorough review of orchid-euglossine relationships).

After it was established that the male bees were not gnawing on the petals, investigators hypothesized that the oils might contain scents that mimicked odors of females or nests (Vogel, 1966a), but this idea was discounted when it was shown that the bees were collecting chemical substances (Dodson & Frymire, 1961b; Dodson et al., 1969). A second hypothesis proposed by Vogel (1966b) was that the floral oils were used by the male bees in the production of pheromones. Williams (1980, in press) has recently elaborated on this hypothesis and proposed on the basis of preliminary chemical results that the males modify the floral monoterpenes in the legs, transport them within the body, and then again chemically alter the compounds in the mandibular glands. The mandibular gland secretions are species specific pheromones. At the same time that Vogel put forth his second hypothesis, Dodson (1966) suggested that the oils were metabolically important for the male bees and prolonged their lives. This idea is now, however, generally discounted (Williams, in press). A final theory about the use of the oils later proposed by Dodson (1975) was that they were used by specific males to attract other males into leks that subsequently attracted females with which they would mate. While the failure of field researchers to observe leks as a common phenomenon argues against this idea, it has not yet been disproved.

The associations between euglossine bees and orchids is often very precise and appears to be a highly coevolved system involving precise mixtures of floral compounds and very species specific taxa of bees. The syndrome is not, however, limited to the Orchidaceae. The collection of floral scents by male euglossine bees has been reported in the Araceae (*Spathiphyllum, Anthurium,* and *Xanthosoma,* Dodson, 1966), Gesneriaceae (*Gloxinia,* Vogel, 1966b; *Drymonia,* Williams, in press), Solanaceae (*Cyphomandra,* Williams, in press), Euphorbiaceae

(*Dalechampia*, Armbruster & Webster, 1979), and Haemodoraceae (*Xiphidium*, Buchmann, 1978, 1980). In *Dalechampia* (Armbruster & Webster, 1979) a somewhat unusual situation pertains in that the oils are produced by a gland on the pseudanthium rather than by a gland within a flower. Williams (in press) also mentions some Cyclanthaceae that may use floral volatile oils as rewards for pollinating insects.

Nutritive Substances

Floral substances consumed by animals that can serve as pollinators range from various kinds of flower tissues to complex secretory products. In our discussion of nutritive floral rewards, we will consider first unspecialized tissues of flowers or inflorescences, then modified tissues, and finally, particular secretory products.

The actual tissues of a flower or an inflorescence can be consumed by animals that play varying roles in the pollination of the plants on which they feed. As in the case of other types of floral reward-pollinator interactions, these associations cover the spectrum from casual encounters to obligately interdependent relationships.

Brood Places (Larval Food Sources)

We will consider first brood place associations involving tissues that do not appear to have been modified for any particular nutritive function. However, it has been shown that the adults which oviposit in the flowers serve as pollinators while searching for, and ovipositing in, host plants. The larvae themselves rarely effect pollination as they are usually confined to a flower or inflorescence during development and are generally mobile only after the periods of anthesis and stigma receptivity have ended. When we talk of brood place-pollinator relationships, we are not speaking of simple parasitism of flowers and the developing ovules such as occurs with bruchids and legumes (Zacher, 1952) or tephritid flies and species of the Compositae (Christenson & Foote, 1960). While adults of these insect groups are often associated with the flowers of the species on which they oviposit and are usually quite specific in their choice of host plant, they do not constitute significant pollinators in terms of the number of visits per flower per unit time or in terms of amounts of pollen carried from flower to flower. Our use of brood place as a floral reward is restricted to cases in which the adults have been shown to be one of the most important, or the only, pollinator of the flowers involved.

Perhaps the two most famous examples of plants dependent on ovipositing adults as pollinators are the *Yucca* (Agavaceae)—yucca moth (*Tegiticula* spp.) and the *Ficus* (Moraceae)—fig wasp (Blastophagidae) associations. The intricate relationships between these taxa and their pollinators have fascinated botanists for many years and have been described numerous times (e.g., Proctor & Yeo, 1972; Faegri & van der Pijl, 1979). In both cases it is now known that pollen, a traditional floral reward is gathered, but not consumed, by the females of both the yucca moths and fig wasps. In *Yucca* a pollen ball is gathered by a female moth from a flower or series of flowers. She then carries the completed ball to

another flower and begins to oviposit. She usually interrupts the ovipositing process to climb to the top of the style and force the pollen ball into the stigmatic cavity. The larvae which hatch feed on the developing seeds (Riley, 1872; Powell & Mackie, 1966). Unlike the yucca system in which one species of moth pollinates the vast majority of *Yucca* species, figs are pollinated by species-specific female wasps. The tiny females become dusted with pollen (active packing of pollen into pockets on the thorax and coxae also occur in many taxa, Ramírez, 1969) when they leave the syconium in which they developed and mated. After entering a different syconium in search of oviposition sites, these females pollinate numerous flowers. The larvae develop in, and feed on, the ovarian tissues of female fig flowers.

The jackfruit, *Artocarpus heterophyllus* (Artocarpaceae), likewise appears to have adapted to the use of brood-place seeking females as pollinators. Van der Pijl (1953) reported that clusters of male flowers in which females of the genus *Dettopsomvia* (Drosophilidae: Diptera) oviposit are enlarged relative to other members of the genus and provide a medium of floral tissue for larval development. A similar association between flies of the genus *Atherigona* (Anthomyideae: Diptera) and *Alocasia pubera* (Araceae) was also reported by van der Pijl (1953). Other plant species, with perfect rather than unisexual flowers, also use floral tissue as larval food as a reward for pollinating female insects. Thrips that oviposit in flowers have been suggested as the pollinators of different species of *Calluna*, *Phyllode*, and *Erica* (Ericaceae) by Hagerup & Hagerup (1953), but Haslerud's (1974) results indicate that the female insects effect little or no pollination except, perhaps, in *Erica*. In *Trollius europaeus* (Ranunculaceae), larvae of its major pollinator *Chiastochaeta trollii* (Thysanoptera) consume receptacular tissue and developing ovules later in the season (Hagerup & Peterson, 1956). Recently, Brantjes (1976a, 1976b) carefully described the relationship between *Melandrium album* (Caryophyllaceae) and its principal pollinator, female *Hadena bicruris*, a noctuid moth. The females visit the flowers for nectar and to lay their eggs in the receptacle. After hatching, the larvae consume an appreciable portion of the potential seed crop. In this particular case Brantjes concluded that there is a precarious balance between pollinator service and simple seed predation. In *Thuranthos* (Liliaceae) an equally hazardous system exists. The two species of this African genus appear to depend on noctuid moths (i.e., *Diaphone eumela*) for pollination (Stirton, 1976). The adult females, which feed on nectar of open flowers, oviposit on young, unopened buds at the apex of the flowering inflorescences. The developing, voracious larvae crawl down the rachises, consuming ovaries and maturing fruits.

In contrast to plant species which are pollinated primarily by insects feeding on completely unspecialized floral parts, are several taxa that have a proliferation of certain tissues as food sources for the larvae of pollinating insects. These plants are often obligately dependent upon their pollinating-parasitizing visitors. One of the cases in which this sort of syndrome is most dramatically exhibited is in the Hydnoraceae. Both of the genera of this family, *Hydnora* and *Prosopanche* are obligate root parasites of other angiosperms and both appear to depend upon beetles for successful pollination. None of the species of the family has leaves. Flowers and fruits are the only portions of the plants borne above

ground. In *Prosopanche americana*, nitidulid beetles (*Neopocadius nitiduloides*) and weevils (primarily *Oxycorynus hydnorae*) feed as adults first on the outer walls of the perianth and, when the flowers open, on the staminal column inner perianth walls. Once they have crawled into the flowers, the insects become temporarily trapped, but continue feeding and simultaneously oviposit into the inner perianth walls. Occasionally, a female which has arrived dusted with pollen will crawl into the lower chamber of the flower and contact the flat stigmatic surface. The anthers of *Prosopanche* dehisce a day or so after the flower opens, dusting females who have completed oviposition. The insects then crawl or chew their way out of the flower (Simpson & Neff, 1977). During the period of fruit maturation, the larvae of these groups feed on the particularly thick layers of floral parenchyma. Bruch (1923) described a similar sequence involving the same beetles for the second member of the genus, *P. burmeisteri*. *Hydnora*, the other genus in the family, also appears to be pollinated by beetles, but the accounts of both Marloth (1907) and Vogel (1954) indicate that it attracts carrion beetles and flies because of its fetid odor and red-purple color. It is not clear if the white, fatty structure inside the flower described by Marloth (1907) functions simply as a source of an odor attractant, or if it acts as a food body. Similar structures in *Prosopanche americana*, which lack a strong odor, are involved in the floral trap mechanism.

ADULT FOOD SOURCES

While floral or inflorescence tissue may be enlarged for larval nutrition, there appear to be no proved cases in which there is a special type of tissue produced as a source of food for the larvae of potential pollinators. For tissues other than pollen that serve as nutritive rewards for adult animals, this is not the case. The pandanaceous genus *Freycinetia* has fleshy bracts surrounding the flowers. These "food bracts" were initially hypothesized by Porsch (1930) to serve as food for birds and bats. Recently, Cox (1980) has shown that flying foxes feed on the bracts and simultaneously pollinate the flowers of the dioecious plants. Likewise, Baker (1978) reported that the fleshy sepals of male flowers of the palm *Bactris major* are eaten by pollen-carrying beetles, and Purseglove (1968) proposed that the staminodes in cacao flowers (*Theobroma cacao*, Sterculiaceae), are pierced by pollinating certopogonid midges. In several species of Araceae, parts of the spadixes have been modified into food tissues (Faegri & van der Pijl, 1979) that are gnawed by pollinating beetles. These tissues are on the lower part of spadix in *Amorphophallus variabilis* and form projections above the female flowers in *Typhonium trilobatum* (van der Pijl, 1953). A final example is the sweet corolla of *Madhuca* (Sapotaceae) species (Faegri & van der Pijl, 1979).

Beach (in correspondence) has found that species of *Bactris* (Palmae) have glandular trichomes on the inflorescence rachises that are consumed by scarab beetles (*Cyclocephala*) while they mate on, and also pollinate, the flowers.

About thirty years ago, Grant (1950) demonstrated that the flowers of *Calycanthus occidentalis* (Calycanthaceae) are primarily pollinated by a nitidulid beetle (*Coleopterus truncatus*) that feeds on the tepal tips that have become modified into food bodies. McCormack (1975) later demonstrated that many species of beetles are initially attracted to the flowers by a complex array of volatile com-

pounds which may mimic fungal odors, rather than by the food bodies themselves. Rickson's (1979) study of the composition of the food bodies showed that they were rich in protein with low levels of starch and lipids. Starchy food bodies serve as rewards for pollinating beetles in several species of *Nymphaea* (Nymphaeaceae) (review in Schneider, 1979).

In the Orchidaceae a number of cases of specialized food tissues have been reported, but many of these appear to need substantiation. The reports indicate that some orchids have a sugar-rich food tissue that must be pierced in order to obtain the sweet fluids (van der Pijl & Dodson, 1966). The aspect of these cells is similar to that of normal epidermal nectaries, but the nectar is not secreted. Among genera reported to have this type of tissue are *Cattleya, Epidendrum,* and *Sobralia.* In *Diuris* a similar tissue forms a ring on the top of the receptacle (Coleman, 1932). Various workers have indicated that many *Orchis* species may also have a type of tissue that must be pierced to obtain a sweet liquid (Knoll, 1956; van der Pijl & Dodson, 1966), but other investigators have concluded that the spurs of the flowers are empty and attract pollinators only by deceit. Other species of the Orchidaceae have been reported to have trichomes called food hairs that are collected or consumed by pollinating bees. At least two species of *Polystachya* (Porsch, 1906; Beck, 1914) have trichomes on the labellum that have been hypothesized to serve this function. However, Vogel (1978), after observing *P. pobequini,* decided that the trichomes are "empty," of no food value, and serve as pollen mimics rather than as a food source. In *Maxillaria rufescens* studied by Porsch (1905), the floral trichomes were shown to contain starch and lipids. Van der Pijl & Dodson (1966) list several other species of *Maxillaria* for which they indicate they have evidence of food hairs being consumed by pollinating bees. A final purported food tissue in the Orchidaceae reported by Beck (1912) is in the form of food scales on labellum of *Vanilla planifolia* which appear to contain sugars and starches. Van der Pijl & Dodson (1966) also list *Coelogyne* and *Cymbidium* as having scales or hairs that are grazed by bees.

Pseudopollen.—Closely related to food trichomes is pseudopollen. We should mention here that the term pseudopollen has been used in two somewhat different ways. Van der Pijl & Dodson (1966) defined pseudopollen as a pollenlike mass of cells that results from the disintegration of multicellular trichomes. In the cases they cite of *Maxillaria* (see also Porsch, 1909; Dodson & Frymire, 1961b), the pollenlike cells appear to contain starch and serve as an actual nutritional reward for bees that collect them. Porsch (1909) cited a similar case in *Rondeletia* (Rubiaceae). Vogel (1978) later used the term pseudopollen for trichomes that mimic pollen and attract pollinators by deceit. Among groups that use pollen-mimicking trichomes in this way are members of the Commelinaceae (*Tradescantia* and *Commelinantia*) and orchids such as *Calopogon.* Following Vogel's usage no reward is, of course, obtained.

Nonfunctional, Dimorphic Pollen.—A number of species of angiosperms have dimorphic pollen associated with a dimorphism in pollen function. One form of the pollen serves as the male gametophyte, the other, sterile form, serves as a reward for pollinators. Vogel (1978) described several cases of plant species which have sterile pollen that is used as a mimic of pollen to lure potential pollinators into appropriately visiting the flowers. However, here we are concerned with a

derivitive of functional pollen that serves as a reward in its own right. Classical cases of food pollen occur in *Cassia* (Leguminosae, Tischler, 1917) and *Melastoma* (Melatomataceae, Forbes, 1882). However, the extent of the phenomenon in these large genera is unknown, and it has not been investigated recently. We have been unable to verify the presence of dimorphic pollen in any of the species of *Cassia* we have examined.

More recent cases of dimorphic pollen have been reported in *Tripogandra* (Commelinaceae, Lee, 1961), *Tetracera* spp. (Dilleniaceae, Kubitzi & Baretta-Kuipers, 1969), and *Lecythis pisonis* and *Couropita guianensis* (Lecythidaceae, Mori et al., 1980). In *Tripogandra* there is only the supposition that the two pollen forms serve different functions, and in *Tetracera* the sterile pollen is found in perfect flowers of New World species that are labeled as being androdioecious, but which are functionally dioecious. The sterile pollen type could, therefore, be simply the remnant of the former, sexual flower, a form of deception, or an actual reward. Within the Lecythidaceae, there is ample documentation of large, pollinating bees feeding on the sterile form of the pollen while becoming dusted on the back with functional pollen.

Secretions Other than Sugar from Floral Nectaries.—The locations and types of floral nectaries have been thoroughly discussed by Fahn (1952) and Kartashova (1965). However, sugar-dominated secretions from structures other than typical floral nectaries can serve the same function. The lapping of stigmatic fluid from *Ephedra campylopoda* (Porsch, 1910), *Gnetum* (van der Pijl, 1953), and some palms (e.g., *Chamerops humilis*, personal observation) by insects has been linked with pollination. Copious, sweet stigmatic secretions of *Anthurium* (Araceae) that serve to attract pollinators have been reported and illustrated by Dauman (1930) and Croat (1980). All of these secretions are predominantly sugar solutions, but apparently can also contain amino acids as well (Baker, 1978). According to Martin (1969) and Fahn (1979), secretions of wet stigmas are usually composed primarily of oil and amino acids with small amounts of sugar. While it is apparent that more chemical analyses are needed, it is possible that there has been a selective modification of the composition of stigmatic secretions that are used as pollinator rewards.

Secretions from extrafloral structures that are parts of a compound inflorescence that functions as a flower (e.g., in the Araceae and the Euphorbiaceae) can also serve as "floral" rewards.

Oils.—The last nonpollen and nectar reward that we want to discuss is floral oil. This group of florally secreted chemicals was only recently recognized, but since its first report (Vogel, 1969) has been intensively studied by Vogel (1974) and our laboratory (Simpson et al., 1977, 1979; Seigler et al., 1978; Neff & Simpson, 1981). The term floral oils, it should be pointed out, is now used only for nonvolatile oils, not the essential oils that serve as odor attractants (although these may be mixed with floral oils), or as sexual attractants. It is becoming increasingly apparent that floral oils are one of the most widespread alternatives to pollen and nectar used as rewards for flower-visiting insects. We will, therefore, discuss floral oils in more detail than the other rewards mentioned above. In particular we will look at the taxonomic distribution of oil-secreting flowers, the structures of the organs that produce the oils, and the nature of the compounds
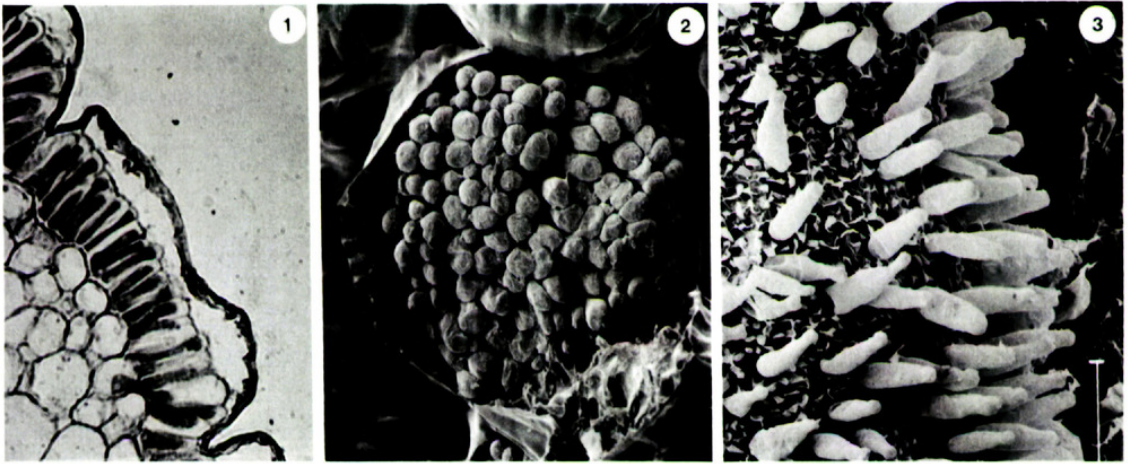
FIGURES 1–3. Types of elaiophores, or oil-secreting floral glands.—1. An epithelial elaiophore shown in cross-section, showing the highly differentiated layer of epidermal secretory cells covered by a common cuticle (×180).—2. A portion of an epithelial elaiophore of *Krameria grayi* (Krameriaceae) viewed under SEM (×181). See Fig. 4 for a view of an entire elaiophore.—3. Trichome elaiophores of *Trimezia* sp. (Iridaceae) from Goias, Brazil (×62).

produced. We will also elaborate upon the collection of the oils by specialized bees and indicate what is known about oil use.

It has been known for at least 200 years that various angiosperms such as the members of the Malpighiaceae and the genus *Krameria* have large glandular structures on the flowers. Before 1969, it was assumed that these structures were nectaries or remnants of functional nectaries. Vogel (1969) was the first to demonstrate in convincing detail that structures which he named elaiophores secreted lipids rather than nectar. In his later treatment (1974), he provided a detailed description of two kinds of oil-secreting organs, trichome and epithelial elaiophores, and listed five angiosperm families in which he thought they occurred. Trichome elaiophores (Fig. 3) are glandular trichomes that secrete lipids. They usually occur in patches on the corolla, but they can also occur on the stamens or ovary bases. The apical cell (or cells) of each trichome secretes oil that collects under the surrounding cuticle or in spaces between the trichomes. Vogel (1974) found evidence of these elaiophores in the Iridaceae, Orchidaceae, and Scrophulariaceae.

Epithelial elaiophores (Figs. 1, 2) are areas of glandular tissue with lipid-secreting epidermal cells. In this case the oils accumulate under the collective cuticle. Vogel (1974) listed three families, Orchidaceae, Malpighiaceae, and Krameriaceae, with taxa that appeared to have this type of elaiophore. On the basis of anatomical evidence, Vogel (1974) hypothesized that the oils were physically secreted from both types of elaiophores through pores in the cuticle. The oils seemed to be forced through the pores by female anthophorine bees equipped with a scraper of bristles on the front and/or mid legs or sopped up by pads of absorbant hairs on the forelegs. He diagrammed (1974: 468) what he believed to be the motions of the legs of *Centris* during the process of forcing oils through the pores of an epithelial elaiophore of *Stigmaphyllon* (Malpighiaceae).

In addition to his morphological studies of elaiophores, Vogel (1974) called attention to the fact that these oils are collected only by certain female bees of

the family Anthophoridae. Both the production of floral lipids and their collection appeared to be restricted to the New World although he indicated two genera of Scrophulariaceae (*Diascia* and *Bowkeria*) native to South Africa which may have flowers that secrete oils. Nothing is known of the pollinators of either genus. In several instances Vogel documented oil production with various chemical tests and personally observed oil collection by anthophorines in South America. In other cases, such as *Krameria,* he postulated oil production and its collection on the basis of floral anatomy and distributional records of bees.

Vogel ascertained for several genera that the secretory products were lipids by showing their lack of miscibility with water. His subsequent use of thin layer chromatography demonstrated that the secretions contained mixtures of several compounds. In most cases one or two of the components was present in greater quantities than the others. For *Calceolaria* he carried the analyses further and, in collaboration with Dr. F. Caesar (Vogel, 1974: 88–121), investigated the structures of the compounds involved. They concluded that the lipids of *Calceolaria pavonii* consisted primarily of diglycerides (which they called monoglycerides) with a β-hydroxy fatty acid and an acetate attached to each glycerol backbone. They also reported small amounts of free fatty acids in the mixtures.

Finally, Vogel hypothesized that the oils are used in place of nectar as the liquid component of the larval provisions of the solitary anthophorine bees. He examined the nests of several species, including fresh nests of *Tapinotaspis caerulea* and older, somewhat degraded, nests of a *Centris* and analyzed their contents. In addition to lipids he found traces of sugars that included fructose, sucrose, and di- and triglycerides. Only triglycerides are uncommon in plant nectars. Nevertheless, because the sugars were present in such small concentrations, Vogel (1974) concluded that the oils were a replacement for nectar in the larval food.

Since 1974, Vogel has reported three genera in two additional families, the Primulaceae and Cucurbitaceae (Vogel, 1976a, 1976b), which appear to have trichome elaiophores. In contrast to all of the groups reported before, one of these genera, *Lysimachia,* is almost entirely temperate in distribution. Both of the members of the Cucurbitaceae (*Momordica* and *Thladiantha*) are restricted to the Old World tropics. Moreover, entirely different groups of bees from those in the New World tropics, species of *Macropis* (Melittidae) and *Ctenoplectra* (Ctenoplectridae) reportedly collect the oils of these genera.

We have been investigating the phenomenon of floral oil secretion in the Krameriaceae and other New World groups for several years. In many cases our studies have confirmed Vogel's observations and conclusions. However, our data differ in some cases from his and we have been able to add to his observations. We have, for example, recently confirmed that the Solanaceae contains at least one genus, *Nierembergia,* that produces floral oils (Seigler, Simpson and Neff, in preparation). *Nierembergia gracilis* in Argentina is visited primarily by oil-collecting anthophorines (*Tapinotaspis* spp. and *Centris* spp.). Our chemical analyses of the extracts of the portions of the petals with secretory trichomes have shown that they produce, among other things, the same types of oils as other oil flowers.

Most of our studies, however, have centered around *Krameria* and *Centris,*

its primary pollinator. *Krameria* is the sole genus in the Krameriaceae, a small group of about 15 species that has been variously aligned with the Leguminosae and the Polygalaceae. A synthesis of morphological and anatomical data suggests that a placement in the Polygalales is most realistic (Simpson & Skvarla, 1981). The flowers of all *Krameria* species are zygomorphic with five, separate, showy sepals. The five (or four) petals are reduced, two or three of them form a flag above the superior ovary and the remaining two have become lens-shaped glands flanking the ovary (Fig. 4). The glandular petals are 2–4 mm in diameter and can contain a milligram of oil per flower (not 0.9 mg per gland as reported in Simpson et al., 1977). In this case, therefore, entire petals have been modified into elaio-phores.

We have examined in detail, by light and scanning electron microscopy, the structure of the elaiophores of the Krameriaceae (Figs. 1, 2, 4) and Malpighiaceae. In neither case did we find evidence of pores in the cuticle. Schnepf (1969) earlier found no pores in the cuticle of the trichome elaiophores of *Calceolaria*. Unvis-ited flowers, particularly those of the Krameriaceae, do not have free oils on the gland surface. Observations of glands after bee visitation clearly shows that dur-ing the collection process, female *Centris* rupture the cuticles (Fig. 5) while scraping the surface.

We have also examined the glands of *Krameria* using transmission electron microscopy (Simpson & Johnson, in preparation). The only previous work of the ultrastructure of oil-secreting glands was carried out by Schnepf (1969). He sec-tioned and described the multicellular apices of oil-secreting trichomes of *Cal-ceolaria rugosa*. He pointed out the large quantities of endoplasmic reticulum (ER) in the dense cytoplasm and described what he termed complexes of endo-plasmic reticulum and leucoplasts. Dictyosomes were especially noticeable in young secretory cells. The outer cell wall of the secretory cells was uneven, but generally thick compared to the walls of the nonsecreting stalk cells of the gland. He hypothesized that the oils were somehow able to penetrate through the thinner parts of the cell wall and collect under the cuticle. Despite his efforts, Schnepf (1969) was unable to locate large areas of oil accumulation within the cells or any apparent precursors of the oils.

Our studies showed many of the same features described by Schnepf. How-ever, it should be pointed out that dense cytoplasm and relatively large amounts of ER are characteristic of plant secretory cells in general (Fahn, 1979). We have also noticed what appear to be leucoplasts in the cytoplasm and evidence, par-ticularly in young cells, of vesicle formation by the ER. With the exception of normal lipid droplets, we have also been unable to pin-point areas of lipid ac-cumulation within the cells. Fresh sections cut with a freeze microtome and stained immediately with Sudan black, a stain specific for lipids, showed a dis-tribution of the stain throughout the cytoplasm. In older cells, there is a con-spicuous shrinking of the cytoplasm from the outer cell walls producing a space between the plasmalemma and the cell wall. Schnepf found no such pulling away in the cells of *Calceolaria*. He did, however, find a similar structure in the se-cretory glands of *Salvia pratense* (Schnepf, 1972). The glands of *Salvia* are not oil glands and Schnepf postulated that the material which accumulated in the space between the plasmalemma was mucilage. We have stained fresh, freeze-
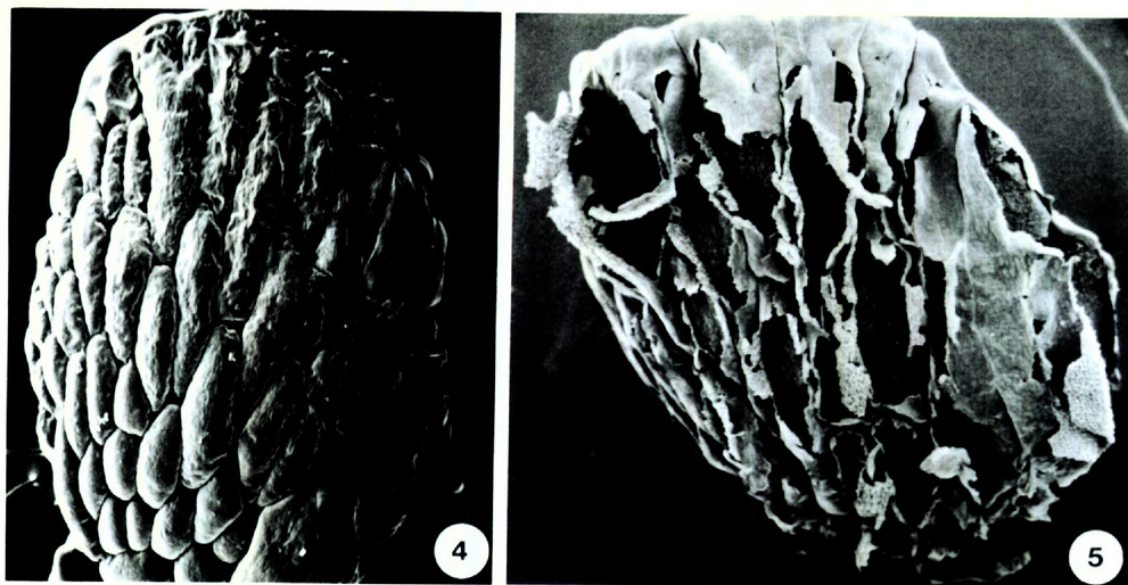
FIGURES 4–5.   Epithelial elaiophores of *Krameria cuspidata* before (Fig. 4) and after (Fig. 5) visitation by an oil-collecting *Centris*. The cuticle under which the oils collect (Fig. 4) has been ruptured (Fig. 5) by the scraping movements of the fore and mid legs of the bees. Both ×20.

sectioned material with both ruthenium red (indicative of aqueous materials) and Sudan black. The space between the plasmalemma and the cell wall stained with neither. We must conclude therefore, that, unlike tissues of oil seeds that accumulate oil within the cells (e.g., *Sinapis*, Rest & Vaughn, 1972), oil-secreting cells transport the oils as soon as they are manufactured, or store very small quantities at a time uniformly throughout the cell. We know that oil secretion begins before the flowers open because unopened buds are forced open by bees who scrape the glands. Likewise, it appears that even after the cuticle is ruptured by an initial visit, the glands continue secreting, at least through the initial part of anthesis.

Our chemical analyses of the lipid secretions of *Krameria*, several Malpighiaceae, Iridaceae, and *Nierembergia* showed that the principal components of the oils differ from those reported by Vogel (1974) for *Calceolaria*. Vogel and his collaborator concluded that the majority of the oil they analyzed was in the form of a glyceride. While we found traces of glycerides in some samples (Seigler et al., 1978), we estimate that about 90% of the lipids is in the form of free fatty acids. Free fatty acids are relatively rare in plant tissues. Moreover, the fatty acids have an acetyl group in the β position, an unusual position for substitutions in fatty acids. We should mention, however, that the β-acetoxy fatty acids we have found (saturated acids with chain lengths of C16, C18, and C20), are the same as the fatty acids which Vogel found to be constituents of his glycerides. Analyses of epithelial elaiophore secretions of *Malpighia glabra* and *Mascagnia macroptera* (Malpighiaceae) and trichome elaiophore secretions of *Trimezia* sp. (Iridaceae) and *Nierembergia* all showed that they, like *Krameria*, contained β-acetoxy fatty acids. *Nierembergia*, however, contained a wider array of lipids and phenolics than the other species.

We also analyzed the oils of *Lysimachia ciliata* proposed by Vogel (1978) to

be an oil-producing species that is collected by female *Macropis*. Like the neotropical taxa visited by anthophorine bees, this species seems to contain free acetoxy fatty acids, but the extracts contain many other compounds as well. The principal components of the oils appear to be terpenes. It is, therefore, not clear that the system in *Lysimachia* is strictly comparable to that of the neotropical species visited by anthophorine bees. We are presently attempting to analyze other purported Old World species of oil flowers.

Buchmann (1978; Buchmann & Buchmann, 1981) recently reported that female anthophorine bees of the oil-collecting genus *Paratetrapedia* visit *Mouriri myrtilloides* (Melastomataceae) in Panama and he analyzed the secretions of glandular areas on the connectives of the anthers. His analyses demonstrated an array of classes of chemicals in the secretions, including fatty acids, amino acids, short chain acids, glycosides, and saponins. On the basis of the studies carried out by Buchmann, it is not possible to determine if *Mouriri* actually possesses the same syndrome of oil production as the other New World taxa Vogel (1974) and we have examined. The extracts he examined did contain numerous fatty acids, but he did not indicate if they were substituted or not. In addition, many of the components that he found in the oils of this species appear to be rather toxic (as food) to insects. His hypothesis (in press) that the bees which collect *Mouriri* oils may have to detoxify them suggests a use different from that of the oils of the other plants studied. Finally, Buchmann & Buchmann (1981) observed *Trigona* bees collecting *Mouriri* oils and placing them in the scopae separate from pollen. *Trigona* has never been reported collecting floral oils from any of the flowers previously investigated. Consequently, it appears that *Mouriri* and its relatives have a system of floral rewards different from that currently considered as floral oils.

Because of conflicting reports, we also tried to determine if the glandular secretions of *Krameria* contained sugars. Analyses of nest contents of oil-collecting bees have shown that some contain appreciable amounts of glucose and fructose (Simpson and Neff, unpublished). It is known that adult oil-collecting bees visit plants other than their oil hosts for nectar, and it has consequently been tacitly assumed that any sugars in the larval provisions came from nonoil plants. If there are sugars in the elaiophore secretions, they may account for the sugars found in nest provisions. Percival (1961) and Baker (1978) have reported the presence of sugars in the ''nectar'' of several species of supposed oil flowers of the Malpighiaceae. Since Vogel (1974: 531) hypothesized that the elaiophores of the Malpighiaceae are derived from extrafloral nectaries, sugars might logically be expected to still be present in their secretions. However, if sugars are present in large quantities in the elaiophore secretions, Vogel's suggestion that the oils are used instead of nectar is unfounded. What is necessary to determine is the quantity of sugars in elaiophores if they are present. Small quantities of sugars are found in most plant secretions such as gums, latexes, etc. Likewise, lipids are commonly found in nectar (Baker & Baker, 1975), but their quantities are usually very small relative to the total solution.

We therefore analyzed simple gland extracts, material from squashes of entire glands, extracts of macerated glands, and extracts of macerated calyx lobes (of Malpighiaceous species from which the glands had been removed) of species including *Krameria lanceolata, Malpighia glabra,* and *Stigmaphyllon* sp. (ex-

amined by both Percival and Baker). Whenever extracts were made, over fifty glands or calyx lobes were used. The plant material was extracted with distilled water, and the decanted extracts evaporated to dryness. The residue which remained was taken up in a very small quantity of methanol and spotted on cellulose 300 N plates (Stahl, 1969: 814) and visualized with standard reagents. In no case have we been able to find any traces of sugars. Further study is obviously required, but clearly sugars are not significant components of the mature elaiophore secretions of the species we have examined.

When oil collection was first reported by Vogel (1969), and its presence in anthophorine nests confirmed (Vogel, 1974), it seemed assured that the primary role of the oils was to serve as a larval food source. The fact that nectar is now known to be present in significant quantities in some of these nests (Neff and Simpson, in press), raises some doubts about nutrition as the sole use of the oils. Floral oils should provide a concentrated energy source that could allow foragers to show a higher energy profit than bees foraging just for pollen or nectar. Available data on this point is sparse and inconclusive. Raw (1979) found that *Centris dirrhoda* foraging for oil and pollen on *Malpighia punicifolia* in Jamaica had very high floral visitation rates (41.8 flowers per minute) and was estimated to be able to complete a pollen-oil foraging run in seventeen minutes. In our studies, principally on *Krameria* species and several different species of the Malpighiaceae, we typically find much lower floral visitation rates (3.4–7.5 flowers per minute on *Krameria* and 5.0–19.2 on *Malpighia glabra*). We have also not observed foragers which collect pollen from their oil hosts. In addition, individual oil-foraging bouts are quite prolonged (occasionally over 30 minutes). As yet, it is thus impossible to formulate an energy budget for any oil-collecting bees, but we are planning to attempt this in the immediate future. Since floral oils may have qualities other than a high caloric value, we have proposed a number of alternative, but not mutually exclusive, possibilities for floral oil use. Alternative explanations we have proposed are: that the oils are incorporated into the nest linings, that the oils serve a fungicidal, bacterial or anti-predator function, or that the oils help to prevent water from being absorbed into the nest provisions (this last was suggested to us by Jerry Rozen). To date the only one of these we have been able to test is the possible fungicidal activity. We have tested (with the help of Robert Slocum) *Krameria* gland extracts against three species of fungi (*Aspergillus flavus*, *Saccharomyces cerevisiae*, and *Fusarium* sp.) known to be pathenogenic in solitary bee nests (Batra et al., 1973). The tests proved to be negative. Consequently, while many short chain fatty acids have a fungicidal activity (Wyss et al., 1945), those of *Krameria* appear to have no such effect. In fact, in the agar cultures on which we placed filter paper discs impregnated with *Krameria* oils, the fungi appeared to be fully capable of metabolizing them.

We have not yet been able to test the other hypotheses, but think that it is unlikely that the bees are incorporating the lipids into the nest lining because closely related anthophorines which do not collect oils construct virtually identical kinds of nests. Moreover, pollen is frequently incorporated into the scopal loads with the oils, yet pollen is not part of the nest linings of the taxa we have examined. At the present time therefore, it still appears most likely that the oils are used as one of the primary larval metabolites. The nutritional hypothesis gains support from the recent finding that the larvae of certain species of *Anthophora*
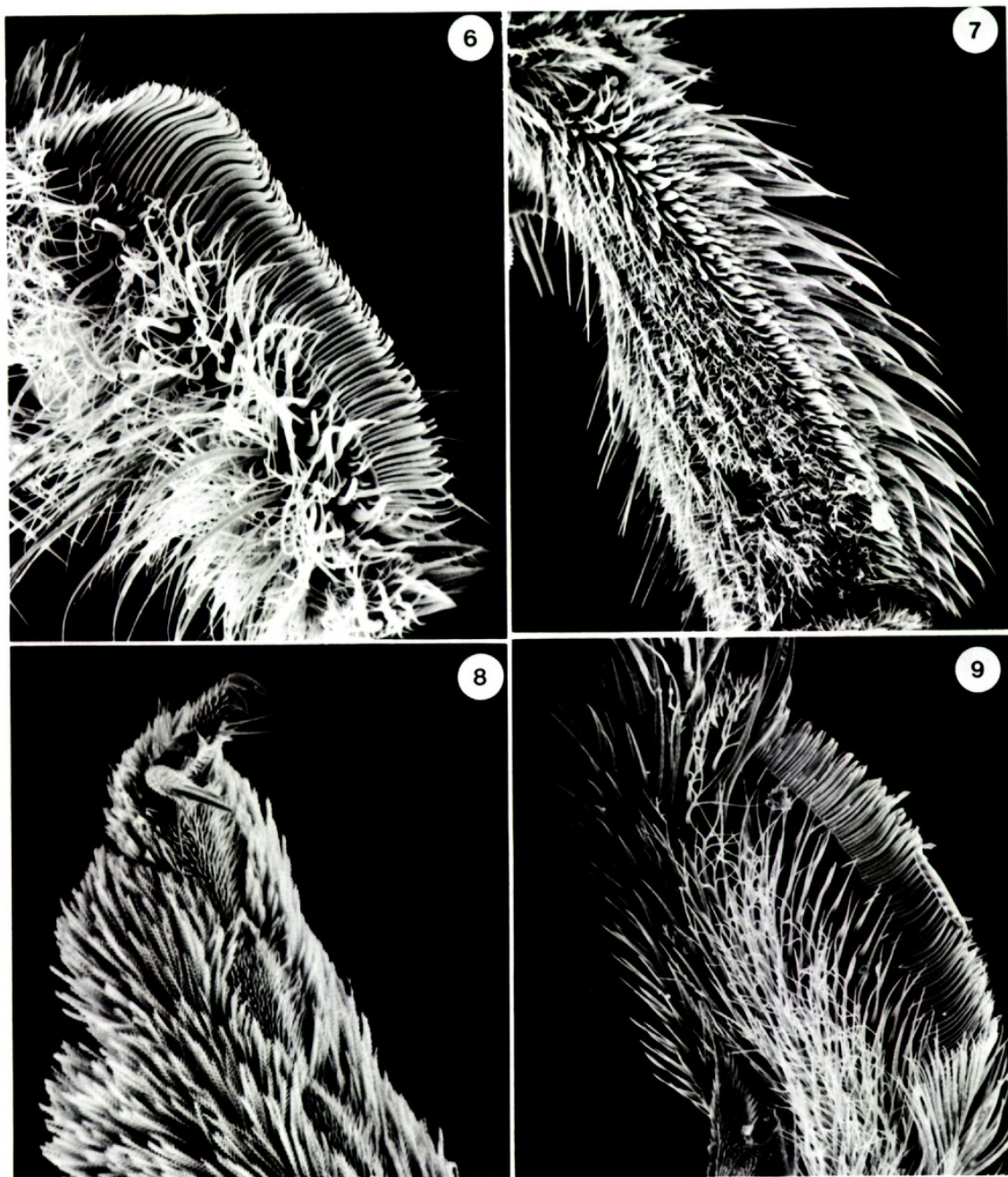
FIGURES 6–9. Oil-collecting structures of female anthophorine bees.—6. Right forebasitarsus of *Tetrapedia maura*, Tetrapediini (×79).—7. Right forebasitarsus of an undescribed *Tapinotaspis*, (*Tapinorhina*) Exomalopsini (×65).—8. Tarsus, left midleg (distal portion) of *Tapinotaspis* (*Tapinotaspis*) *chalybaea*, Exomalopsini (×43) showing the brushlike collecting hairs of this species.—9. Basitarsus, left foreleg of *Paratetrapedia maesta*, Exomalopsini (×83).

consume the maternally secreted fatty lining of their larval cells (Norden et al., 1980). *Anthophora* is a genus of nonoil collecting bees closely related to the oil-collecting anthophorines.

The oil-collecting structures of female Anthophorinae exhibit a wide array of morphologies ranging from long, sickle-shaped, relatively straight rows of simple setae to hoodlike cups of highly modified setae or pads of finely branched hairs
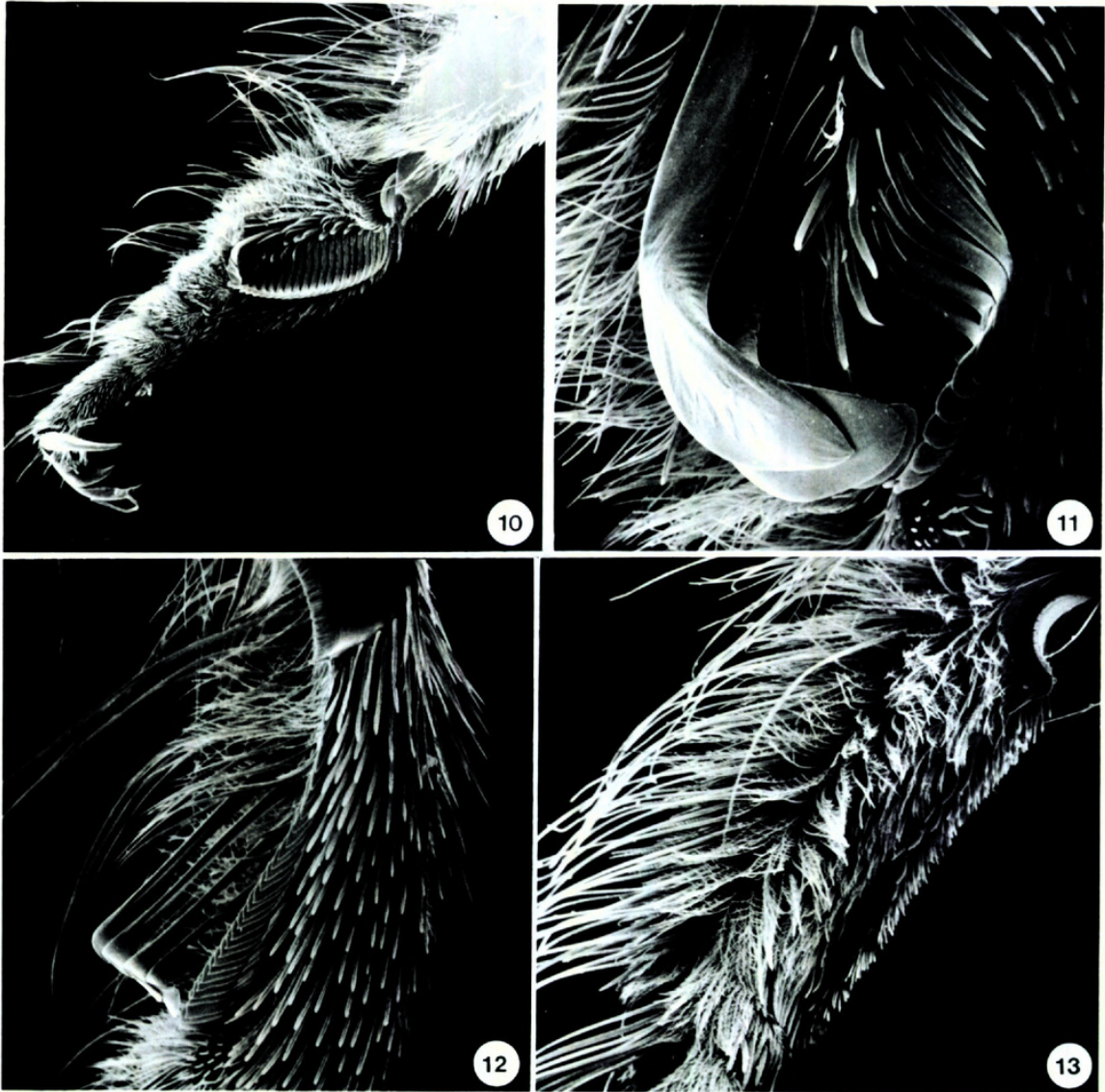
FIGURES 10–13.   Forelegs of species of *Centris* species (Anthophorini, Centridini) showing the variations of the oil-collecting structures present in this genus.—10. Tibia and tarsus of a *Centris* aff. *tricolor* which collects on flowers with epithelial elaiophores (×24).—11. Left basitarsus of *C.* aff. *autrani* which collects oils from flowers with trichome elaiophores such as *Calceolaria* spp. (×121).— 12. Left basitarsus of *C. versicolor*, a collector of oils from species of the Malpighiaceae, all of which have epithelial elaiophores (×62).—13. Left basitarsus of a nonoil-collecting *Centris, C. pallida* showing the loss of the oil-collecting structures (×62).

(Figs. 6–13 and Neff & Simpson, in press). As pointed out by Vogel (1974), there is a good correlation between the type of collecting structure and the type of elaiophore of the plants visited. Species of bees with only pads of hairs on the basitarsi visit only flowers with trichome elaiophores, presumably because they are incapable of scraping and rupturing the cuticles of epithelial elaiophores. On the other hand, species with scraping combs can, and do, visit plants with either type of elaiophores.

    We have examined in detail the collecting structures of oil-collecting antho-phorines (Neff & Simpson, 1981). These studies suggest that oil-collecting

may have arisen only once, or at most twice, in this family and that collection on plant species with trichome elaiophores preceded that of collection from epithelial elaiophores. Within *Centris* (Figs. 10–13), however, there is an ancestral association with epithelial elaiophores, particularly those of Malpighiaceae, independent losses of the ability to collect oils (with a corresponding reduction or loss of the collecting structures), and a variety of modifications of the oil-collecting apparatus related to the radiation in the spectrum of oil-producing hosts (Figs. 6–13).

We have studied in some detail the foraging behavior of marked females of *Centris atripes* in mapped populations of *Krameria lanceolata* in Austin, Texas. While oils are frequently incorporated into the scopal loads of pollen foraging bees, extensive observations indicate that oil foragers rarely carry significant amounts of pollen in their scopae. In this case at least, pollen foraging, which invariably involves plants other than *Krameria*, must occur after *Krameria* visitation. Oil foragers usually show extreme site constancy in our study area. One bee that was followed for 34.5 minutes, visited 119 consecutive *Krameria* flowers and buds within an area of 10 m². However, some individual foragers move on a regular basis between populations 50 to 100 m apart. The same marked female bees were observed day after day in the same populations of *Krameria* which are composed of what appear to be 10 to 25 flowering individuals. Controlled pollinations have shown that *Krameria lanceolata* is self-compatible but not autogamous. Within a plant, therefore, geitonogamy appears to be unavoidable as individual bees usually visit a high proportion of the open flowers on any particular plant. However, individual bees may frequently approach, but rarely revisit, flowers they have recently visited on a given plant.

We have performed a series of preliminary experiments to help to understand what are the specific attractants of *Krameria* flowers and how female *Centris* are able to recognize flowers they have recently visited. The experiments have involved removal of various floral parts as well as exposure of gland secretions on filter paper discs to foraging bees. Observations of the antennae dipping activities of female *Centris* indicates that the primary short-range cues are olfactory, although the isolated gland secretions on filter paper never attract female bees. Scent production, at least to a human nose, seems to be localized in the elaiophores in *K. lanceolata* and *K. grayi*, yet, typical oil gathering motions of female *Centris* were still observed when either the elaiophores or the stamens were removed from flowers. In the former case the bees simply went through the scraping motions with the legs grazing only the sides of the ovary. Current evidence suggests that a hierarchy of cues is involved which includes floral form and color, an odor (volatile oils) mixed with the fatty oils, and scent marking, either passive or active, by the bees themselves. Further experiments are planned to unravel the sequential effects of these factors.

In the Austin area *Krameria lanceolata* is the only native oil plant. To study the relative constancy of female *Centris* when presented with two potential oil hosts, we placed potted, blooming plants of *Malpighia glabra* in a patch of *K. lanceolata*. *Malpighia glabra* (Barbados cherry, or acerola berry), is not native in central Texas, but it is planted in Austin as an ornamental. *Centris atripes*, our primary study bee, is quite widespread in the southwestern United States and throughout Mexico and does occur naturally in areas where *Malpighia glabra* is

native. We assume, however, that the bees with which we were working were naive to *Malpighia* since we have found none planted near the research station. After a few minutes exposure to the potted plants, the *Centris* foragers switched from *Krameria* to *Malpighia* and proceeded to scrape repeatedly all the open *Malpighia* flowers. After this initial active bout of foraging, the bees began to move back and forth between *Krameria* and *Malpighia*. These preliminary experiments suggest that these bees lack a strong innate preference for a particular oil host, at least among flowers of similar size and color. It is therefore possible that, as in many other pollination systems, constancy in foraging may be mediated by levels of resource availability.

Knowledge of the blooming patterns of oil plants in a community should be particularly enlightening in view of the fact that *Centris* and its relatives are major pollinators of many tropical species (Frankie et al., 1976). Our own work in the arid scrub vegetation in northwestern Argentina indicates that a single oil-collecting species, *Centris brethesi,* is one of the dominant pollinators of the entire community, and its interactions with various pollen, nectar, and oil hosts have led to fairly complicated phenological patterns. These kinds of interactions should be even more interesting in more mesic tropical environments where both the diversity of oil collecting bees and oil flowers increase markedly. We therefore plan to pursue studies of oil plants as a requisite component of the pollination of tropical communities.

CONCLUSIONS

While pollen and nectar are without doubt the primary floral rewards, selection has promoted the use of numerous alternative rewards in an impressive number of plant species. We conclude, as have others, that selection favored the elaboration or use of these rewards because plants which possessed them were able to capture a segment of the pollinator community not used by other plants in a community and/or achieve greater constancy of visitation.

If the use of alternative rewards insures greater constancy and, presumably, more effective pollination, we might ask why more plants have not turned to them. We believe the answer is two-fold. First, many alternative rewards are more expensive (energetically) than pollen and nectar, and, second, the use of an alternative reward often locks both the plant and the pollinator into a one-to-one relationship. While in the short run such specificity might be advantageous, it provides a situation conducive to relatively rapid extinction. It is likely that in such systems as those involving orchids and euglossines or figs and fig wasps, that coevolutionary radiation can occur rapidly, but that extinction also eliminates many species pairs.

For oil plants the situation is somewhat more complex since oil species have now radiated and oil-collecting bees do not appear to be species specific in their choice of oil hosts. If several oil plants co-occur within a community, they now appear to partition their pollinator fauna along the lines often observed for plants offering traditional rewards, namely, by temporal, spatial, or size displacements. Oil flowers also often have more options than some other plants which offer alternative rewards because their pollen can be, and is occasionally, used as a reward by oil-collecting bees. Consequently, they are not locked into a system involving a single, specialized reward.

If we ask why bees have turned to the collection of oils, the answer is not straightforward and final resolution of the question must await the accumulation of more data on the life histories of oil-collecting bees. If, however, larval nutrition is the primary use of the collected oils, it appears likely that their high energy content per unit weight relative to carbohydrates makes its use profitable. The discovery that non-oil-collecting anthophorine bees secrete maternally synthesized fatty oils from the Dufour's glands which are subsequently fed upon by the larvae provides support to the idea that fats are a superior food. On the basis of present reports, few groups of flower-visiting bees appear to be capable of metabolizing high lipid diets. More work is needed to assess the utilization of lipids by other groups of bees and to determine the degree of dependency of oil-collecting anthophorines on floral oils.

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