Pollination in the plants of the Golfo Dulce area

Polinización en las plantas del área de Golfo Dulce

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Abstract: A brief survey is given of the pollination of flowers in the Golfo Dulce area. As in any tropical country, animal pollination prevails by far, while wind and water pollination play an insignificant role. Animal pollination includes birds (especially hummingbirds) and bats. Pollination by non-flying mammals has not yet been recorded in the Golfo Dulce area, but certainly occurs in some primarily bat-pollinated species. Irrespective of significance, the present treatment follows textbook patterns, starting with abiotic vectors (wind, water) and referring to the particular animal groups (bees, flies, beetles, butterflies, moths, birds, bats and non-flying mammals). The large group of bee-pollinated flowers is classified according to the floral reward provided (pollen, nectar, perfume, oil, resin and deceptive flowers). Exemplary species which are frequent and easily encountered in the Golfo Dulce area are described in some detail and illustrated.

Key words: Costa Rica, Golfo Dulce, pollination, flowers.

Resumen: Se realizó un breve investigación sobre la polinización de las flores en el área de Golfo Dulce. Como en cualquier país tropical, la polinización por animales prevalece, mientras que la polinización por el viento y el agua tiene un rol insignificante. La polinización por animales incluye aves (especialmente picaflores) y murciélagos. La polinización por mamíferos no voladores no ha sido registrada para el área de Golfo Dulce hasta el momento, pero ciertamente ocurre en algunas especies primariamente polinizadas por murciélagos. Independientemente de su significado, el presente trabajo sigue los patrones de los textos, partiendo con vectores abióticos (viento, agua) y refiriendose a los grupos de animales en particular (abejas, moscas, escarbajos, mariposas, polillas, aves, murciélagos y mamíferos no voladores). El principal grupo de flores polinizadas por abejas es clasificado de acuerdo a la recompensa floral proporcionada (polen, nectar, perfume, aceite, resina, engaño floral). Ejemplares de especies que son frecuentes y facilmente encontradas en el área de Golfo Dulce son descritas con algún detalle e ilustradas.

Palabras clave: Costa Rica, Golfo Dulce, polinización, flores.

Preface

The present article is a condensed version of a more detailed (but by no means exhaustive) treatment of the topic which will be published in the booklet series of the Tropenstation La Gamba, in which field guides to the amphibians, reptiles and birds have already appeared (ALBERT et al. 2006, SAUBERER et al. 2007). Condensation not only means shortening of the text, but a rigid selection of examples, illustrations and references. The result is a skeletal survey on a topic the adequate treatment of which would fill a many-volumed book. Though the area considered (ACOSA region, including three national parks: 1 – Bahia Ballena National Park, 2 – Corcovado National Park, 3 – Piedras Blancas National Park, and several protected areas, e.g. Golfito Nature Reserve) is relatively small, the plant and animal diversity and the diversity of their synecological interrelations are extremely high, covering a considerable portion of what is known from the floral biology of Central and tropical South America.

Some of the anthecological discoveries are closely associated with a historical event: the Costa Rica expedition 1930, led by the Austrian botanist Otto Porsch (1875-1959) (see papers of DÍAZ 2008 and WEBER 2008a, this volume). It should be remembered that this expedition formed a milestone in the foundation and development of tropical anthecology.

Introduction

Reproduction of any flowering plant is tied to two crucial events: (1) fertilisation of ovules, and (2) seed dispersal. The pre-requisite of fertilisation and the formation of seeds and fruits is pollination, i.e. the transport of pollen grains to the stigma. Theoretically, the route for a pollen grain to the stigma is very short, measuring a few millimetres in a normal, bisexual flower. However, this only applies to the small proportion of plants that are self-fertilising. In outcrossing plants, the pollen grain's route is a "long and winding

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road", and manifold and sophisticated patterns have evolved to ensure successful pollination. Plants were extraordinarily inventive in utilising wind, water and animals as vectors for pollen transport. As in any tropical region, we encounter an enormous diversity of pollination systems in the Golfo Dulce area.

The goal of the present account is to provide some background information on the pollination of flowers that can be seen frequently seen in the rainforest, on the beach or on the roadside. It will give the functional meaning of the varied shapes and different colours of flowers. Most of their characters reflect a long history of survival and adaptation to special agents that serve for pollen transport.

Subdivision of the topic and arrangement of the chapters follows a conventional pattern, irrespective of the biological significance in the area under consideration. In the tropics, animal pollination is greatly dominant, while pollination by abiotic vectors as well as self-pollination is rather insignificant. The diversity of animals involved in pollination is much higher than in temperate plants. While in the latter only insects (bees, butterflies, moths, flies) are observed, additional insect groups such as beetles, specialised bees and vertebrates (birds, bats, non-flying mammals) play a significant role in tropical plants.

For the sake of brevity and easy reading, quotation of literature has been kept at a minimum. General information on the topics can obtained from the textbooks and summarising treatments such as KUGLER (1955/1970), FAEGRI & VAN DER PIJL (1966, 1979), PROCTOR & YEO (1973), RICHARDS (1978), BARTH (1982/1985), HESS (1983), REAL (1983), ENDRESS (1994), PROCTOR, YEO & LACK (1996), ZIZKA & SCHNECKENBURGER (1999), and LEINS & ERBAR (2008). The magnificent book "Life in the Cerrado" by GOTTSBERGER & SILBERBAUER-GOTTSBERGER (2006), the second volume of which is devoted to pollination and seed dispersal is warmly recommended. Though, at a superficial glance, the book deals with a completely different ecosystem, much can be learned for the Golfo Dulce area, as this comprises also arid and cerrado-like parts. In fact, ample comparison is made in the book with the Guanacaste province in Costa Rica, from which many floristic elements are also found in the drier parts of the Golfo Dulce area. More specifically addressed to rainforests is the brief survey on the pollination of Amazonian plants by PRANCE (1985). An overview on the reproductive biology of a Costa Rican rainforest (La Selva) was given by BAWA et al. (1985).


Fig. 1: *Myriocarpa longipes* (Urticaceae), branch with strings of female flowers. Photo: A. Weissenhofer.

Regarding the flora of the Golfo Dulce, the classic book "The rainforests of Golfo Dulce" (ALLEN 1956), the booklet "Arboles de la Peninsula de Osa" (QUESADA et al. 1997) and the "Introductory Filed Guide to the Flowering Plants of the Golfo Dulce Rainforests" (WEBER et al. 2001) are important complements. In the latter book, some basic information on pollination and seed dispersal has been included in the family treatments.

Pollination by wind (anemophily)

It is generally known that wind pollination is rare in the tropics, especially in rainforests. WHITEHEAD (1969) and JANZEN (1975) even believed that wind pollination would be completely absent in neotropical lowland rainforests. The reasons were mainly seen in the fact that wind is an inefficient pollen vector in species-rich tropical plant communities where plants of the same species are usually widely spaced.

BAWA & CRISP (1980) were the first to document wind pollination in a Costa Rican rainforest tree, namely in *Trophis involucrata* (Moraceae) (possibly conspecific with *T. racemosa* of the Golfo Dulce area). The authors also referred to *Chamaedorea* species (Arecaceae; Golfo Dulce: 11 spp.) and ***Myriocarpa longipes*** (Urticaceae; common in the Golfo Dulce area) as being wind-pollinated. In the latter, both the male and female inflorescences represent pendent spikes or catkins, the female ones being up to 60 cm long and forming conspicuous strings (Fig. 1). As in *Trophis*, the female flowers lack a perianth and bear feathery stigmata.

Anemophily is more common in plants growing in forest gaps, secondary growth, mangroves and dry forests. The fast-growing *Cecropia* species (Cecropiaceae), found in every forest gap and at forest edges, may serve as examples. In disturbed, marshy places the peculiar *Bocconia frutescens* (Papaveraceae) is found, whose pendulous stamens, thin filaments and absence of petals suggest wind pollination. In the mangrove, the flowers of *Rhizophora mangle* are both wind- and self-pollinated (MENEZES et al. 1997).

Anemophily becomes more significant at higher altitudes (Osa Peninsula), where families and genera of predominantly temperate alliances turn up, e.g. Fagaceae (Golfo Dulce: *Fagus insignis*) and Juglandaceae (*Alfaroa*, *Oreomunnia*). The dioecious or polygamodioecious *Ticondendron incognitum* (Ticondendraceae), a species/family recently described and best referred to the order Fagales (GOMEZ-LAURITO & GOMEZ 1989, 1991; HAMMEL & BURGER 1991), also seems to be wind pollinated.

Further examples of families comprising anemophilous trees and shrubs include Anacardiaceae (*Astronium graveolens*), Chloranthaceae (*Hedyosmum*), Euphorbiaceae (*Acalypha*, *Alchornea*, *Alchorneopsis*, *Croton*, *Hyeronima*), Flacourtiaceae (now mostly Salicaceae) (*Xylosma*, *Caseara*, *Lacistema*) and Rutaceae (*Zanthoxylum*). Wind pollination occurs also in some herbaceous plants, e.g. Amaranthaceae (*Amaranthus*, *Iresine*) and, of course, grasses (Poaceae) and sedges (Cyperaceae) (though some rainforest grasses have apparently switched to insect pollination: SODERSTROM & CALDERÓN 1971). In these plants, insects (small bees, flies) can almost always be observed collecting pollen and it is difficult to assess whether or not they contribute to pollination. Perhaps both wind and insects are relevant ("ambophily").

Pollination by water (hydrophily)

True water pollination, that is pollination of flowers which open in a submerged position and in which the pollen is transported underwater or on the water surface is only known from a few (mostly marine) macrophytes (see surveys of COX 1986, 1993). Relevant families are Cymodoceaceae, Hydrocharitaceae, Najadaceae, Zanichelliaceae and Ceratophyllaceae. Species of these families are found in a few sites in Costa Rica, but their distribution is insufficiently known and only one or two have been recorded from the Golfo Dulce area. The chance of a visitor seeing a hydrophilous plant is very low. Therefore, no details are given here.

Animal pollination (zoophily) – introductory remarks

Principally, animals visit flowers in expectation of a reward. The classical floral rewards are pollen and nectar (SPRENGEL 1793). In recent decades, additional rewards have been discovered, which are exclusively addressed to bees: fragrance (perfume) (VOGEL 1966), fatty oil (VOGEL 1969c), and resin (SKUTCH 1971, ARMBRUSTER 1984). As noted by SPRENGEL (l. c.), some flowers only pretend to provide a reward. This is the group of deceptive flowers.

The reward, however, is usually not the agent to attract the visiting animals. Attraction is usually by completely different agents: (1) visual cues, and (2) olfactory cues (scent). Only in the case of perfume flowers are the attraction agent and the reward identical. Olfactory cues usually serve for long-distance attraction (especially in insect-pollinated flowers), while visual cues mainly serve for short-distance attraction. In bird-pollinated flowers, only visual cues are relevant.

Depending on the position of the stamens and anthers in the flower, the pollen is deposited on the animal's body at different, but fairly strictly defined places. Bees usually try to groom themselves and to comb out the pollen grains from the hair cover. This pollen (along with that intentionally gathered) is lost for pollination. However, some grains always survive this grooming, and some flowers have been inventive enough to place the pollen on parts of the insect's body which cannot be easily reached by the bee's legs.

In contrast to wind- or water-pollinated plants, animal-pollinated plants are usually bisexual. Prevention of self-pollination is by spatial or (more commonly) temporal separation of the floral organs (protogyny, protandry). Dioecy is rare in tropical zoophilous plants. Good examples are the species of *Clusia*. For a detailed list and a discussion of the possible driving forces towards dioecy in zoophilous tropical plants, see BAWA (1980b) and RENNER & FEIL (1993). For a general survey of the breeding systems represented in neotropical lowland rainforests, see BAWA (1974, 1980a).

Generalist flowers (allotropy)

The term "generalist flowers" refers to flowers which are not specialised to a certain species or group of animal pollinators. A definition is rather difficult, as there are "many ways to be a generalist flower" (OLLERTON et al. 2007). For a long time, allotropy has received little attention, but more recently interest was revived by several papers (e.g., WASER et al. 1995, WASER & OLLERTON 2006, FRAME 2003, HERRERA 2005) and a symposium devoted to that topic was held during the IBC 2005 in Vienna (FRAME & GOTTSBERGER 2007).

The visitor spectrum of "classical" generalist flowers includes a variety of insects such as bees, flies, beetles and butterflies. Flies and beetles always form a significant component. The flowers are usually small and of a simple architecture, flat or bowl-shaped, with easy access to the nectar and/or pollen. Flower colours are mostly greenish, whitish or brownish. Such flowers are well known from cosmopolitan or temperate plant families (e.g., Apiaceae, Araliaceae, Asteraceae, Ranunculaceae, Rosaceae) and it is therefore no surprise that taxa from these families which ocur in the tropics also possess generalist flowers. Examples are the Sambucaceae, with tropical species of *Viburnum* (Golfo Dulce: *V. costaricanum*) or Rhamnaceae, with tropical species of *Rhamnus* (Golfo Dulce: *Rh. oreodendron*) and *Ziziphus* (Golfo Dulce: *Z. chloroxylon*). But there also exist essentially tropical families with generalist flowers, e.g. Lauraceae (*Nectandra*, with some ten species in the Golfo Dulce area), Anacardiaceae (Golfo Dulce: *Tapirira myriantha*), or Combretaceae (*Terminalia* spp.).

In many cases, a certain group of the visitor spectrum attains some dominance and transitions to specialised flowers are manifold. It is a matter of definition whether these flowers are categorised as generalist flowers with prevalence of, say, beetles or as cantharophilous flowers with a low degree of specialisation.

In the palm family (Arecaceae), beetles, flies and small bees play a dominant rôle in pollination (sometimes along with wind: "ambophily"). In some palms, the three insect groups are of ± equal significance, while in others the proportion shifts towards one of these, especially beetles. In *Bactris* (Golfo Dulce: 7 spp.), for instance, there is a clear preference of beetles (weevils, Curculionidae: Deleromini), but flies still act as co-pollinators (see, e.g., MORA URPI & SOLIS 1980, HENDERSON 1986, 2000, HENDERSON et al. 2000, LISTABARTH 1992, 1993). Beetles apparently also prevail in the mentioned genera of Lauraceae and Anacardiaceae. In Panamá, ØDEGAARD & FRAME (2007) collected specimens of no fewer than 177 beetle species (belonging to Cerambycidae, Chrysomelidae, Brentidae, and Curculionidae) on the flowers of *Nectandra umbrosa* and *Tapirira guianensis*, 65 being common to both trees.

Generalist flowers with a prevalence of flies and bees found in *Smilax* (Smilacaceae; Golfo Dulce: 6 spp.). The flowers are small, greenish and star-like. Nectar is produced at the base of the stamens or staminodes and/or by septal nectaries. The flowers of some species emit a foetid odour. SAWYER & ANDERSON (1998) observed that the carrion-like odour of *S. herbacea* attracts a wide range of beetles, hymenopters and flies, from which andrenid and halictid bees as well as anthomyiid and stratiomyiid flies can be assumed to be the most significant pollinators.

Similar flowers are found in *Dioscorea* (Dioscoreaceae, Golfo Dulce: 8 spp.). Though several authors assumed wind-pollination, the sticky pollen, the presence of septal nectaries and the emission of a sweetish scent are clearly in favour of insect pollination. BARROSO et al. (1974) observed only stingless bees (*Melipona*, *Hypotrigona*) visiting the flowers of several *Dioscorea* species, but SEGNOU et al. (1992) reported also beetles and flies as visitors of the African *Dioscorea rotundata*.

Pollination by bees (melittophily)

Bees are the dominant animal pollinators in the temperate regions and play a significant rôle in the tropics too. With more than 20.000 species, they represent a considerable group of insects. Their life is intimately associated with flowers, in that they feed on nectar and collect pollen for the brood. There are many specialisations in the morphological relations and interactions between bees and flowers.

The classification of bees is still under debate and the taxonomic status of some groups is not settled. Based on molecular studies, DANFORTH et al. (2004, 2006a,b) distinguished 7 families, forming the superfamily Apoideae within the Hymenoptera. In contrast, MELO & GONÇALVES (2005) treat the bees as a single family, comprising 7 subfamilies, 51 tribes and 27 subtribes. Representatives of most (sub)families are found in the Golfo Dulce region.

The largest bees are found in the Xylocopini (carpenter bees; characterised by a black body), the Centridini and the Bombini (bumblebees) within the family Apidae. The large and middle-sized "euglossine bees" (Apidae-Euglossini) are perhaps the most conspicuous bees in the neotropics. Except *Eulaema*, which resemble temperate bumblebees, most species have a body of metallic green, golden, red or blue colour. Their name refers to the long proboscis, which is often longer than the body and carried in reflexed position between the legs during the flight. A common name is "orchid bees", as the bees (males only) are often found on orchid flowers (for collecting flower fragrances, see below). On the opposite end of the size range, there are small bees such as sweat bees (Halictidae) and stingless bees (Apidae-Meliponini).

The classic floral rewards provided for bees are nectar and pollen. Nectar is an energy-rich substance serving for energy supply, pollen is usually not collected for the bee's own needs, but – mixed with nectar – as fodder for the brood. The recently discovered new floral rewards (fragrance, fatty oil and resin) are exclusively addressed to bees.

In the present treatment, the flowers and floral syndromes are essentially classified according to the reward provided. The last section is devoted to flowers that do not provide a reward but pretend to do so (deceptive flowers).

Pollen flowers with numerous stamens (polyandrous pollen flowers)

Pollen is the most ancient floral reward. Especially in primitive flowers, a surplus of stamens and pollen is produced, so that the pollen collected by the bees (and thus being lost for pollination) is of no consequence. This is the group of "polyandrous pollen flowers", characterised by numerous stamens, anthers dehiscing by an apical pore, non-adhesive (powdery) pollen, usually large flower size, and lack of a nectary and nectar. Such flowers are found in primitive angiosperm families, but also (or even predominantly) in families with secondary increase of stamens (secondary polyandry). Such families are rare in the monocots, but more frequently found in the dicots. Examples from the Golfo Dulce area include: Bixaceae (*Bixa orellana*), Clusiaceae (*Calophyllum*), Cochlospermaceae (*Cochlospermum vitifolium*), Dilleniaceae (*Davilla*, *Doliocarpus*), Lecythidaceae (*Gustavia*), Muntingiaceae (*Dicraspidia*, *Muntingia*) and Myrtaceae (subfam. Myrtoideae, to which most of the neotropical genera belong).

Cochlospermum vitifolium (Cochlospermaceae), occurring in drier parts of the Golfo Dulce area, has large, deep yellow flowers with numerous stamens and a long central style curving upwards (Fig. 2). The stamens are long, with the anthers mostly curved inwards. The anthers open by four apical pores, from which the pollen is released by buzzing (see below). Large bees (*Xylocopa*, *Bombus*, *Oxaea*, *Centris*) grasp as many stamens as they can and vibrate while hanging on them, while small bees vibrate single anthers only (GOTTSBERGER & SILBERBAUER-GOTTSBERGER 1997).

Pollen flowers with few stamens (oligandrous pollen flowers)

Flowers with few stamens have to be economical with their provision of pollen. These flowers are shaped according to a fairly uniform type, called the *Solanum* type (cf. *Solanum tuberosum*, *S. dulcamara;* some 15 species of *Solanum* are present in the Golfo Dulce area). Typical characters include: nodding flower position, (sub)actinomorphic corolla, petals spreading or forming a bell, corolla white or violet (purple), stamens upright, with short filaments and large yellow anthers forming a bunch or cone, anthers opening apically by a pore or a short slit, powdery (not sticky) pollen, and the lack of nectary and nectar (VOGEL 1978c).

The bees approach the nodding flowers from below. After landing, they clasp the flower with their legs and – by using the thoracic muscles (without moving the wings) – release the pollen by vibrating the anthers. The buzzing (audible from a short distance) causes the pollen to gush out from the apical pores ("buzz pollination", "vibratile pollen collection": PROCTOR et al. 1996). The pollen is caught among the hairs of the bee's body. Finally, the bee combs the pollen from its body and packs it into the pollen baskets on its hind legs. As the bee cannot reach all places on the body, some pollen grains remain and these are enough to serve for pollination. For a survey on buzz pollination and the many angiosperm families involved, see BUCHMANN (1983).

Fig. 2: *Cochlospermum vitifolium* (Cochlospermaceae); (**a**) flower (polyandrous pollen flower), (**b**) close up of lower stamens, showing the anthers opening by four apical pores. Photos: A. Weissenhofer.

In the Golfo Dulce area, this type of pollination is found (with some modifications) in the Haemodoraceae (*Xiphidium*), Fabaceae-Caesalpiniaceae (*Cassia*, *Senna*, *Chamaecrista*), Melastomataceae (*Miconia* and many others), Myrsinaceae (*Ardisia*), Ochnaceae (*Ouratea*), Solanaceae (*Lycianthes*, *Solanum*, *Physalis*, *Witheringia*), and others. The bees involved in pollination are mainly medium-sized to large bees including *Centris* and oth-

Fig. 3: *Solanum* sp. (Solanaceae); flowers (oligandrous pollen flowers); note yellow anther cone contrasting with bluish corolla. Photo: A. Weissenhofer.

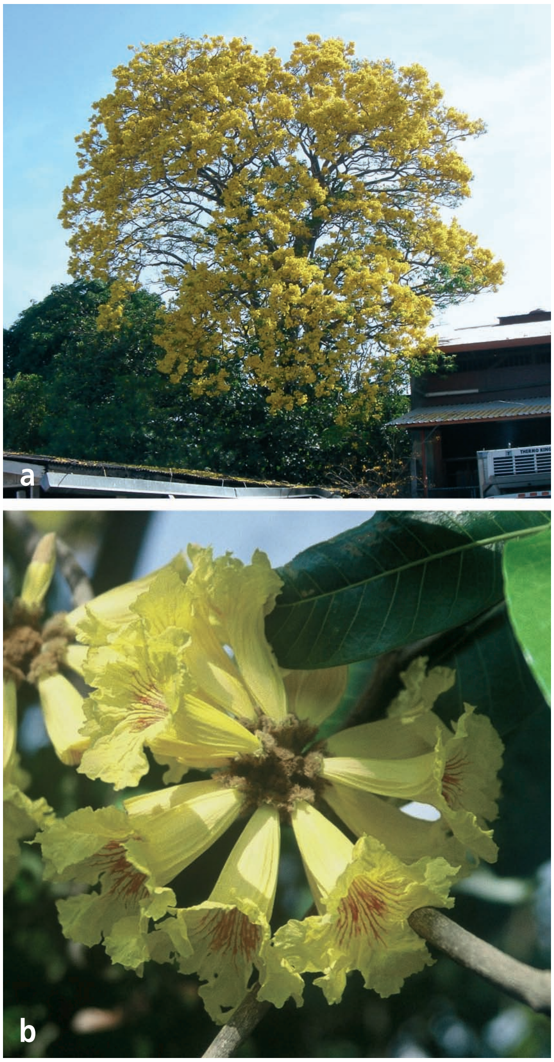

Fig. 4: *Tabebuia chrysantha* (Bignoniaceae), (**a**) flowering tree ("big bang" flowering), (**b**) bunch of flowers (nectar flowers, adapted to pollination by large bees). Photos: A. Weber (a), W. Huber (b).

Fig. 5: *Canavalia rosea* (Fabaceae-Faboideae), resupinate papilionoid flowers (operating as lip flowers) adapted to the pollination by *Xylocopa* bees. Photo: A. Weber.

er anthophorids, euglossines, bumblebees, colletid bees (*Ptiloglossa*) and meliponid bees.

Solanum (Solanaceae; Fig. 3), ***Ardisia*** (Myrsinaceae) and ***Ouratea*** (Ochnaceae), though they belonging to different families and orders of angiosperms, have morphologically and functionally extremely similar flowers. They exhibit perfectly the character syndrome described above, and there is only some variation in the stamen number (5 in *Solanum* and *Ardisia*, 10 in *Ouratea*).

Nectar flowers

Nectar is the most common floral reward and used by all kinds of bees. In the course of evolution, nectar flowers have adapted to bees in various ways and vice versa. In particular, there is a close relation between size and robustness of flowers and bees. Large flowers, e.g., of *Tabebuia* (see below), *Jacaranda*, *Tecoma* (Bignoniaceae), and *Ipomoea* (Convolvulaceae), are visited by a wide range of large bees (*Xylocopa*, *Centris*, *Euglossa* etc.), those of *Thunbergia* (Acanthaceae), the frequently cultivated "blue trumpet vine", are more specifically addressed to *Xylocopa* bees (FAEGRI & VAN DER PIJL 1966). The latter also applies to *Canavalia rosea* (Fabaceae), the Beach Bean (see below).

Other flowers are visited by medium-sized bees (including male and female euglossine bees) and small bees. This kind of relationship is well known from the temperate flora and will not be discussed in detail here.

Tabebuia chrysantha*, *T. ochracea (Bignoniaceae). These magnificent trees have not only paradigmatic large, yellow nectar flowers of the gullet type, but present them synchronously in the leafless condition. This results in a mass flowering and a breathtaking "big bang" effect (GENTRY 1974, 1976, 1990) (Fig. 4). Pollination (by various large bees, but also by hummingbirds) has been studied by FRANKIE et al. (1983).

Canavalia rosea (Fabaceae-Faboideae). The "beach bean" (Fig. 5) is frequently found as a creeping pioneer plant on sandy beaches. Its flowers are remarkable for two reasons: (1) the switch of the papilionoid flower to a different functional type: a lip flower (by resupination, the flag petalum forms the lower lip, the keel petal the upper lip; the latter contains the stamens and the style), and (2) the adaptation to large bees: all flower parts are thick and robust, and the flower can be worked only by large and strong insects such as *Xylocopa* bees. Only these are able to press the lower lip down and get access to the nectar. The stamens/style are released by this movement from the upper lip and contact the bee's back. For general aspects of "keel flowers" and the forces required to handle them, see WESTERKAMP (1997).

Perfume flowers

The phenomenon that specialised bees (male euglossines) collect and use floral fragrances was discovered by Stefan Vogel in the 1960s (VOGEL 1966). He was the first to correctly interprete former observations that male euglossine bees visit particular orchid flowers and move their forelegs in an enigmatic way. VOGEL (l.c.) found that the flowers secrete fine droplets of terpenes. These are mopped up by the bees with feathery brushes on their tarsi. During a short up-flight the collected droplets are transferred via the mid-legs to the hind legs. The tibiae of these legs are conspicuously pouched. The substance is transferred through an opening (occluded by a hair cover) into the interior of the pouch and stored there. As the tibia bears secretory ducts, the flower fragrance is apparently mixed with the bee's own secretions. Thus it is transformed to a characteristic, species-specific (or even individual-specific) perfume. This perfume is connected in some way with mating and is thought to play a rôle in territorial display and courtship (olfactory marking of the swarm routes), but many details are not yet known.

Chemically, the scents consist of monoterpenes (e.g., cineole, limonene) and benzenoids (e.g., benzaldehyde, methyl benzoate). They do not attract other insects than euglossines, and from these exclusively the males.

Vogel's first observations related to orchids (some are described below) and *Gloxinia perennis* (Gesneriaceae). Later, he and associated authors found additional families that contain perfume flowers: Araceae (*Spathiphyllum*, *Anthurium*), Solanaceae (*Cyphomandra*), and Euphorbiaceae (*Dalechampia* sect. *Cremophyllum*, e.g., *D. spathulata*). Of the orchids, over 50 genera are now known to bear perfume flowers, and in the Gesneriaceae the genus *Monopyle* is also presumed to have this flower type (WIEHLER 1983). Except species of *Dalechampia* sect. *Cremophyllum* (the recorded *D. dioscoreifolia* belongs to a different section and produces resin as floral reward, see below), all families and genera listed are found in the Golfo Dulce region.

Coryanthes*, *Gongora* and *Stanhopea (Orchidaceae). Each of these genera is represented by a single species in the Golfo Dulce area. *Coryanthes* plants usually grow in ant gardens. Their large, waxy flowers are pendulous. One part of the three-parted lip (epichile) forms a bucket. Drops of a slimy liquid, secreted by a pair of protuberances at the base of the column, fall into the bucket, collect there and form a pool. Attracted by the strong fragrance, male euglossine bees (*Euglossa*, *Eulaema*) get attracted. By the localised fragrance they are guided to a small area at the base of the column and the basal part of the lip (hypochile). While scratching the scent from the surface, the bees get more and more excited. They often lose their foothold, slip and fall into the liquid-filled bucket. They cannot climb the walls and have to swim to reach the only way out. This is through a narrow opening at the tip of the lip, close to the tip of the column. In squeezing through this with force, the bee has to pass first the stigma, and then the anther. If laden with pollinia from another *Coryanthes* flower, the pollinia are deposited at the stigma. When passing the anther, the orchid presses and glues its own pollinia onto the thorax or abdomen of the bee. DODSON (1965) reported that that the time from entering a freshly opened flower and leaving it with the pollinia may take 15-30 minutes. Once the pollinia are removed, the way out is much quicker. Apparently, the bees never learn their lesson, and visit flower after flower, every time taking an involuntary bath.

Fig. 6: *Gongora tricolor* (Orchidaceae), one of the most bizarre orchids of the Golfo Dulce area; the flower (perfume flower) represents a "fall-through flower", it attracts male euglossine bees searching for flower frangrances; the bees alight in upside-down position on the basal part of the lip (white arrow), lose their foothold when scratching off the fragrance, and fall down along the curved column; when passing the tip of the column (yellow arrow), the pollinia are fixed on its body. Photo: A. Weber.

In the related genera *Gongora* and *Stanhopea*, the flowers represent what is called "fall-through" flowers. In both genera the lip (labellum) is in the upper position, but does not curve down and does not form a bucket. In *Gongora* (Fig. 6), it spreads horizontally to form a kind of roof. The column situated below the lip is long and curved. The anthers and stigma are at the lowest point. Male euglossine bees alight on the lower surface of the lip in upside-down position. In the course of scratching the scent, the bee slips and falls down in such a way that its back touches the column. When passing the tip of the column, the pollinia are fixed on its back.

Gloxinia perennis (Gesneriaceae). See paper of WITSCHIG, HICKEL & WEBER (2008, this volume).

Fig. 7: *Bunchosia cornifolia* (Malpighiaceae), section of pendulous inflorescence with an open flower and flower buds (oil flowers); note flower buds with conspicuous (green) elaiophores on the outside of the calyx. Photo: A. Weber.

Oil flowers

The fact that fatty oil is provided as a floral reward by specialised flowers was discovered about four dacades ago (Vogel 1969c). Since then, a huge amount of information has accumulated, mainly by the studies of Stefan Vogel and collaborators (e.g., Vogel 1974, 1986, 1990a,b, Vogel & Cocucci 1995), including documentation on film (Vogel 2002a-d). To date, there are about 10 known angiosperm families that contain oil flowers. Only one of them plays a major role in the Golfo Dulce region: the Malpighiaceae (as an exception, oil flowers occur also in Melastomataceae-Memecyleae, including *Mouriri myrtilloides* from the Golfo Dulce area: Buchmann & Buchmann 1981). Principally, the oil is collected by female bees, mixed with pollen and used as a fodder for the larvae. The oil collectors include apid bees such as Centridini, Tetrapediini and Tapinotaspidini. Generally, the oil is harvested in a characteristic way with the specialised fore and middle legs and stored and carried away in the hairy scopae of the hind legs.

Malpighiaceae. The members of this family (Golfo Dulce: *Banisteriopsis*, *Bunchosia*, *Byrsonima*, *Heteropterys*, *Tetrapterys* and others; Fig. 7) are easily recognised by the characteristic flowers of a highly conservative structure. They are usually yellow (less frequently pink or white) and consists of five free sepals, five free petals, ten (rarely five) stamens and a 2-5-merous, syncarpous gynoecium. Superficially, the flowers look radially symmetrical, but closer inspection shows that one (the "upper", median-adaxial) petal is somewhat different in size and shape ("flag petal"). The large oil glands (elaiophores) are located in pairs on the sepals (either on all five, or more commonly only on four sepals). The oil is secreted and stored under the cuticle covering the surface of the oil glands. Finally, the cuticle bursts, and the oil is released, covering the elaiophore surface as a thin film. The petals are spoon-like, with a narrow stalk and an orbicular or elliptical, concave apical part ("clawed" petals). Oil collection proceeds as follows: after alighting on the flower, the bees grasp the stalk (claw) of the flag petal with their mandibles and position themselves in the flower center. With their hairy fore and middle legs, they pass between the clawed petals, touch the surface of the oil glands and scrape off the oil from the elaiophore surface. The oil is then transferred to the hind legs and mixed with the collected pollen in the scopae. During the collection activity, the bees get dusted with pollen and/or touch the stigma.

Resin flowers

Flowers providing resin as a floral reward were discovered in the 1970s. In his recommendable book "A naturalist in Costa Rica", Skutch (1971) reported an

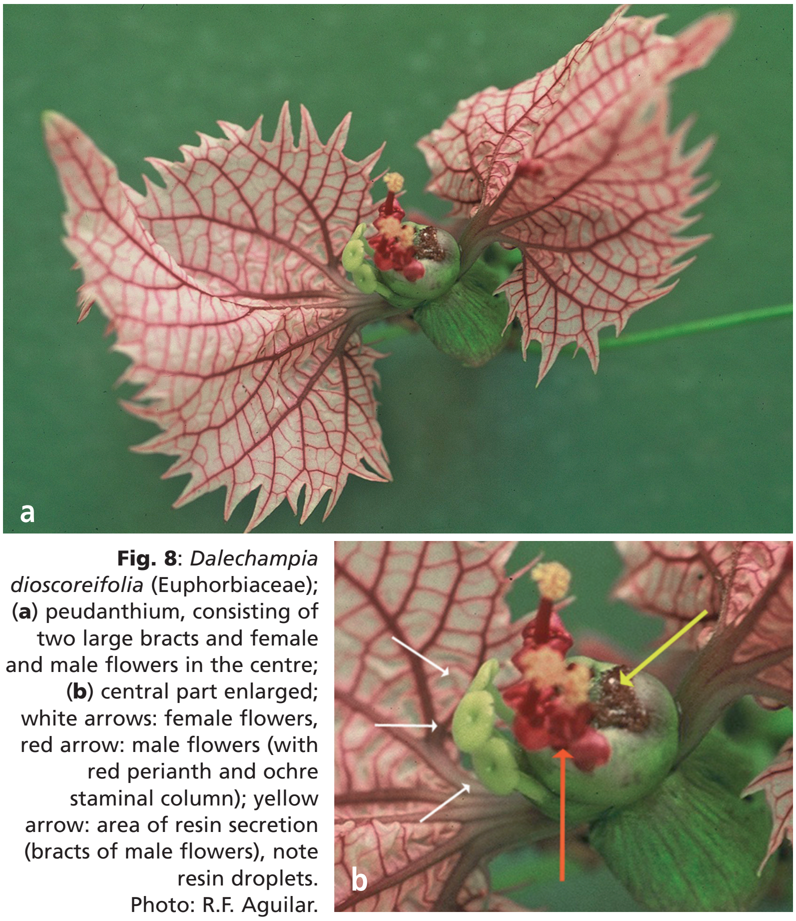

Fig. 8: *Dalechampia dioscoreifolia* (Euphorbiaceae); (**a**) peudanthium, consisting of two large bracts and female and male flowers in the centre; (**b**) central part enlarged; white arrows: female flowers, red arrow: male flowers (with red perianth and ochre staminal column); yellow arrow: area of resin secretion (bracts of male flowers), note resin droplets. Photo: R.F. Aguilar.

early observation of his that stingless bees (Meliponini) repel aggressive ants with a "sticky substance" and that their nests consist of the "stickiest stuff imaginable". Years later, he observed that the sticky substance was resin collected by the bees in flowers. An initial summary of the knowledge of resin flowers was given by ARMBRUSTER (1984). Since then, a number of papers have appeared on the topic.

As far as is known, resin flowers are restricted to two angiosperm families: Clusiaceae and Euphorbiaceae. Even here, they are found in very few genera and mostly only in certain species. In the Clusiaceae, these are *Clusia* (pro parte), *Clusiella*, *Chrysochlamys* (1 sp.) and *Tovomitopsis* (1 sp.) (BITTRICH & AMARAL 1996, 1997, GONÇALVES-ALVIM 2001). In the Euphorbiaceae, only particular (usually viny) species of *Dalechampia* produce resin flowers (ARMBRUSTER & WEBSTER 1979, SAZIMA et al. 1985, STEINER & WHITEHEAD 1991, ARMBRUSTER & STEINER 1992), including *D. dioscoreifolia* found in the Golfo Dulce area. In terms of the bees collecting resin, three groups are involved: Meliponini (*Trigona*), Euglossini (*Euglossa*, *Eulaema*, *Eufriesea*), and Megachilidae (*Hypanthidium*).

The bees do not collect resin exclusively from flowers, but also from other sources. The resin remains sticky for an almost unlimited time, is waterproof and has fungicidal and bactericidal effects (LOKVAN & BRADDICK 1999). Chemical analyses of the floral resin have been performed both in *Dalechampia* (ARMBRUSTER et al. 1997) and *Clusia* (e.g., NOGUIERA et .al 1997, PORTO et al. 2000).

Dalechampia dioscoreifolia (Euphorbiaceae). No information is available on this particular species occurring in the Golfo Dulce area, but the facts known from other species, especially *D. scandens* from drier parts of Costa Rica (ARMBRUSTER 1983) will probably apply to that species as well.

In *Dalechampia*, the resin is not produced by the flowers, but by elaborate parts of the inflorescence. In fact, the genus has much condensed and highly complicated inflorescences that operate as functional units. They form pseudanthia of a very special structure, which has been clarified by FROEBE et al. (1983). A simplified description is given here. Flanked by two large white or (in *D. dioscoreifolia*, Fig. 8) pinkish bracts with darker venation, a conglomeration of flowers and tiny modified bracts is situated in the centre. In the lower part, there is a complex of three female flowers, each subtended by a tiny bract and arranged in a simple dichasium (triad). In the upper part, there are groups (double cincinni) of male flowers, each with a perianth and a central staminal column. Above the complex of male flowers, there is a cushion of secretive structures. Closer inspection shows that the cushion is made up of three units, each composed of distinct layers of different width and thickness. By sharp-witted considerations and ontogenetical data, FROEBE et al. (l.c.) provided evidence that these layers correspond to the bracts of the male flowers. These are the structures secreting the resin by papillae or glands at their upper margin.

Clusia (Clusiaceae). *Clusia*, a neotropical genus of some 300 species (peculiar by their dioecy), is represented in the Golfo Dulce area by 10 species. At least three of them possess resin flowers: *C. minor*, *C. peninsula* (ined.) and *C. valerioi*. Detailed studies have been carried out in the latter species (HOCHWALLNER & WEBER 2006; HOCHWALLNER et al. in prep.). The resin is secreted both by the stamens of the male flowers and the staminodes of the female flowers (thus visitation of both sexes is ensured). It is collected by meliponine bees (e.g. the common *Trigona fulviventris*) which bite off pieces with their mandibles, form globules and transport them in packets on the hind legs to the nests. See also paper of WEBER (2008b, this volume).

Deceptive flowers

Deception of flowers, that is the pretence of an unavailable reward, is not rare in flowers. For a long time, the category of "deceptive flowers" was largely ignored, but has received new attention recently. VOGEL (1978) re-openend the field by documenting various evolution-

Fig. 9: *Begonia* sp. (Begoniaceae), a genus with female deceptive flowers (intersexual mimicry); (**a**) inflorescence of male flowers; (**b**) female flowers; the stigmas of the latter mimic the anthers of the former. Photos: A. Weber.

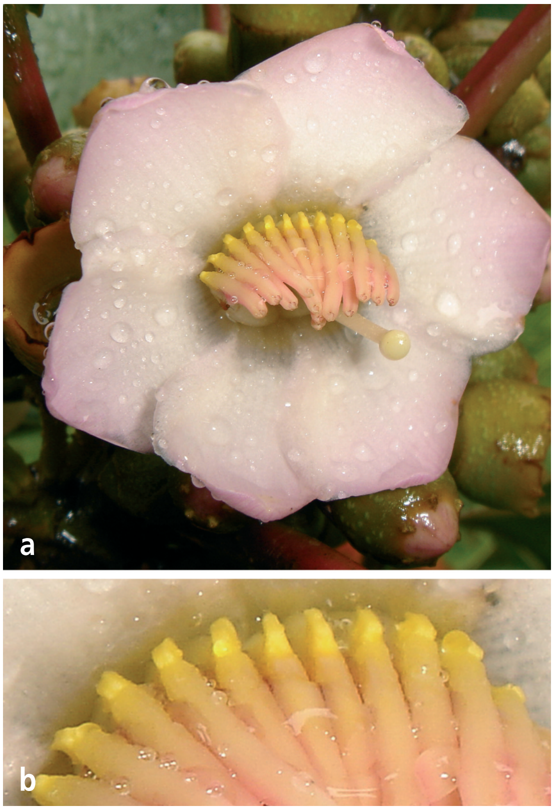

Fig. 10: *Topobea maurofernandeziana* (Melastomataceae); (**a**) flower (partially deceptive pollen flower), (**b**) base of anthers enlarged, note solid (pollen-sterile) yellow appendages, the remaining parts of the anthers are ± of the same colour as the corolla. Photo: A. Weissenhofer.

ary steps from reward to deception in pollen flowers. More recently, he presented an exciting survey on deceptive flowers on a broad scale (VOGEL 1993).

Principally, we must discriminate between deceptive nectar flowers and deceptive pollen flowers (there are also cases of deceptive oil flowers: orchid flowers (*Oncidium*, *Tolumnia*) mimicking those of Malpighiaceae, ACKERMANN 1986, SILVERA 2002; deceptive perfume or resin flowers are not known). The former look like "normal" nectar flowers, but do not produce nectar. Either they resemble nectar flowers in a general way or they mimic a specific extant nectariferous species (floral mimicry). In both cases, they rely on the ignorance, inexperience or bad memory of insect visitors and are apparently successful in doing so. An example is described in the section "Pollination by butterflies" in which a trinity of similar flowers (two with nectar, one without) is involved.

Deceptive pollen flowers are more common and more varied. Deception creeps in by small steps. A first step is the advertisement of pollen presence by yellow structures other than pollen grains. A bright yellow anther (or anther cone), as present in most buzz-pollinated flowers, is suggestive of copious pollen – more than is really available. The degree of deception is higher when the yellow signal is transferred to a flower part other than the anther, e.g. a yellow filament portion or yellow blotch on the corolla. The ultimate degree of deception is reached, when three-dimensional yellow structures broadcast the presence of anthers or pollen, while the true anthers are cryptic.

When trying to release the pollen from the showy structures, the bee is dusted with pollen from the cryptic pollination anthers, preferably at a place from which the bee cannot remove the pollen grains when grooming.

Deceptive flowers are found in the Commelinaceae (*Tradescantia*, *Dichorisandra*, *Commelina* and *Cochliostema*), Begoniaceae (*Begonia*, see below), Fabaceae (*Cassia*, *Senna*), Lythraceae (*Lagerstroemia*), Lecythidaceae (*Lecythis*, *Couroupita*, *Eschweilera*), Melastomataceae (see below) and others.

Begonia (Begoniaceae). The species of *Begonia* are predominantly monoecious. The male and female flowers look extremely similar (Fig. 9). While the centre of the flower is made up of conspicuous yellow anthers in males, it consists of yellow stigma lobes in the female flowers. As both male and female flowers do not provide nectar, the hypothesis was proposed that the female flower mimic the male ones, pretending there is copious pollen (VAN DER PIJL 1978, VOGEL 1978c, WIENS 1978). This hypothesis was supported by experimental studies and field observations in Costa Rica (Monte Verde) in *Begonia involucrata* (ÅGREN & SCHEMSKE 1991).

Melastomataceae. In this family a full range from simple pollen flowers to highly sophisticated deceptive pollen flowers can be found. A nectary is generally lacking in the family (but a substitute may be produced by wounded or broken filaments, VOGEL 1998). Pollen is released by vibration. The primitive condition is found in the many species of *Miconia* present in the Golfo Dulce area. The flowers are relatively small, white and exhibit a bunch of 10 stamens with yellow anthers. In the course of evolution, the androecium experienced manifold modifications and variations. A first step towards deception is that the anther elongates and experiences a colour differentiation. Only the (somewhat exserted) base remains yellow, while the tapering upper part takes on a cryptic coloration. By progressive enlarging of the anther base and forming a yellow sterile appendage (while the pollen-bearing part of the anthers takes on a cryptic colour), a pollen dummy is formed (rather small in *Topobea*, Fig. 10). In some taxa, an additional modification is the differentiation of the androecium (di- and trimorphy). The anthers differentiate into those producing pollen for pollination and those producing pollen for rewarding the insect visitor.

Pollination by flies (myiophily)

Flies (Diptera) are a much varied group of insects and many taxa have become involved in pollination. The range is from the large carrion flies, house flies, horse flies and hoverflies (Calliphoridae, Muscidae, Tachinidae, Syrphidae) to tiny gnats (Cecidomyiidae, Cer-

Fig. 11: Orchids with myiophilous flowers; (**a-c**) *Stelis* spp., (**d**) *Trigonodium egertonianum* (reddish form), (**e**) *Pleurothallis* sp. Photos: A. Weissenhofer (a-e), A. Weber (d)

atopogonidae, Mycetophilidae etc.). Flies are important pollinators of generalist flowers, but often there are more specific relations. The flowers provide different kinds of rewards to attract flies: nectar, pollen or – deceptively – brood sites. As was pointed out by KUGLER (1955), only in the "carrion flowers" are there intimate relations between flowers and pollinating flies, constituting the syndrome of "sapromyiophily". In four families (Orchidaceae, Aristolochiaceae, Sterculiaceae, Aristolochiaceae), floral structures have evolved which are unambiguously associated with fly-pollination: flickering bodies. A detailed survey on these structures has recently been published by VOGEL (2002). Small flies are essentially involved in the pollination of flowers mimicking fungi. This phenomenon, was recently evinced by exciting new data (VOGEL 1973, 1978a,b).

(Sapro-)myiophilous flowers occur in many alliances of angiosperms represented in the Golfo Dulce area. Perhaps the most important are Araceae (*Anthurium* spp., *Dracontium pittieri*) Burmanniaceae, Orchidaceae, Ascepiadaceae, Aristolochiaceae (*Aristolochia*), Siparunaceae (*Siparuna*) and Sterculiaceae. Of these, only examples from the orchids and the Sterculiaceae are given here.

Orchids. The orchid family includes a large number of flowers which exhibit myiophilous characters. The following genera of the Golfo Dulce area can be included: *Dichaea*, *Dresslerella*, *Dryadella*, *Macroclinium*, *Pleurothallis*, *Stelis*, *Trichosalpinx* and *Trigonidium*.

Species of *Pleurothallis* (Fig. 11e) are often encountered in the Golfo Dulce forests, growing on tree trunks, mossy rocks etc. and sometimes forming mats of one-leaved shoots. The small flowers are produced singly or in small groups closely attached to base of the single foliage leaf. They exhibit a range of colours typical of fly pollination: whitish, cream, greenish and brownish. Studies of *Pleurothallis* pollination, focussing on pollinator specificity and convergence, have been performed recently in Brazil, where flies of the Chloropidae (*Tricimba* sp.) and Photidae (*Megaselia* spp.) have been identified as significant pollinators (BORBA & SEMIR 2001). Species of *Trigonidium* (Golfo Dulce: *T. egertonianum*) and *Stelis* (Golfo Dulce: one unidentified species

Fig. 12: *Sterculia apetala* (Sterculiaceae/Malvaceae); inflorescence (**a**) and individual flowers (**b**, **c**) with fly visitors. Photos: A. Weissenhofer.

recorded, but apparently several present) are also certainly fly-pollinated (Fig. 11a-d).

Theobroma, Guazuma and ***Sterculia*** (Sterculiaceae, now Malvaceae). Fly pollination plays an essential role in the Sterculiaceae (in its former sense). In fact, with the exception of the two *Melochia* species (bee-pollinated, VOGEL, pers. comm..), all species represented in the Golfo Dulce area seem to be fly-pollinated. One example is cocoa, *Theobroma cacao*, which is frequently cultivated in the Golfo Dulce area (origin: Amazonia). The small white-reddish flowers are borne on the trunk and on old branches (cauliflory). They are very small (measuring a few millimetres in diameter) and actinomorphic, but nonetheless of a surprisingly complex structure. Functionally, they represent miniature "roundabout" flowers. The insects enter the flower and, in seeking and feeding on the nectar (secreted by microscopic nectaries), circuit the flower centre below the petal pouches which form the roof of an ambulatory. The anthers are placed in the petal pouches, so that the insects get laden with pollen on the back. Several small midges (Ceratopogonidae, Cecidomyiidae), stingless bees (Meliponinae) and miner bees (Halictidae) have been recorded as flower visitors and pollinators (YOUNG et al. 1984, 1986; YOUNG 1994). YOUNG & SEVERSON (1994) assumed that the flowers of ancestral or wild species of *Theobroma* (incl. non-cultivated *T. cacao*) attract bees, while those of cultivated *T. cacao* have lost most of its original floral attraction system and are pollinated by midges. There are four wild species of *Theobroma* in the Golfo Dulce area and it would be worthwhile to test this hypothesis by detailed studies.

The common *Guazuma ulmifolia* has equally tiny and still more sophisticated flowers . Its complex floral structure was recently described by WESTERKAMP et al. (2006). The tiny flowers form female and male chambers with separate entrances.

Little is apparently known about the pollination of the widespread Panamá tree, *Sterculia apetala*. In its flowers, the wide, bowl-shaped calyx functionally replaces the absent petals. The flowers are held in a nodding position and are of a red-brown colour, with white lines running towards the centre (window effect!). From photos taken by A. Weissenhofer (Fig. 12), it is evident that various flies gather in the flowers. They are attracted by a foetid odour, feed on nectar secreted around the stamens and style, and try to escape through the apparent radial windows. During these activities, they make contact with the pistil and anthers (the flowers are andromonoecious).

Pollination by beetles (cantharophily)

Beetles (Coleoptera) are the largest group of insects living on earth, numbering more than 350.000 described species (and amounting perhaps to 1 million species, ØDEGAARD 2000). Moreover, beetles are one of the

Fig. 13: *Carludovica drudei* (Cyclanthaceae); (**a**) young inflorescence with spaghetti-like staminodia of the female flowers (stage of weevil attraction); (**b**) same enlarged, note weevils (*Phyllotrox* sp.) on and between the staminodia; (**c**) inflorescence with dropping staminodia (through the holes the weevils get access to the cavities with the female flowers). Photos: A. Weber (a, b), A. Weissenhofer (c).

Fig. 14: An inflorescence of *Philodendron* sp. with two *Cyclocephala* beetles inside. Photo: A. Weissenhofer.

most ancient groups of insects phylogenetically, known in the fossil record since the Lower Permian. Their life and life cycle is commonly associated with plants. It is, therefore, no surprise that they became integrated in the pollination of flowers. While in temperate regions, beetles are a rather insignificant guild of pollinators (only forming a ± regular component of the visitors of generalist flowers), they play a much more significant rôle in the tropics, particularly in the neotropics. Here, we find plants which are strictly adapted to the pollination by beetles, and one angiosperm family is even exclusively cantharophilous: the cyclanth family (Cyclanthaceae). However, beetles play a significant, but not exlusive rôle in pollination in many cases. These flowers can be qualified as generalist flowers with predominant beetle pollination (see above).

The most important families (and genera) of beetles involved in pollination are: Curculionidae (weevils or snout beetles, e.g. *Phyllotrox*), Nitidulidae (sap beetles), Staphylinidae (rove beetles) and Scarabaeidae (scarabs or scarab beetles; especially *Cyclocephala*). Only the last family includes beetle pollinators of large size. For convenience, some authors make a distinction between pollination by small (microcantharophily) and large beetles (macrocantharophily). This seems to make sense when the Cyclanthaceae are considered. Here, in a single species, *Cyclanthus bipartitus*, pollination is by large *Cyclocephala* beetles, while in the rest of the family, tiny beetles (especially weevils) are the principal pollinators (see below). But such a distinction cannot be upheld in other families.

As far as plants of the Golfo Dulce area are concerned, beetle pollination is restricted to few families (or genera therein): Cyclanthaceae (all genera), Araceae (*Dieffenbachia*, *Xanthosoma*, *Philodendron*, *Syngonium*, *Monstera*), Annonaceae (*Anaxagorea*, *Annona*, *Duguetia*, *Guatteria*, *Xylopia*), Magnoliaceae (*Talauma*) and possibly Myristicaceae (*Virola*).

Only two examples are given here: one (*Carludovica drudei*) illustrating a "microcantharophilous" plant, the other (*Philodendron*) a "macrocantharophilous" plant.

Carludovica (Cyclanthaceae; Fig. 13). The pollination of *Carludovica* remained enigmatic for a long time. Even in 1982, SCHREMMER referred to the pollination of *Carludovica* as an "ecological paradox". He only observed meliponine bees visiting the inflorescences and collecting pollen, and concluded that no bee or the pollen carried along could reach the stigma hidden in the small and inaccessible chamber beneath the male flowers. The first to assume that beetles (particularly weevils) act as pollinators of *Carludovica*, was HARLING (1958), but convincing evidence was only provided much later, by GOTTSBERGER (1990, 1991) and ERIKSSON (1994).

The spadix bears three or four "spathes" (bracts) which cover the flowers completely before anthesis. The flowers are unisexual and cover the whole spadix surface tightly. The flowers form a mosaic, with four male flowers surrounding a central female flower situated in a depression below the male flowers. The male flowers comprise numerous stamens and do not possess a vestigial gynoecium. In contrast, the female flower possesses structures of both sexes: four long staminodia and a four-carpellate gynoecium. Like the male flowers, the carpels and the stigmas are placed in a diagonal position.

Anthesis lasts two days, with the female phase on the first and the male phase on the second morning. The flowering process starts the day before, when the spathes begin to unfold. During the following night, the staminodes of the female flower protrude between the male flowers and surround the spadix as a mass of white, spaghetti-like threads. Apart from the visual attraction, the staminodes function as osmophores. In the early morning hours the emitted scent – enhanced by thermogenesis of the spadix – attracts tiny beetles: mainly weevils of the genus *Phyllotrox* (Curculionidae-Derelomini) and members of Staphylinidae. In the late morning, the staminodes begin to wither and drop subsequently. Through the holes left by the staminodes, the weevils gain access to the chambers containing the female flowers. They lick the sweetish exudate of the scars of the staminodes and feed on the exudate of the receptive stigma. If covered with pollen from another inflorescence, the beetles deposit the pollen on the stigmas. The beetles then stay in the "female chambers" throughout the day, crawling around, feeding and copulating. They are not visible from outside and thus are well protected against predators. In the early morning of the second day, the inflorescence progresses to the male stage: the numerous anthers open synchronously and the pollen is released. The weevils crawl onto the surface where they become dusted with pollen, and then fly away, visiting another inflorescence in the female stage.

Philodendron (Araceae; Fig. 14). This genus is represented by some 18 species in the Golfo Dulce area, about half of them being fairly common. None has been studied with regard to its pollination, but there is little doubt that they are pollinated in a similar manner as described here for *Philodendron bipinnatifidum* and *P. selloum* (based on NAGY et al. 1972, WALKER et al. 1983, GOTTSBERGER & AMARAL 1984, GOTTSBERGER 1986, 1990, GOTTSBERGER & SILBERBAUER-GOTTSBERGER 1991). One day before anthesis, the spadix starts to heat up to a temperature of 39-46°C (sometimes more than 30°C above air temperature!), combined with strong odour emission. The beetles (*Erioscelis emarginata*, *Cyclocephala cribrata* and *C. variolosa*) are guided to the female zone of the inflorescence, where they stay for 24 hours, copulating and feeding on the stigma exudations. In the evening of the next day, they leave the inflorescence after getting covered with pollen by crawling over the fertile male flowers.

Pollination by butterflies (psychophily)

The life of butterflies is intimately connected with plants: the juvenile forms of butterflies, the caterpillars, feed on plants (often with specialisation to a single plant species), and the adult forms suck nectar from flowers. *Heliconius* and *Laparus* butterflies also feed on pollen (GILBERT 1972, KRENN & PENZ 1998, PENZ & KRENN 2000; details are being investigated by Harald Krenn and his students from the University of Vienna.). Flowers, therefore, have generated manifold contrivances which make butterflies regular visitors and pollen vectors. Butterflies are diurnal insects. They utilise daylight and are thus prepared to recognise and remember colours (including red) and shapes. The long proboscis (curled when not feeding) is able to suck nectar from deep cavities. Nectar uptake occurs while the insect rests on the flowers. Flowers have responded to these characteristics and developed manifold accomplishments and adaptations. Psychophilous flowers thus usually possess a long narrow tube topped by a flat limb (hypocrateriform flower shape). The limb fulfils two essential functions: firstly, it serves as a visual cue for long-distance attraction; it is therefore, brighly coloured (a characteristic colour combination is red and yellow), and, secondly, it serves as a landing and resting place for the butterfly.

Fig. 15: *Lantana camara* (Verbenaceae) visited by various butterflies; (**a**) *Anartia fatima*; (**b**) *Anartia jatrophae* (Nymphalidae-Nymphalinae); (**c**) *Urbanus proteus* (Hesperiidae); (**d**, **e**) *Urbanus* sp. (Hesperiidae). Photos: A. Weber.

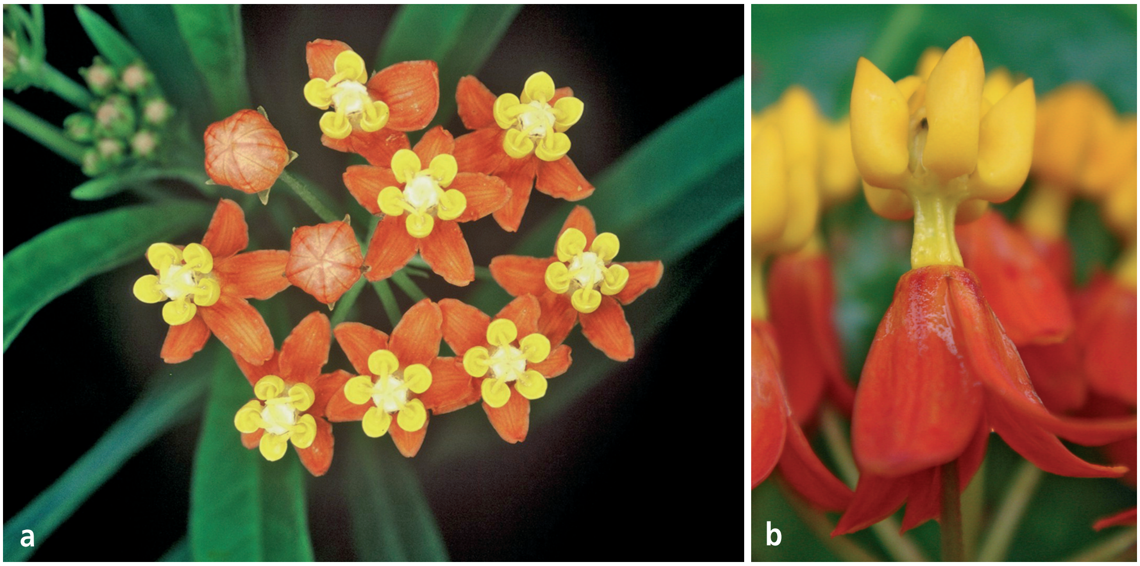

Fig. 16: *Asclepias curassavica* (Asclepiadaceae); (**a**) flower head seed from above; (**b**) close-up of flower in lateral view; note red petals and yellow paracorolla enclosing the stamens and the large stigmatic head. Photos: A. Weber (a), A. Weissenhofer (b).

Though butterfly diversity abounds in the tropics, relatively few flowers have adapted to pollination by butterflies, or at least many fewer than have to moth pollination. The reasons for this are not fully understood. One reason may be that butterflies resting on a flower and sucking nectar are an easy prey for predators. Another is that the plant's "costs" for the formation of a long-tubed flower with a large limb are comparatively high. A third possible cause could be that bees or birds are more reliable and more rapid flyers. There is no tropical family with exclusively butterfly-pollinated flowers. Psychophily has evolved occasionally in large and small families scattered across monocotyledons and dicotyledons. Important families in the Golfo Dulce area include: Orchidaceae (*Epidendrum radicans*), Asclepiadaceae (*Asclepias curassavica*), Chrysobalanaceae (*Hirtella*), Cucurbitaceae (*Gurania*, *Psiguria*), Fabaceae (*Caesalpinia pulcherrima*), Loganiaceae (*Strychnos*), Nyctaginaceae (*Abronia*), Rubiaceae (*Psychotria* spp.), Styracaceae, Verbenaceae (*Lantana*) and others. The evolutionary switch from butterfly to moth pollination (sphingophily) – and vice versa – is easily accomplished and psychophilous and sphingophilous genera/species occur often side by side (e.g. *Hirtella* and *Cuepia* in the Chrysobalanaceae).

Fig. 17: *Epidendrum radicans* (Orchidaceae), flower head; note different colours of tepals (orange), lips (orange-yellow) and old (postanthetic) flowers (red). Photo: A. Weissenhofer.

Lantana camara (Verbenaceae). The easiest way to see a variety of butterflies "at work" is to walk on a sunny day across a pasture or along an old road of a village. Almost certainly, you will come across the "red sage" (*Lantana camara*), a noxious weed of rural areas all over the tropics (being probably of West Indian origin, MOLDENKE 1973). The attraction unit is not a single flower, but a dense head of small flowers (capitulum). The attractiveness is due to a conspicuous colour contrast and colour change. Flower buds are bright red, anthetic flowers are yellow and post-anthetic flowers again change to red. A young capitulum, consisting of flower buds only, is therefore plain red. Subsequently, the opening peripheral flowers form a yellow ring around the central red buds. With age, the yellow ring progresses to the centre, surrounded by a red ring outside and a red centre.

The heads of *Lantana camara* are eagerly visited by butterflies of various kinds (Fig. 15). On a sunny day in September 2005, the following butterfly visitors were recorded at a place near the Tropenstation La Gamba: *Anartia fatima*, *A. jatrophae* (Nymphalidae-Nymphalinae), *Agraulis vanillae*, *Dryas iulia*, *Heliconius melpomene rosina*, *H. hecale zuleika*, *H. hewitsoni* (Nymphalidae-Heliconiinae), *Nymphidium ascolia* (Riodinidae-Riodininae-Nymphidiini), and two species of *Urbanus* (Hesperiidae). The latter were among the most frequent visitors of *Lantana*. More detailed observations were made by SCHEMSKE (1976) on the Osa Peninsula. He recorded no fewer than 24 butterfly species visiting *Lantana*.

One can readily observe how the butterflies roll out their proboscis after landing and immerse it deeply into the floral tube. Though the tube is not very deep, bees scarcely visit the *Lantana* heads. An exception is the common meliponine bee *Trigona fulviventris*, which, however, is useless for pollination, as it steals nectar by biting holes through the corolla (for quantatative data of nectar robbing in *Lantana* see BARROWS 1976).

Asclepias curassavica (Asclepiadaceae) and ***Epidendrum radicans*** (Orchidaceae). The red and yellow colour contrast is obviously a strong visual signal for butterflies and occurs also in unrelated flowers such as *Asclepias curassavica* (Fig. 16) and *Epidendrum radicans* (Fig. 17), the flower architecture of which is completely different. It is notable that *Epidendrum radicans* does not produce nectar. It has therefore been suggested that *Lantana*, *Asclepias* and *Epidendrum* form a floral mimicry complex (BOYDEN 1980). *Asclepias* and *Lantana* are presumed to be Müllerian mimics of each other, while the nectarless *Epidendrum* is thought to be a Batesian mimic of the first two. Although the three species have overlapping ranges and share pollinators, BIERZYCHUDEK (1981), however, showed that visitation frequencies in stands of different floral composition do not support this hypothesis. Flowers in high-density stands of the "Müllerian mimics" are not visited more often than flowers in low-density stands, so the apparent increase in population density through mimicry does not appear to confer an advantage. The "Batesian mimic" (*Epidendrum*) is not visited more often when interspersed with the model than when alone. Consequently, other reasons seem to be responsible for the resemblance of the three plants.

Like in *Lantana*, in *Epidendrum radicans* (Fig. 17) the red and yellow colour contrast is time-dependent. At anthesis, the lip (labellum) is of a much lighter colour (orange) than the rest of the flower. After a flower has been pollinated, the colour of the lip turns darker and adjusts to the colour of the other floral parts. Moreover, as in *Lantana* it is not the individual flower, but the inflorescence which operates as a functional unit (TODZIA 1983). Lower (peripheral) flowers of the almost flat, umbel-like inflorescence open first and thus are visited first. After pollination, they turn a uniform dark colour, forming a dark ring around the centre with freshly opened flowers having bright orange lips. The inflorescence thereby becomes more of a target for the butterfly. Thus, a similar effect is reached as in *Lantana*. Little is known about the identity of the pollinating butterflies, but pollinia (apparently of *Epidendrum*) are often found on the proboscis of common roadside butterflies (DEVRIES in TODZIA 1983).

Pollination by moths (sphingophily)

In the tropics, moth pollination is much more frequent than butterfly pollination. Both floral syndromes are closely related to the shape of the flowers, but each has its distinctive features. The sphingophilous syndrome includes: white (or cream, yellowish or greenish) flower colour, emission of a strong, sweetish scent in the evening and night hours, and presence of nectar. The corolla limb is usually actinomorphic or only slightly zygomorphic. Even when flat (in hypercrateriform flowers), the limb does not serve as a landing place, but only as a visual cue. There is, however, a second, completely different type of sphingophilous flowers: the brush type. The flowers of that type have numerous, long protruding stamens which form a white brush. The nectar is located a the base of the filaments.

The most important (but not the only) moth family involved in pollination are the Sphingidae (hawk moths). Hawk moths hover in front of the flower when sucking the nectar via an extremely long, thin proboscis.

In the Golfo Dulce area, sphingophilous flowers are found in many families, both of monocotyledons and dicotyledons. Regarding the former, there is one family in which all three genera/species represented in the Golfo Dulce area are sphingophilous: the Amaryllidaceae (*Crinum erubescens*, *Eucharis bouchei* and *Hymenocalls* sp., see below). Otherwise, sphingophily is found in some orchids (*Habenaria monorhhiza*, *Brassavola nodosa*) and in the naturalised *Hedychium coronarium* (Zingiberaceae). In the dicotyledons, families with (a) sympetalous flowers (or with an hypanthium forming a tube), or (b) with a polyandrous androecium are suitable groups for the evolution of sphingophilous flowers. Examples for (a) are Apocynaceae (*Plumeria rubra*, with strongly fragrant, but deceptive nectarless flowers), Campanulaceae (*Hippobroma longiflora*, the "Star of Bethlehem"), Caricaceae (*Carica cauliflora*, *Jacaratia. spinosa* and *J. dolichaula*, with unisexual flowers, the nectar-less female flowers mimicking the male nectariferous flowers; BAKER 1976, BAWA 1980c, 1983, BULLOCK & BAWA 1981) and Rubiaceae (*Amphydasia ambigua*, *Cosmibuena grandiflora*, *Gonzalagunia brenesii*, *Guettarda crispiflora*, *Isertia laevis*, *Pentagonia tinajita*, *Posoqueria latifolia*, *Psychotria chiapensis*, *Tocoyena pittieri* and others). Examples for (b) are Capparaceae (*Capparis cynophallophora*), Caryocaraceae (*Caryocar costaricense*), Cactaceae (*E. grandilobum*, *E. phyllanthus*), and Fabaceae-Mimosoideae (most species of *Inga* and allied genera).

Crinum*, *Eucharis and ***Hymenocallis*** (Amaryllidaceae) (Fig. 18). *Crinum erubescens* and *Hymenocallis* (only one unidentified species has been recorded from the Golfo Dulce area) are plants of sandy seashores,

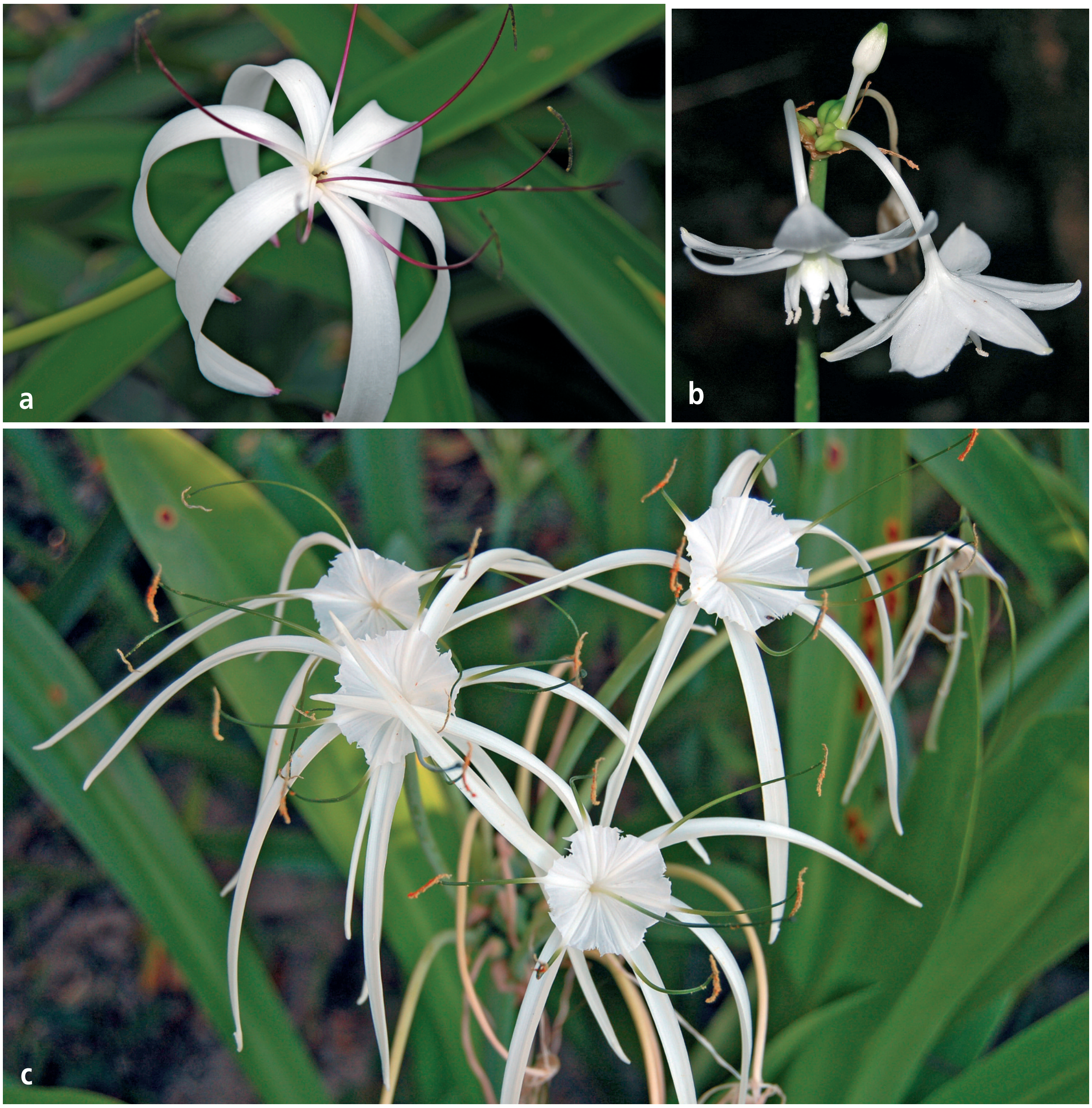

Fig. 18: The sphingophilous flowers of the three genera/species of Amaryllidaceae occurring in the Golfo Dulce area; (**a**) *Crinum erubescens*; (**b**) *Eucharis bouchei*; (**c**) *Hymenocallis* sp. Photos: W. Wurzinger (a), A. Weber (b, c).

while *Eucharis bouchei* is a forest plant of higher altitude. All have white flowers with a long, slender, perianth tube (made up of six fused tepals) and a hexamerous limb. In *Crinum*, the tepals are recurved, while in *Eucharis*, they form a flat corona (the flowers are nodding). In *Hymenocalls*, the tepals are rather inconspicuous, while a large paracorolla forms the most conspicuous showy element of the flower. In *Crinum* and *Hymenocallis*, the stamens are exserted a long way. Pollination studies in *Crinum* have been performed in the African species *C. jagus* and *C. variabile* (BRANTJES & BOS 1980, MANNING & SNIJMAN 2002), and in *Hymenocallis* on *H. coronaria* (North America) where the plebian sphinx moth (*Paratrea plebeja*) and the pipevine swallowtail butterfly (*Battus philenor*) have been observed to visit the flowers during the evening, night and morning hours (DAVENPORT 1966, MARKWITH & SCANLON 2007). Pollination is effected by the wings which touch the stamens in the act of hovering or fluttering. Smaller insects, although they also visit the flowers (to collect pollen; the flowers are also open during the day), do not effect pollination, since the stamens and the style are too widely separated.

Posoqueria latifolia (Rubiaceae (Fig. 19). This shrub or treelet growing commonly along streams and on river banks has not only paradigmatic flowers of the sphingophilous syndrome, but exhibits an interesting mechanism of explosive pollen release. The plain white corolla has a very narrow cylindrical tube up to 18 cm long with a 5-merous limb. The petal lobes are somewhat unequal, with the uppermost one being the broadest. When entering anthesis, the lobes are held in a plane, but later become reflexed. The explosive pollen release was described and illustrated by FRITZ MÜLLER in 1866 [under the name *Martha* (*Posoqueria*?) *fragrans*] (see BEACH 1983). The flowers start opening before dusk and emit an intoxicating sweet odour during the following night hours. The anthers of the five stamens

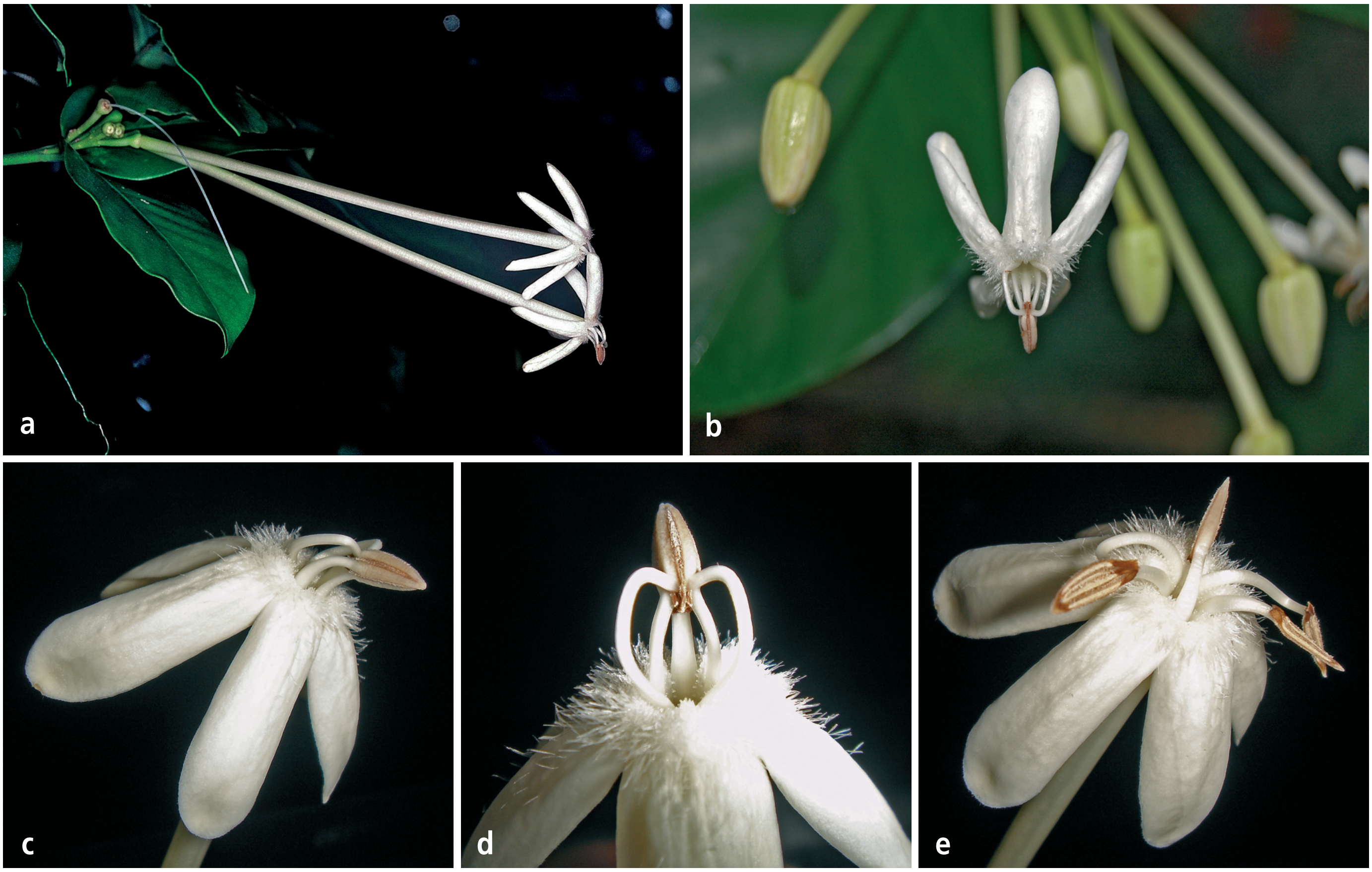

Fig. 19: *Posoqueria latifolia* (Rubiaceae); flower and explosive release of anthers and pollen; (**a**) flowers in lateral view, note the extraordinarily long, narrow tube and somewhat reflexed corolla lobes; (**b**) flower in frontal view, note coherent anthers and five curved filaments under tension, the lower (middle) one has a broader, shorter and stronger filament; (**c**, **d**) close up of flower before triggering, seen from the side and from above; (**e**) close up of flower after triggering, note reflexed position of lateral stamens and upright position of the fifth (lowermost) stamen. Photos: A. Weber (a, b), A. Weissenhofer (c-e).

cohere along their lateral margins and are held in a slightly reflexed downward position. The filaments are under a strong tension. On – even very slight – touching, the anther cone splits apart explosively. The lateral stamens remain connected in pairs and curve immediately outwards, left and right of the corolla entrance. The fifth, lower stamen, however, curves upwards and forcefully ejects the cohesive pollen mass into the flower visitor.

***Inga* and allies** (Fabaceae-Mimosoideae) (Fig. 20). In this alliance, the highest concentration of sphingophilous in the legume family is found. The brush type of flowers is characteristic of the whole subfamily Mimosoideae, but there is a considerable range of pollination types and pollinators: birds (*Calliandra. grandifolia*), bats (*Parkia pendula*), bees (*Mimosa pudica*) and moths. However, it is clear that moth pollination is dominant, especially as it is characteristic of the most species-rich genus *Inga* (with no fewer than 34 species in the Golfo Dulce area, ZAMORA 1991, ZAMORA & PENNINGTON 2001). Other genera to be mentioned here (each usually represented by several species in the Golfo Dulce

Fig. 20: *Inga spectabilis* (Fabaceae-Mimosoideae); inflorescence with a ring of multistaminate flowers opening at dusk. Photo: A. Weber.

area) are *Acacia*, *Albizia*, *Cojoba*, *Enterolobium*, *Zapotheca* and *Zygia*. In most cases, the attraction units are not the flower themselves, but flower aggregations (heads forming spherical "puffballs", racemes or racemes made up of flower heads).

Pollination by other insects

Apart from the insect groups addressed above, there are still others involved in the pollination of Golfo Dulce plants. Perhaps of major importance are wasps and thrips. A survey and comparison of bee and wasp pollination in Costa Rica was given by HEITHAUS (1979a, b). Particularly interesting are the chalcid wasps pollinating the species of *Ficus*. The complicated symbiosis and mutual dependece cannot be addressed here. Thrips (Thysanoptera) are common flower visitors (feeding mainly on pollen), but usually ineffective or at most accessory pollinators. However, in *Castilla elastica* (Moraceae) thrips seem to play the main rôle as pollinators (SAKAI 2001) and this may also be relevant for *Castilla tunu* in the Golfo Dulce area. As has been recently observed by Verena Schmelz, *Tetrathylacium macrophyllum* (Flacourtiaceae/Salicaceae) has nocturnal flowers which are regularly visited (and probably pollinated) by bush crickets (katydids) (see WEBER 2008b, this volume).

Fig. 21: Hummingbirds visiting *Heliconia* flowers; (**a**) *Amazilia tzacatl* (Trochilinae) visiting *Heliconia rostrata*; (**b**) *Threnetes ruckeri* (Phaetornithinae) visiting *Heliconia bihai*. Photos: Gregor Baumgartner.

Pollination by birds (ornithophily)

Costa Rica harbours an enormously rich bird fauna. The numerically richest group is formed by the hummingbirds (Trochilidae) which is also the main (though not exclusive) group relevant for pollination. Non-humminbird pollinators inlude the honeycreepers (Drepaniidae), the orioles (Icteridae), the bananaquits (Coerebinae) and the tanagers (Thraupinae). Due to considerations of space, only pollination by hummingbirds is addressed here.

The hummingbirds (with 102 genera and 328 species in total) have some 50 species in Costa Rica, and over 20 are known for the Golfo Dulce region (HOYO et al. 1999, KASTINGER 2005). In fact, Otto Porsch chose Costa Rica as his expedition destination because of the richness of hummingbirds. Several years before the expedition, Porsch had already made remarkable predictions on pollination by hummingbirds, based on the functional interpretation of flower morpholoy. In the 1960s, K. and V. GRANT carried out out field studies at a broad scale und published them in their classic book "Hummingbirds and their flowers" (GRANT & GRANT 1968). Since then, a huge literature on bird pollination, especially hummingbird pollination has accumulated.

Bird flowers are principally nectar flowers. Nectar is the essential food, drink and energy supply for the hummingbirds. The nectar is usually dilute, with low viscosity, low concentration of sugars and low content of amino acids (BAKER & BAKER 1973, 1975, BAKER 1978, STILES 1981). Pollen and insect visitors may be eaten as a side diet for taking up ammonium.

Hummingbirds commonly take up the nectar while hovering in front of the flower, while other birds perch on a floral or extra-floral part. However, many exceptions occur: there are hummingbird species which regularly perch while sucking nectar, and there are non-hummingbirds which are able to hover (FEINSINGER & COLWELL 1978, WESTERKAMP 1990).

(Humming-)bird flowers are generally diurnal, scentless, and brightly coloured. The colours are mostly red or yellow, a combination of both, or contrasting "parrot colours". It is remarkable that there is no innate preference for colours, the birds have to learn to associate colour with the presence of a reward (BENÉ 1941). Floral form is varied, the main types include gullet flowers (e.g., *Costus*, *Columnea*, *Aphelandra*, *Razisea*), tubular

Fig. 22: Selection of ornithophilous dicot flowers; (**a**) *Hamelia patens* (Rubiaceae), (**b**) *Russelia sarmentosa* (Scrophulariaceae), (**c**) *Scutellaria costaricensis* (Lamiaceae), (**d**) *Malvaviscus arboreus* (Malvaceae), (**e**) *Calliandra grandifolia* (Fabaceae-Mimosoideae). Photos: A. Weber (a-c), A. Weissenhofer (d), W. Huber (e).

flowers (*Guzmannia*, *Malvaviscus*, *Russelia*, *Hamelia* etc.) and brush flowers (*Calliandra*). In all types, the nectar is usually concealed at the flower bottom.

The nectar is taken up via a more or less long, narrow (sometimes needle-like) beak, which may be decurved or straight. The tongue is deeply split into two parts, each forming a slender tube. In the process of sucking the nectar, the tip of the bill is slightly opened and the tongue tip moves rapidly in and out. The nectar is held in the double tube by capillarity until the tongue moves back into the beak. Now the nectar can be sucked back into the mouth and swallowed.

The hummingbirds can be divided into two groups (subfamilies): the "hermits" (subfam. Phaetornithinae) and the "non-hermits" (called "exhibitionists" by Proctor et al. 1996) (subfam. Trochilinae). The two groups differ in beak shape, colouring, distribution, habitat and flower preference and behaviour (Bené 1946, Pickens 1944, Snow & Snow 1972). The "hermits" usually have a decurved beak and are drably coloured, occur predominantly in the lowlands, spend most of their time in the forest, a few metres above the ground, and visit mainly shade-tolerant plants with large flowers. The "non-hermits" have a straight beak and brightly-coloured and iridescent plumage. They are of the type commonly associated with hummingbirds. They are typically found in rather open places, often high above the ground. They hold strict territories and aggressively defend their feeding places. The territories are small and sometimes measure only a few metres across. During the Austrian Costa Rica expedition of 1930, it was observed that a single flowering tree was parcelled out territorially between numerous hummingbird individuals belonging to three species (Moller 1931).

Hummingbird-pollinated plants are abundant in the Golfo Dulce area and pollination can be observed conveniently in many places. There are some plant families that are almost exclusively pollinated by hummingbirds. In the monocotyledons, this applies to the Heliconiaceae (*Heliconia*) in which only a few Old World species are bat-pollinated (KRESS 1985b), while all Costa Rican species are hummingbird-pollinated (LINHART 1973, KRESS 1985a, STILES 1975, 1979; Fig. 21). With the exception of *Costus laevis* (though having red flowers, with some yellow venation of the labellum, this species is adapted to pollination of the euglossine bee *Euglossa imperialis* and rarely – and illegitimately – visited by hummingbirds; SCHEMSKE 1983), all species of the Golfo Dulce area obviously are hummingbird-pollinated (plain red flowers and bracts in *C. pulverulentus* and *C. osae*, cream flowers and red bracts in *C. stenophyllus*). Bird pollination is common in the Bromeliaceae (*Aechmea*, *Chevaliera*, *Guzmannia*). In the orchid family, there is a single ornithophilous genus in the Golfo Dulce area: *Hexisea*. The same applies for the ginger family (Zingiberaceae): *Renealmia* (*R. cernua*).

In the dicotyledons, ornithophily and hummingbird-pollination occurs in many families. Those of major importance include Acanthaceae (*Aphelandra*, *Razisea*), Ericaceae (*Cavendishia*, *Satyria*), Cucurbitaceae (*Gurania makoyana*), Fabaceae-Faboideae (*Erythrina*), Fabaceae-Mimosoideae (*Calliandra grandifolia*), Gesneriaceae (*Columnea*, *Kohleria spicata*), Lamiaceae (*Scutellaria costaricana*), Loranthaceae (*Psittacanthus*), Malvaceae (*Malvaviscus*), Passifloraceae (*Passiflora vitifolia*), Rubiaceae (*Hamelia patens*, *Isertia haenkeana*), Scrophulariaceae (*Russellia*), Simaroubaceae (*Quassia*) and Solanaceae (*Jullanoa*). A small selection of dicotyledonous hummingbird-pollinated flowers is shown in Fig. 22.

Heliconia (Heliconiaceae). The easiest and most convenient way to observe hummingbirds at work, is to take a seat on the veranda of the Esquinas Rainforest Lodge or one of the buildings of the Tropenstation La Gamba, with a glass of cool beer, binoculars and a camera within reach. Within a few minutes, a hummingbird will turn up at one of the cultivated *Heliconia* plants and hover in front of a flower. *Heliconia* species are indeed perfect examples of adaptation to bird pollination. Attraction is not only by the (usually yellow) flower, but also by the brightly-coloured bracts of the inflorescences. A combination of red and yellow is common (Golfo Dulce: *H. irrasa*, *H. lathispatha*, *H. longiflora*, *H. trichocarpa*). In species such as *H. imbricata* and *H. nigripraefixa*, there are three colours forming a conspicuous contrast: yellow (flower), red and black (bracts). The colour combination in *H. wagneriana* is rather strange: green (flowers, edges of bracts), (orange-)red (central parts of bract flanks) and yellow (surroundings of the red parts).

Columnea (Gesneriaceae). The species of this large genus (over 270 species) are almost exclusively hummingbird-pollinated. Remarkable is the shift of the attraction cues from the flower to the leaves in some species. Detailed studies have been recently carried out in the Piedras Blancas National Park by C. Kastinger (see WEBER 2008b, this volume).

Pollination by bats (chiropterophily)

Today, everybody knows that bats are significant pollinators in the tropics. It should be remembered, however, that this realisation is relatively young and that Otto Porsch and the Austrian Costa Rica Expedition of 1930 played a pioneering rôle in the exploration of this phenomenon. Porsch was the first to present definite proof that flowers exist which are strictly adapted to bat pollination (which he predicted in 1922, based on observations of cultivated *Kigelia africana* trees in Java) (PORSCH 1931, 1932, 1939). *Crescentia cujete* and *C. alata* were treated as exemplary cases and visitation/pollination by *Glossophaga soricina* was reported (PORSCH 1931). Nonetheless, Porsch did not realise how significant bat-pollination really is. The full recognition was reached by Stefan Vogel nearly 30 years later, based on field studies in Colombia, Brazil and Bolivia (VOGEL 1958a,b, 1968, 1969a,b). Today, we are quite well informed about the pollination of tropical plants by bats. For general information, see the book of DOBAT & PEIKERT-HOLLE (1985). These authors recorded about 750 (actually or presumably) chiropterophilous species in 270 genera and 64 families, and additional ones have been found since then. HELVERSEN (1993) estimated that in the neotropics between 0.5% and 1% of the angiosperms are pollinated by bats. The chapter “Glossophagine bats and their flowers: costs and benefits for plants and their pollinators” by HELVERSEN & WINTER in KUNZ & BROCK FENTON (2003) is particularly recommended. HELVERSEN and collaborators conducted many studies on the behaviour, flight distances, physiology, energy turnover etc. of flower-visiting glossophagine bats. These zoological aspects are most interesting and instructive, but cannot be addressed here in detail.

Bats visit flowers essentially for the consumption of nectar, so bat-pollinated flowers are essentially nectar flowers. Pollen is sometimes consumed too, and in rare cases extra-floral fruit-like tissue is provided as a reward (the palm *Calyptrogyne*, TSCHAPKA 2003).

The flowers usually open just before dark, display dull or dingy colours and usually emit a (to the human nose) “unpleasant” smell. In some features, they resemble hawkmoth-pollinated flowers, but are generally more robust. As an adaptation to the sonar-based navigation of neotropical bats (Microchiroptera), they are held in an exposed position: either on the trunk or branches ("cauli flory" and "ramiflory", e.g., *Amphitecna*, *Crescentia*), on long stalks standing out from the crown (e.g., *Caryocar*), or on long pendulous "strings" ("penduliflory" or "flagelliflory"; e.g., *Mucuna*, *Markea*).

The main floral types are gullet flowers (actinomorphic or slightly zygomorphic funnel-shaped or campanulate flowers (e.g. *Amphitecna*, *Crescentia*, *Markea*) and brush flowers (the brush formed by numerous, long and stiff stamens, e.g. *Pachira*, *Pseudobombax*, *Caryocar*, *Hymenaea*, *Parkia*, *Lafoensia*), but other types (e.g., papilionaceous flowers: *Mucuna*) occur as well. The nectar of neotropical bat-flowers is glucose-rich or glucose-dominated (which is not always true of Old Word genera).

All neotropical bats involved in pollination belong to the suborder Microchiroptera and here to the family Phyllostomidae. Important genera are (subfamilies in brackets): *Phyllostomus* (Phyllostominae), *Artibeus* (Stenoderminae), *Glossophaga*, *Leptonycteris* and *Musonycteris* (Glossophaginae). *Glossophaga soricina* is among the smallest flower-visiting bats, with a weight of ca. 10 grams, *Artibeus jamaicensis* the largest (ca. 45 g). According to their size, the bats behave differently in the exploitation of flowers: the larger (*Phyllostomus* etc.) perch on the flowers (leaving characteristic claw marks), while the smaller (glossophagine) bats usually hover while taking up the nectar. Flower visitation takes place at dusk or at night. Visitation by large bats can be often deduced from the presence of claw marks on fallen flowers.

In the Golfo Dulce area, bat pollination is rather rare in the monocotyledons. Examples include *Calyptrogyne ghiesbreghtiana* (Arecaceae) (TSCHAPKA 2003), and *Werauhia gladioliflora* (Bromeliaceae) (TSCHAPKA & v. HELVERSEN 2007). In the dicots, one family seems to be exlusively bat pollinated: the monogeneric Caryocaraceae (*Caryocar costaricense*) (VOGEL 1958, GRIBEL & HAY 1993). In Bombacaceae, bat pollination prevails (*Ceiba pentandra*, *Ochroma pyramidale*, *Pachira aquatica*, *Pseudobombax septenatum*), and in most other families it is found here and there among other pollination systems (e.g., Bignoniaceae: *Amphitecna*, *Crescentia*, Cactaceae: *Weberocereus*, Capparidaceae: *Cleome*, Chrysobalanaceae: *Couepia*, Cucurbitaceae: *Cayaponia*, Euphorbiaceae: *Mabea*, *Sapium*, Fabaceae-Caesalpinioideae: *Hymenaea*, Fabaceae-Mimosoideae, *Parkia*, *Inga* p.p., Fabaceae-Faboideae: *Mucuna*, *Erythrina fusca*, Gesneriaceae: *Kohleria allenii*, Lythraceae: *Lafoensia*, Marcgraviaceae: *Marcgravia*, Sapotaceae: *Manilkara*, Solanaceae: *Datura*, *Markea*, Piperaceae: *Piper* p.p.). In total, bat pollination can be assessed to occur in ca. 20 families represented in the Golfo Dulce area.

Fig. 23: *Amphitecna latifolia* (Bignoniaceae); (**a**) flower on plant ; (**b**) fallen flower with claw marks of bats. Photos: A. Weissenhofer.

In the following, a few examples representing different floral types are described in some detail.

Amphitecna and ***Crescentia*** (Bignoniaceae) The large family Bignoniaceae, represented by over 20 genera and ca. 35 species in the Golfo Dulce area includes (*inter alia*) two very common bat-pollinated species: *Amphitecna latifolia* and *Crescentia cujete*. The two genera were already recognised by PORSCH (1931) to be bat pollinated and *Crescentia* was dealt with in great detail, with observation of "regular and rich" bat-visitation (*Glossophaga*) in the field. The flowers of both species are very similar. They belong to the gullet type, are bell-shaped (with a distinct fold at the ventral side) and yellowish in colour (Fig. 23).

Bombacopsis, ***Pachira*** and ***Pseudobombax*** (Bombacaceae). The flowers of these genera (represented by *Bombacopsis sessilis*, *Pachira aquatica* and *Pseudobombax*

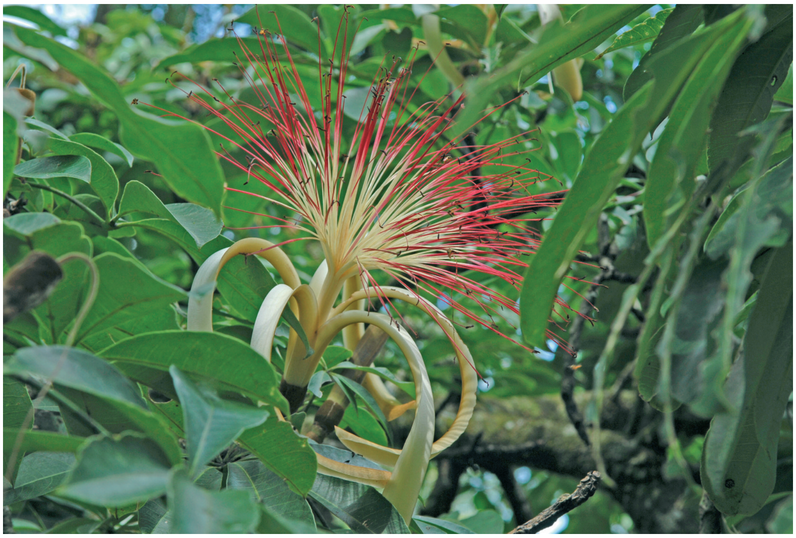

Fig. 24: *Pachira aquatica* (Bombacaceae), a large nocturnal flower pollinated by bats. Photo: W. Wurzinger.

septenatum in the Golfo Dulce area) have large brush flowers. The bunch of long stamens is white, turning purple toward the tips in *Pachira* (Fig. 24). At the base of the stamen mass, it is easy to see that there are distinct stamen bundles connected to each other (indicating secondary increase of stamen number). The free petals roll back and eventually fall off. In the morning after anthesis (the flowers last only one night), the androecium drops as a whole, while the petals drop individually.

Mucuna (Fabaceae-Faboideae). The pan-tropically distributed genus *Mucuna* (ca. 100 species) is represented by two species in the Golfo Dulce area, *M. holtonii* and *M. mutisiana*. The species are conspicuous by the dense racemes of flowers hanging on a long peduncle and greenish-white papilionoid flowers. Pollination has been studied in great detail in *M. holtonii* by V. HELVERSEN and collaborators. It is particularly remarkable that the flag petalum serves as a mirror reflecting the sonar waves sent out by the bat and thus facilitates the location of the flower.

Pollination by non-flying mammals (therophily)

Pollination by mammals other than bats has been discovered only recently. Although it has known for a long time that arboreal marsupials in Australia visit flowers of trees and feed on nectar and pollen, it remained unknown for a long time whether they play an effective rôle in pollination or whether flowers adapted to the pollination of non-flying mammals exist. Otto Porsch discussed this question on several occasions and assumed marsupials to be legitimate pollinators of flowers in Australia (PORSCH 1934, 1935, 1936a-c). Today, evidence is available from many instances and several continents. Most cases have been described from Australia and southern Africa. The first report from the neotropics was by STEINER (1981). He found that the small, primarily bat-pollinated tree *Mabea occidentalis* (Euphorbiaceae) (also present in the Golfo Dulce area, see the similar *M. klugii*, Fig. 25) is almost certainly effectively pollinated by the red woolly oppossum (*Calomys derbianus*) in Panama. The importance of this marsupial may vary over the flowering period, depending on the prevailing rate of bat visitation. In Amazonia, *Mabea fistulifera* was found to be potentially pollinated by the brown capouchin (*Cebus apella*) and woolly spider monkey (*Brachyteles arachnoides*) (TORRES DE ASSUMPÇAO 1981). In the Golfo Dulce area, three species of *Mabea* are present (*M. excelsa*, *M. klugii* and *M. occidentalis*) and it would be worthwhile to investigate the kind and rate of pollination by the two animal groups. *Calomys* (*C. lanatus*) has been observed in Amazonia as a ± regular visitor of other neotropical plants. Those shared with the Golfo Dulce area include *Hymenaea courbaril* (Fabaceae-Caesalpinioideae), *Ceiba pentandra* and *Ochroma pyramidale* (Bombacaceae) (JANSON et al. 1981, GRIBEL 1988). All these are primarily bat-pollinated, but this may not apply to *Quararibea cordata* (Bombacaceae), in which, apart from *Calomys*, other marsupials (*Didelphis*), monkeys (*Cebus*, *Aotus*) and procyonid carnivores (*Potos*, *Bassaricyon*) have been observed to visit the flowers. The rôle of bats and opossums in the pollination of syntopic *Marcgravia* species in Costa Rica has been discussed recently by TSCHAPKA & HELVERSEN (1999).

Combretum species have brush-like inflorescences with brightly coloured flowers. They are primarily pollinated by birds. PRANCE (1980) reported visitation by *Cebus* monkeys. The monkeys feed rather destructively on the flowers, eating perhaps two thirds of the flowers for the nectar. Nontheless, those remaining stand an excellent chance of being pollinated by the monkeys.

In these examples, the mammals are clearily additional or alternative pollinators and the plants may be qualified as ambivalently adapted to the pollination by bats/birds and non-flying mammals., A case of clearly specialised pollination by non-flying mammals was first described from Monte Verde in Costa Rica: *Blakea chlorantha* (Melastomataceae) (LUMER 1980). In contrast to other species of the genus, which have large showy flowers of white to pink colour and pollinated by a variety of bees gathering pollen, *B. chlorantha* has small, green, bell-shaped, nodding flowers hidden in the foliage. They open at night and provide nectar during the hours of the first and second night, but not during the day. They are visited at night, at dawn or dusk by small rodents (rice-rats). The pollen is released explosively by slight pressure on the outside of the petals when the animals grasp the flowers with their fore-paws, and by pressure at the bases of the filaments, when the animal's snout reached the base of the floral bell. Later, LUMER & SCHOER (1986) expanded these observations to *B. austin-smithii* and *B. penduliflora*, the flowers of which were found to be visited by 5 species (in 4 genera) of rodents. The *Blakea* species mentioned are species of montane forests and do not occur in the Golfo Dulce area. So, at present, no plant species is documented in the Golfo Dulce area, the flowers of which are strictly adapted to the pollination of non-flying mammals.

Concluding remarks

Knowledge of pollination is a substantial part of understanding plant communities all over the world. The diverse strategies by which animal-pollinated plants achieve their fertilisation is the result of a long co-existence and co-evolution of both partners. As shown by the present survey, the plants of Golfo Dulce have involved an enormous faunistic diversity for their successful reproduction and survival, ranging from ancient insects such as beetles to highly evolved vertebrates such as birds and mammals. Apart from the academic interest, study of pollination is also of great economic and conservational value. Plants of economic potential cannot be grown as crops without knowledge of their pollination requirements. Conservation of plants and plant communities is only possible when the pollinators are conserved too. In most cases, destruction of a pollinator means the destruction of the plant species. Therefore, pollination studies are of great importance for conservation projects and conservation planners. The study of pollination is not only a discipline of natural science, but also a basis for the cultural development of mankind. Hopefully, the present account gives some stimulating insight into a fascinating science which forms a link in the understanding of the natural and cultural history of the Golfo Dulce region.

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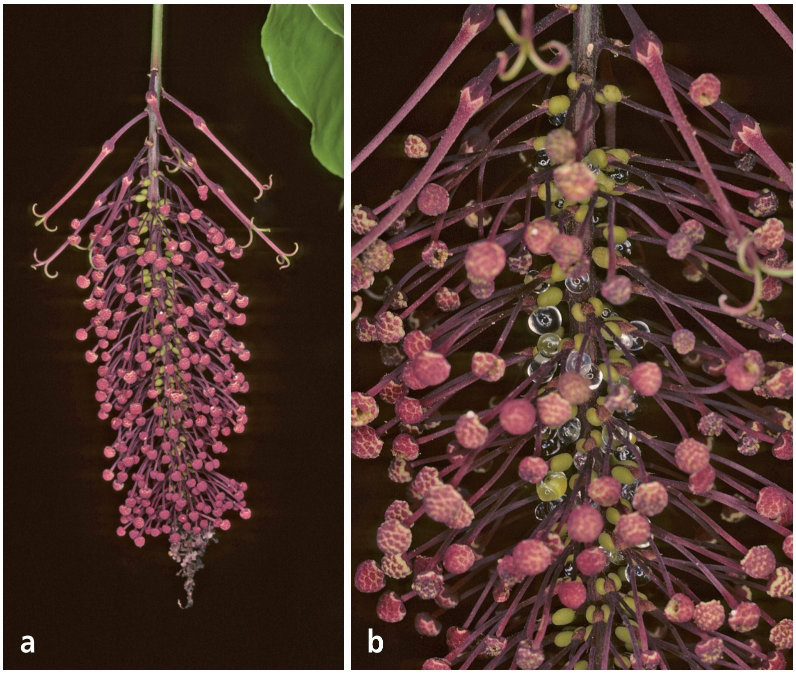

Fig. 25: *Mabea klugii* (Euphorbiaceae), (**a**) bat-pollinated species possibly also pollinated by nocturnal non-flying mammals; a: inflorescence, note female flowers with long style and trifid stigma in the basal (topographically upper) part; (**b**) central part enlarged, note large nectar droplets sectreted by nectaries situated on the rudimentary bracts of the flowers. Photos: A. Weber.

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