

Vertebrate Pollination in Compositae: Floral Syndromes and Field Observations

STEFAN VOGEL*

Abstract: The plant family Asteraceae (Compositae) owes its enormous evolutionary success to the development of the capitulum, in which many florets are combined into a flower-like pseudanthium. Although the details vary enormously, the capitulum adheres to a pattern that does not promote assortative specialisation to pollinators. Most species have a wide pollinator spectrum that includes bees, flies, butterflies, beetles and bugs. Here, I present a survey of tropical and subtropical Compositae that exhibit the floral syndromes of ornithophily (> 60 species in 27 genera), chiropterophily (17 species in 9 genera) and therophily (2–4 species of the genus *Oldenburgia*). In c. 20 cases, bird-pollination is supported by relevant (although mostly casual) observations (literature data and personal observations). The ornithophilous syndrome was convergently achieved by similar means to those seen in other families, albeit limited by the Compositae bauplan. Eight subfamilies (of the 12 presently recognised in the Compositae) and 12 tribes are involved, of which the Neotropical Barnadesioideae, Stiffioideae and Mutisioideae are the most prominent. Around 70% of the ornithophilous species are trees or shrubs. With respect to habitat, higher altitudes with a temperate climate are clearly preferred. Pollination by bats and non-flying mammals is much rarer. Although at least 17 species can be predicted to be bat-pollinated based on their chiropterophilous floral syndrome, visits by bats have only been observed in a single species, *Gongylolepis jauaensis*. In the South African genus *Oldenburgia*, at least two (and possibly all four) species are probably pollinated by non-flying mammals. The capitula of the taxa (presumably) pollinated by bats and non-flying mammals share certain traits with those of the ornithophilous taxa, differing in their whitish colour, musty scents and the bouquet-like divergence of the styles.

Zusammenfassung: Die Korbblütler (Compositae, Asteraceae) verdanken ihren enormen evolutionären Erfolg der Entwicklung des Köpfchens, in welchem zahlreiche Blüten zu einem blütenähnlichen Pseudanthium zusammen treten. Obwohl in den Einzelheiten stark variierend, folgt das Köpfchen einem Muster, das einer Spezialisierung auf verschiedene Bestäubergruppen nicht besonders förderlich ist. Das Bestäuberspektrum der meisten Arten ist groß und inkludiert Bienen, Fliegen, Schmetterlinge, Käfer und Wanzen. In der gegenständlichen Arbeit wird ein Überblick über tropische und subtropische Korbblütler gegeben, welche das Bestäubungssyndrom der Ornithophilie (> 60 Arten in 27 Gattungen), der Chiropterophilie (17 Arten in 9 Gattungen) und der Therophilie (2–4 Arten der Gattung *Oldenburgia*) aufweisen. In ca. 20 Fällen ist Vogelbestäubung durch Literaturdaten und/oder eigene Beobachtungen belegt. Das Syndrom der Vogelbestäubung hat sich konvergent in ähnlicher Weise entwickelt wie in anderen Pflanzenfamilien, wenngleich eingeschränkt durch den vorgegebenen Bauplan des Köpfchens. Betroffen sind 8 (von den gegenwärtig 12 unterschiedenen) Unterfamilien bzw. 12 Triben, von denen die neotropischen Barnadesioideae, Stiffioideae und Mutisioideae die wichtigsten sind. Etwa 70% der ornithophilen Arten sind Holzpflanzen (Bäume und Sträucher). Bevorzugtes Habitat sind höhere Gebirgslagen mit temperattem Klima. Die Bestäubung durch Fledermäuse und nicht-fliegende Säugetiere ist wesentlich seltener. Obwohl bei mindestens 17 Arten auf Grund des Merkmalssyndroms auf Fledermausbestäubung geschlossen werden kann, liegen entsprechende Beobachtungen nur für eine einzige Art (*Gongylolepis jauaensis*) vor. In der südafrikanischen Gattung *Oldenburgia* werden wahrscheinlich mindestens zwei (wenn nicht sogar alle vier) Arten von nicht-fliegenden Säugetieren bestäubt. Die Köpfchen der (vermutlich) chiroptero- und therophilen Taxa haben bestimmte Merkmale mit jenen der ornithophilen Taxa gemeinsam, unterscheiden sich aber hauptsächlich durch die weißliche Farbe, den moschusartigen Geruch und die straußartig auseinanderstrebenden Griffel.

Keywords: Asteraceae, Compositae, bird pollination, bat pollination, pollination by non-flying mammals, ornithophily, chiropterophily, therophily, adaptive radiation, floral syndromes, pollinator guilds.

Correspondence to: anton.weber@univie.ac.at

* Editorial note: To our deep regret we have to inform the readers of the present paper that the author, Prof. Dr. Stefan Vogel, passed away on Nov. 5th 2015 at the age of 90. His former affiliation was: Department of Botany and Biodiversity Research, Division of Structural and Functional Botany, University of Vienna, Rennweg 14, A-1030 Vienna, AUSTRIA

INTRODUCTION

The inflorescences of the plant family Compositae or Asteraceae – ‘capitula’ or ‘heads’ – are commonly considered to be ecologically unspecialised (allotropous). Although the morphological diversity of the heads and their florets is reflected in an enormous species number, their overall appearance is fairly uniform as compared to related families.

Flower-like heads attract a large and diverse assemblage of insects. The flower-like pseudanthium appears to have produced a structure equivalent to a single flower, albeit at a more general level. It has not proceeded (and probably cannot proceed) to the many variations observed in the flowers of euanthous plants, and the diversity of floral styles – adaptation to different pollinator guilds as part of specialisation – is significantly underdeveloped. This restriction has not, however, affected the great reproductive success of the Compositae, not least because variation in seed-dispersal mechanisms is less restricted.

The family Compositae thus shows very little diversification in floral syndromes – adaptations to different guilds as part of specialisation. Not counting here the remarkable contingent of anemophiles, a typical asteraceous zoophilous floret is small, tubular, colourful, nectariferous, fairly rich in pollen and usually scented. It is thus well-adapted to pollination by animals, especially insects. Bees, wasps and non-necrophilous and coprophilous flies make up the bulk of pollinating visitors. MANI & SARAVANAN (1999), based mainly on the Compositae of India, also considered diurnal butterflies to be important and frequent visitors, favoured by long-tubed florets. Hemipterans, orthopterans and beetles that feed on nectar and pollen are also common and significant pollen vectors, although most insects in these groups are destructive.

In terms of floral features, the Compositae may be classified as allotropous, with a tendency towards pollination by bees (melittophily) and butterflies (psychophily). MOLDENKE (1979) presented a preliminary survey of the bee fauna of the Sierra Nevada Mountains of California, where 84 species of oligolectic bees are restricted to the family Asteraceae or to specific Asteraceae genera. WESTRICH (1989) listed 220 oligolectic bees in Baden-Württemberg (Germany) specialised on 66 composite species: many bee species are found on more than one plant species, and several bee species visit the same plant host. These associations are asymmetrical and reciprocal inasmuch as bees receive cues based on the pollen quality of their host and some specific (visual or olfactory) cues, whereas the host’s general appearance represents the near-melittophilous standard within the family, and also attracts polylectic bees and opportunists.

No cases of sphingophily or phalaenophily (pollination by hawkmoths and noctuid moths, respectively) has yet been documented in the Asteraceae, although genera such as *Ainsliaea*, some species of *Prenanthes*, *Brickellia* and *Macroclinidium* are good candidates, and nocturnal insects more generally have been suggested as the pollinators of *Hecastocleis* (cf. FUNK et al. 2009).

Here I discuss floral syndromes of Asteraceae which have received little attention so far: ornithophily (the floral syndrome suggesting bird-pollination), chiropterophily (bat-pollination),

and therophily (pollination by non-flying mammals). I am aware of no recent surveys detailing the occurrence and distribution of these syndromes in the Compositae. In their reviews on pollination in that family, LEPPIK (1970) and LANE (1984) mention some genera to be adapted to bird-pollination, and some field observations on bird visits to certain Compositae have also been published. In contrast, chiropterophily seems never to have been addressed in the literature on Compositae. More and targeted field studies are badly needed, especially as my own experience is confined to the Neotropics, with data for the Palaeotropics being entirely based on literature data.

MATERIALS AND METHODS

Samples were collected in the field, photographed, sketched and preserved in ethanol during numerous visits to tropical and temperate regions of South and Central America: Brazil (seven visits: 1969–2002), Colombia (1964, 2002), Argentina and Chile (1969, 1989–90, 1991), Mexico (1969, 1984), Cuba (2004) and Costa Rica (five visits: 1986–2003). Madagascar was visited 1980 and 2000. Vouchers were deposited at the herbarium of the University of Vienna (WU), and light-microscope samples of nectaries were prepared at the Department of Botany and Biodiversity Research of the University of Vienna. Plants were identified by the author or, in problematic cases, by specialists. Nomenclature follows PRUSKI (1997), ANDERBERG et al. (2007; in KADEREIT & JEFFREY 2007) and FUNK et al. (2009). Additional data were taken from the literature and research at botanical gardens and herbaria (WU, K, MO, US, MEXU, COL, SP, BAA and BO).

All taxa known or suspected to be adapted to bird- or bat-pollination are discussed and illustrated below, in taxonomic order under a classification based on FUNK et al. (2009). They include cases published in the literature as well as personal conclusions based on published diagnoses, photographs and unpublished field notes. The latter include direct observations of pollinator activities and deductions from the floral syndrome. The brief structural comments are not full diagnoses, but rather focus on the biologically relevant traits, namely the processes of animal attraction and reward. Considering the double, sequential function of the style – pollen presentation and as well as pollen receipt – this complex will be termed the ‘polliniferous style’. (Presumably) ornithophilous, chiropterophilous and therophilous taxa are marked in bold on their first mention.

RESULTS

ORNITHOPHILY

The floral syndrome of ornithophily is known from numerous angiosperms and is not in need to be described here in detail. Some specific traits of ornithophilous Compositae are treated in the Discussion. As will be shown in the following, the number of (presumably) bird-pollinated Compositae is most probably much higher as presently thought.

Subfam. Barnadesioideae, (only) tribe Barnadesieae

Barnadesia spinosa L.F. is a shrub or small tree up to 10 m high, with small, entire leaves on short shoots and pairs of axillary spines, growing in the Andean sub-páramo. The flower-heads, 4 cm long and 13 mm in limb diameter, are solitary, terminal or axillary, and held erect or inclined on short, rigid stalks, usually in large numbers. The urn-shaped involucre is multiseriate and densely packed, with dark brown, glossy phyllaries. There are around 10 hermaphroditic, rose-coloured ray florets, with narrow, nectarless tubes and reflexed ligules (Fig. 1A). At anthesis, the rigid styles of the ray florets emerge 17 mm beyond the level of the disc. The disc's centre is occupied by a triad of peculiar nectar florets, which are much shorter, 3–4 mm in inner diameter, thick-walled and zygomorphic (1:4 arrangement). Stamens are rudimentary, and the style is not emergent (Fig. 1B, C, D). The tube of the nectar floret is large enough to accommodate a bird's tongue or beak. The achenes of these florets are larger than those of the rays, and are crowned by an extremely large nectary (Fig. 6A). The pappus consists of thick bristles. It is not clear whether these florets are fertile; pollen is produced, but the stigmatic lobes are almost absent.

Lagerheim (1899) reported from Ecuador that the hummingbird *Colibri coruscans* feeds on *B. spinosa*. I have observed this species (det. Cuatrecasas) being pollinated by the hummingbird *Colibri coruscans* in the páramo at 3500 m near Pueblo de Cumbal (Nariño province, Colombia) (Fig. 1E). As is usual among trochilids, birds hovered above the flower head, sinking their beak into the disc's centre for 1–2 s, touching the stiff styles of the peripheral sexual florets with their face or throat. The observed birds were in courtship (November 1964). Unidentified trochilids were observed to behave similarly at the Tequendama Falls near Bogotá (November 1964).

Barnadesia rosea LINDL. resembles *B. spinosa* in growth habit and the morphology of its pink heads (Fig. 1F). It was studied in the Mainz Botanic Garden.

The occurrence of specialised disc florets in *Barnadesia* was recognised by DELPINO (1890), who called them 'honey muglets'. They were later independently described by GOEBEL (1932) in *B. polyacantha* WEDD., but have rarely been mentioned in the later literature. The nectar source is in the centre of the head, with the sexual functions restricted to the ray florets. The heads thus closely imitate the configuration of a single flower. This is unique among the composites and is characteristic of the genus *Barnadesia*.

It is important to note that not all species of *Barnadesia* are ornithophilous. In cultivated specimens of *B. odorata* GRISEB. in Buenos Aires (flowering in October), the capitula, measuring only 30 mm in diameter, were observed to be white (pale violet with age), strongly clove-scented, and containing on average 14 strongly bilabiate ray florets (2 : 1 = 2 adaxial lobes : 1 abaxial lobe) with polliniferous styles emerging by only around 7 mm. Its three disc florets unfold their flat, 5-dentate limbs (0:5) in the centre, at the same level as the ray florets (Fig. 1G), rather than being cryptic. They form part of the advertisement system and even bear guidemarks in the form of dark purple stripes along the edges of the five teeth. URTUBEY (1999) clearly indicated entomophily for *B. odorata*, as did GOEBEL (1932) for *B. polyacantha*. Another sweet-scented, insect-pollinated species, *B. lehmannii* HIERON., which I studied in Sernambetiba (Guanabara

state, Brazil; cultivated material), has cream-white heads in pendent cymes.

Chuquiraga jussieui J.F.GMEL. is a xerophytic shrub, 2 m high, with very long branches held erect or suberect. It is armed with paired thorns (as in *Barnadesia*) and is densely beset with short, rigid, acute, triangular leaves (Fig. 1I). The heads are terminal, mostly solitary, and sometimes accompanied by sessile lateral heads that also conclude short lateral branchlets. The involucre consists of 150 or more phyllaries, the outermost being small scales, the inner ones increasing in length.

Visual attraction is mainly through the distal part of the involucre, which is dead and dry and varies in colour from straw-like yellow to bright red distally; there are no ray florets. The c. 30 orange disc florets, despite hardly exceeding the involucre, play a role in attraction. They are tubular, relatively wide-mouthed (3 mm), radially five-lobed and nectariferous. Even more spectacular are the extremely prominent, vermilion pollen-bearing styles. I observed *Chuquiraga jussieui* flowering in June at Pueblo de Cumbal, Colombia, Nariño province, but recorded no bird visits.

Chuquiraga calchaquina CABRERA (Fig. 1H) has rufous capitula 3.7 cm long and 2 cm wide. Plants were collected in the aliso (*Alnus acuminata*) zone of the páramo at 3050 m on the Nevado de Cumbal (Nariño province, Colombia) in June, and also in the Valle de Tafi at Infiernillo (Colombia), at 2900 m (det. Hunziger and Barbosa).

In the genus *Chuquiraga*, which contains 19 species, the ornithophilous syndrome is represented only in sect. *Chuquiraga* (EZCURRA 1985, 2002), with the exception of *C. parviflora* (GRISEB.) HIERON. (Fig. 1J). The latter species has inflated yellow heads measuring only 2 × 2 cm, and is apparently melittophilous. Plants were observed flowering in July at Nevado del Chañi, Bolivia, at 4000 m, and in the Garganta del Diablo near Salta, Salta Province, Argentina, at 3000 m; where a male sphecoid wasp, *Trichostictia vulpina*, was seen to sip nectar.

DELPINO (1873–74) was the first to recognise the genus *Chuquiraga* as exhibiting 'caratteros d'ornitofilia' [characteristics of ornithophily]. JAMESON & FRASER (1859) had observed the trochilids *Chalcostigma stanleyi* and *Oreotrochilus chimborazo* on heads of *Chuquiraga insignis* (WILLD.) HUMB. & BONPL. in Ecuador. The visitation of *C. insignis* by *Oreotrochilus chimborazo* is well documented by photographs posted in the internet (e.g. https://es.wikipedia.org/wiki/Oreotrochilus_chimborazo, <https://www.flickr.com/photos/73136015@N05/7037538173/>, <http://www.otromundoesposible.net/wp-content/uploads/2014/01/chiquiragua1.jpg>). *C. longiflora* (GRISEB.) HIERON. also exhibits this syndrome, as observed on the Nevado de Chañi near León at 4000 m in February. *C. spinosa* D.DON is the only food source in winter (June–August) for *Oreotrochilus estella* on the altiplanos of the southern Peruvian Andes. According to CARPENTER (1976), who monographed the life history of *Oreotrochilus estella*, this hummingbird perches on the flower-heads while feeding, apparently in order to save energy; it clings to the involucre or nearby twigs and bends down to the disc. The bird not only profits from the nectar, but also ingests pollen: 'individuals are coated with bright orange pollen on the forehead and chin, and moistly caked pollen occurs in the corners of the mandibles' (CARPENTER 1976). In winter, when insects are scarce, the uptake of pollen proteins is of crucial importance.

The species of the second section, sect. *Acanthophylla*, have small heads similar to those of *C. parviflora*. They are all entomophilous (EZCURRA 1985). *C. erinacea* D.DON, for example, is ‘...visité par les himenoptères’ [visited by hymenopterans] (HAUMAN-MERCK 1913).

Species of *Arnaldoa* are shrubs up to 3.5 m tall, growing in xeric habitats in the Andes of Peru and Ecuador. They bear spines like *Barnadesia* and are densely leafy with alternate, oval or lanceolate, entire, coriaceous phyllomes. The heads are sessile, solitary, terminal and upright.

In the Peruvian *Arnaldoa macbrideana* FERREYRA the heads measure 2.5–4 cm in length (Fig. 1L). My description of this plant is based on diagnoses in the literature (ERBAR & LEINS 2000; ANDERBERG et al. 2007; FUNK et al. 2009). The numerous adaxially tomentose phyllaries are differentiated into a green outer series, where the scales are tightly imbricate and have recurved tips, and an inner series of erect, reddish scales which are about as long as the c. 40 disc florets. These have short, bilobed stigma lobes and a 1:4-lobed limb; they are bright vermilion, including the long, stiffly exerted, simultaneously anthetic styles (ERBAR & LEINS 2000). No data on the nectary are available, but ERBAR & LEINS (2000), who investigated a cultivated plant at the Botanical Garden of Heidelberg, recorded ‘abundant nectar secretion’ and concluded that the species was ornithophilous. Colour photographs (available at: https://www.flickr.com/photos/alej_or/9302533406 and <http://www.nolana.com/images56/1556-82>) are in good agreement.

Two other Peruvian species of *Arnaldoa* also exhibit the ornithophilous syndrome: *A. weberbaueri* (MUSCHL.) FERREYRA and *A. ‘pircapirca’ sine auct.* Both have spectacular, bright red capitula, but differ from *A. macbrideana* in details of leaf form and involucre (see photos at <https://www.flickr.com/photos/manuelroncal/11856600164>). A fourth species from Ecuador, *A. argentea* C.ULLOA, P.JØRG. & M.O.DILLON, is 3.5 m tall, has capitula measuring 40–85 × 35–50 mm, ending in long, exerted ramets, with silvery red to orange-brown involucre and cream-white to orange disc florets (ULLOA, JØRGENSEN & DILLON 2002). It tends towards the chiropterophilous syndrome.

Fulcaldea stuessyi ROQUE & V.A.FUNK is a spiny shrub, 3 m tall, with alternate, elliptic leaves. It occurs in deciduous forests of the Chapada Diamantina, Bahia state, north-eastern Brazil. I rely on the beautifully illustrated description of this recently discovered taxon by FUNK & ROQUE (2011). The plant is characterised by a panicle of clusters (capitulescences) of up to six small, sessile heads. The clusters are borne on elongate peduncles (hypopodia) arising from the upper leaf axils. The cylindrical involucre of each head is 15–17 mm long and consists of tightly appressed phyllaries that are straw-coloured basally but purple towards the apex. The rayless head is remarkable in containing a single disc floret, a peculiarity also seen in some species of *Barnadesia*. This disc floret is actinomorphic, with five long, straight segments (Fig. 1K). Its tube is 20–30 mm long, red and somewhat inflated, and exceeds the involucre for 10–15 mm and so presents a conspicuous signal. A red, plumose, proleptically developing pappus that surrounds it during anthesis is also involved in attraction, in a parallel to *Stiffitia grazielae* (see below). The white style is exerted for another 12 mm and bent downwards distally, suggesting that nototribic pollination is carried out by birds approaching from below. No pollinators have yet been observed, but FUNK & ROQUE (2011) note that the

‘long exerted styles, red color, and damage to the styles hint at possible hummingbird pollination’.

The above diagnosis contrasts with the only other species of *Fulcaldea*, *F. laurifolia* (BONPL.) POIR., which has heads that are smaller in all parts and has pale lilac florets, suggesting entomophily. It lives in the northern Andes, giving the genus an enormous disjunction.

Subfam. Stiffioideae, (only) tribe Stiffieae

Stiffitia chrysantha J.C.MIKAN (det. Cuatrecasas) is a 3 m tall shrub with entire, leathery, lauroid leaves that grows in coastal forests in Brazil. Its flowering heads are 3 cm long and 2–3 mm in diameter, solitary, terminal and horizontally exposed (Fig. 1O). The involucre is smooth, with many greenish-brown, blunt, tightly appressed, imbricate phyllaries, half as long as the disc florets. The c. 12 disc florets are 3 cm long, tubate, radially 5-lobed, with a gaping limb. The lobes are yellow and tightly spirally coiled. The nectar sugar concentration was assessed at 12–15%, with sucrose the dominant constituent. Polliniferous styles rise stiffly 12 mm above the lobes. The golden-yellow pappus is fully developed at anthesis (proleptic) and as long as the disc florets it surrounds, making it very conspicuous.

I observed unidentified hummingbirds as pollinators in Massaguaçu at sea level (São Paulo state) in March (Fig. 1P), approaching the horizontal heads from the side. At the same locality, *Thaluranium glaucopsis*, *Melanotrochilus fuscus* and *Amazilia fimbriata* (Trochilidae) were identified on the plant by M. & I. Sazima (pers. comm.).

Stiffitia grazielae LEITÃO, a 4 m high tree living in the Atlantic rain forest of eastern Brazil, is similar to *S. chrysantha* in its capitulum structure (Fig. 1M), but differs in the deep carmine colour of the peripheral pappi (see above), which contribute strikingly to the overall showiness of the flower heads and which maintain their colour when dispersed. It was collected near Caraguatatuba (São Paulo state) in a forest near the coast (April), where the trochilid *Thaluranium glaucopsis* was observed to visit the capitula (Fig. 1N).

Hyaloseris rubicunda GRISEB. is an Andean shrub native to Argentina with small, sparse, opposite, entire leaves. Numerous sessile heads are unilaterally inserted along spike-like brachyblasts (short shoots), which are in turn borne on long shoots. The heads are usually horizontally orientated. The aspect of the elegant capitula approaches the ornithophilous euanthia of other plant families (Fig. 2 A, B). They are 50 mm long and narrow (5 mm). The brownish-red involucre of the few lanceolate phyllaries, gradually increasing in length, encloses the complex of only 3–4 (up to 5–6 fide ARIZA ESPINAR 1973) scarlet, erect, tubular disc florets, which are deeply cleft and apically ligulate with a five-toothed limb. There are no ray florets. The polliniferous styles emerge 5 mm beyond the corollas and end with the two spirally recurved stigmatic branches.

H. rubicunda was observed in December on stable xeric slopes at 1920–2000 m in the Sierra del Aconquija above Andalgala, Catamarca province, Argentina. The hummingbirds *Chlorostilbon lucidus* and *Sappho sparganura* were seen sipping from the heads of the plant.

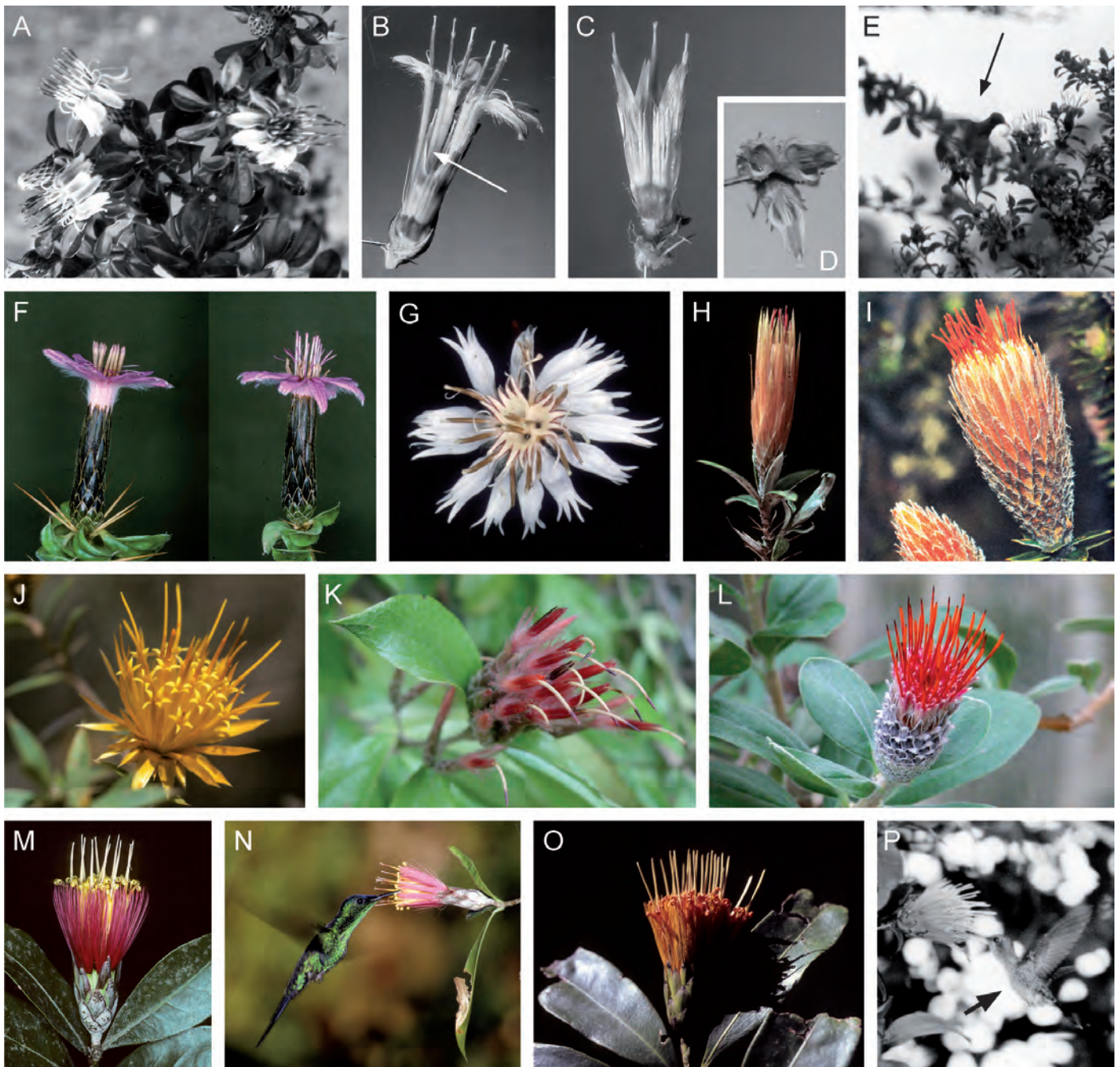


Fig. 1: Ornithophilous Compositae and a selection of entomophilous congeners. A *Barnadesia spinosa*, B Head of the same, cut open to show the central triad of nectariferous florets (x), C the triad alone, D the same, seen from above, E same species, visited by *Colibri coruscans*, F *Barnadesia rosea*, staminate (left) and pistillate phase, G *Barnadesia odorata* (entomophilous), H *Chuquiraga calchaquina*, I *Chuquiraga insignis*, J *Chuquiraga parviflora* (entomophilous), K *Fulcaldea stuessyi*, L *Arnoldoa macbrideana*, M *Stiffitia gracielae*, N same, visited by *Melanotrochilus fuscus*, male, O *Stiffitia chrysantha*, P same, visited by a trochilid bird. (Photo credits: H Erwin Patzelt, I unknown, K Vicki A. Funk, L Michael Wolf, N Silvana Buzato)

I confidently conclude that also *Hyaloseris salicifolia* (GRISEB.) HIERON. (= *Dinoseris salicifolia* GRISEB.) is ornithophilous based on features of the capitula. This shrub, native to the Bolivian and Argentinian cordilleras, is 3–4 m high, has large, lanceolate leaves and large, long-stalked, solitary, termi-

nal capitula (4×2 cm) in horizontal to semi-erect position. The straw-like, light brown to whitish lemon-coloured phyllaries are hardly imbricate, but spread as a loose tuft. The c. 30–60 florets, together with their pappi, form a 35 mm long campanulate bunch exceeding the involucre by 25 mm. The light-yellow

florets are entirely ligulate with five coiled points (Fig. 2D). The polliniferous styles are exerted up to 15 mm and are very stiff, their stigmatic arms extended. ARIZA ESPINAR (1973) describes the flowers as ‘perfumado’ [scented], which would be inconsistent with the syndrome, and which I could not confirm. The nectary is voluminous; nectar rises in the 15 mm long corolla tube. The species was seen flowering in January on dry mountain ridges at 3600 m near Siberia, eastern Bolivia (det. Cuatrecasas), and was also found at 1400 m in the puna of the Quebracho del Toro near Humahuaca (Jujuy province, Argentina) in December.

A close relative, *Hyaloseris cinerea* var. *tomentella* GRISEB. (cf. ARIZA ESPINAR 1973), exhibits an entomophilous syndrome, possibly adapted to nocturnal moths (Fig. 2C). The five white ray florets bear 5-toothed extended ligules, while their styles protrude as a conical bunch 10 mm above. Surprisingly, no disc florets were found. The striking heads are strongly perfumed. Specimens were collected above Andagalá, Argentina, in December.

Duidaea rubriceps S.F. BLAKE is a thick-stemmed shrub that belongs to a series of endemics of the Guiana highlands (tepuis) of Venezuela and northern Brazil. No direct observations on pollination seem to exist, but published photographs (STEYERMARK, BERRY & HOLST 1997; FUNK et al. 2009) leave little doubt that these taxa are bird-pollinated. According to ANDERBERG et al. (2007), *D. rubriceps* has densely foliate (caulirosette) stems with dense tufts of nearly linear, coriaceous leaves and axillary, stalked, cylindrical capitula; these capitula are pendent – a condition which hummingbirds are well-adapted to exploit. The capitula are deep red throughout, including the phyllaries (Fig. 2F). The involucre is three times as long as the exerted parts of the c. 20 bilabiate disc florets, which have coiled lobes (2:3 arrangement). There are no ray florets, as in the following cases. *Duidaea tatei* S.F. BLAKE, with needle-like, tufted foliage and red, terminal capitula also displays the ornithophilous syndrome.

Glossarion rhodanthum MAGUIRE & WURDACK, another endemic of the Guiana Shield, may be inferred to be ornithophilous, because of the similar gross appearance of its heads to those of *Duidaea* (see photograph in GEORGE 1988). The cylindrical, sessile heads are inclined downwards and have a pale, spelt-like involucre and scarlet disc florets with long exerted polliniferous styles (Fig. 2G). The florets are bilabiate (2:3 arrangement) with recurved tips.

Subfam. Wunderlichioideae, tribe Wunderlichieae

Stomatochaeta cymbifolia (S.F. BLAKE) MAGUIRE & WURDACK. This shrub or small tree c. 1 m tall is endemic to the Guianan region. From a description of PRUSKI (1989a) and a photograph published by GEORGE (1988) (Fig. 2E) it can be concluded

that the species is bird-pollinated. It has solitary, terminal, sessile heads, which rise from a rosette of oval, thick and narrow spatulate leaves that terminate the few branches and fall off later. The erect, chaffy scales of the receptacle surround 10–16 pale yellow disc florets that contrast with the red phyllaries. The stiff, yellow polliniferous styles diverge widely above the level of the florets.

Chimantaea spec. nov. aff. *lanocaulis* is a caulirosette tree from the highlands of Guyana which, based on a description/photograph of GEORGE (1988), can be qualified as bird-pollinated. Like in *Stomatochaeta cymbifolia*, the capitulum is terminal, solitary, sessile and sits in a rosette bunch of thick, spoon-like leaves. The multifoliate, cup-like involucre bears a bunch of about 20 ochre-yellow, somewhat divergent disc florets and greatly exerted polliniferous styles. ANDERBERG et al. (2007) mention the presence of a style ‘basally immersed in a large lobed nectary’. Bird pollination is probable, but chiropterophily, or a transition to that mode, cannot be excluded (see below). PRUSKI (1997) recorded the hummingbird *Polytmus milleri* visiting *Chimantaea mirabilis* MAGUIRE, STEYERMARK & WURDACK in the Chimantá massif (Venezuela).

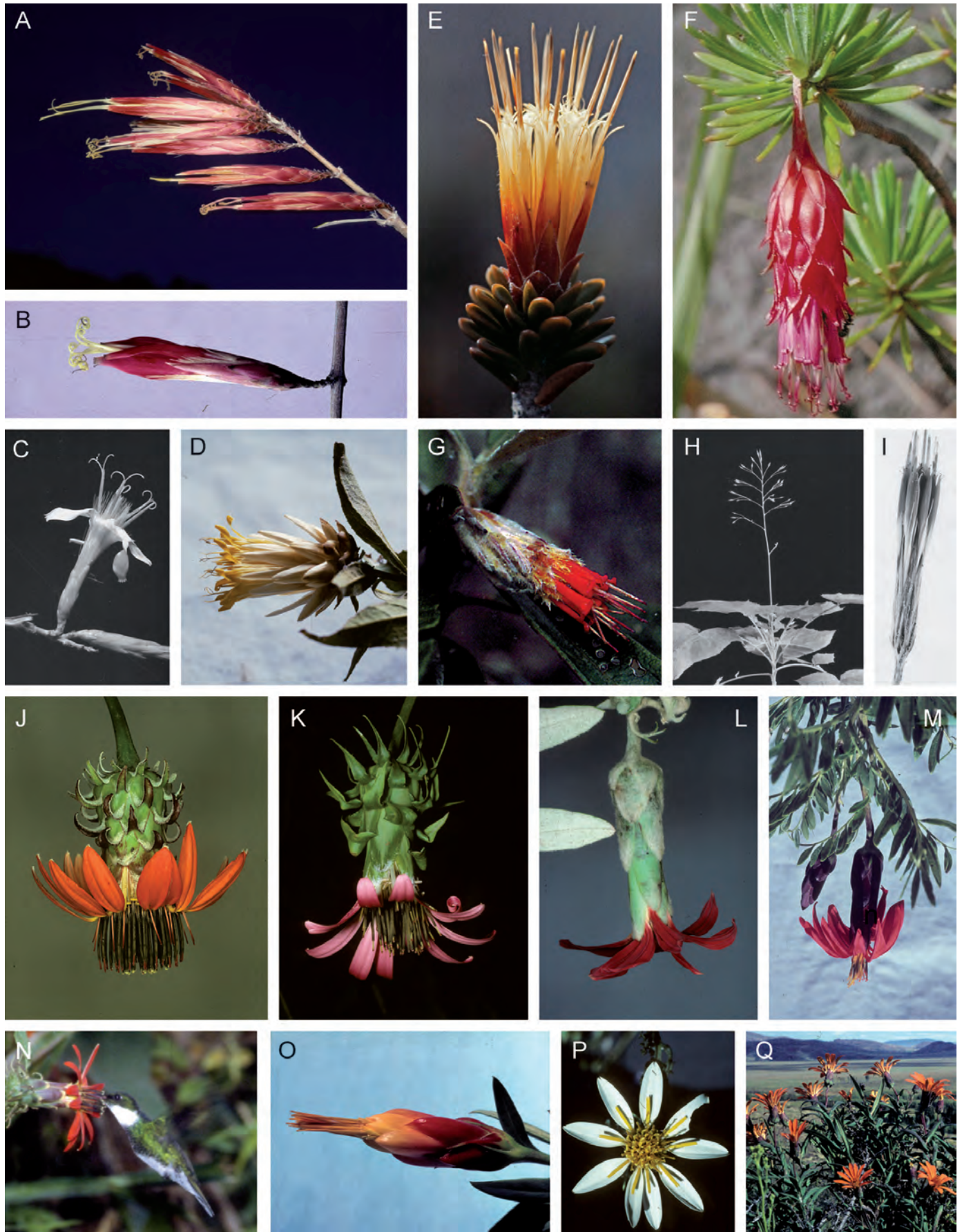
The genus *Stenopadus*, with 14 species of the Guiana highlands (but occurring also in Colombia, Ecuador and Brazil), contains trees up to 25 m high. It joins the previous genera in habit and leaf arrangement, and has handsome, terminal heads. The corollas are actinomorphic. According to ANDERBERG et al. (2007), the disc florets are magenta. Together with the head size, this coloration suggests pollination by birds, at least in species such as *Stenopadus kunhardtii* MAGUIRE.

Subfam. Mutisioideae, tribe Mutisieae

Mutisia, some species of which are found in cultivation, is a long-celebrated example of bird-pollination in the family Compositae. It is a mostly herbaceous genus comprising (as far as known) 62 species from two disjunct parts of South America: one extending from Colombia to Patagonia, and one in eastern Brazil (CABRERA 1965).

The alternate leaves are often pinnatisect and of many shapes, the majority armed with simple or branched tendrils at the end of the leaf rachis, which enable some of the taxa to climb tall trees. The flower-heads are situated at the ends of branches, and have long, cylindrical, imbricate, usually leafy, green (sometimes reddish or brown) involucre, 3–4 cm wide and 5–10 cm long. The florets are heteromorphic: the ray florets are female, very long, nectarless and thin-tubed, with two tiny lateral segments and a large, 3-dentate ligular part that is brightly coloured above (adaxially); the hermaphroditic disc florets are also dorsiventral (2:3), but wide-tubed and nectariferous. The often blackish polliniferous styles emerge stiffly by 15–20 mm.

Fig. 2: Ornithophilous Compositae and a selection of entomophilous congeners. A, B *Hyaloseris rubicunda*, C *Hyaloseris cinerea*, subsp. *tomentella* (entomophilous), D *Hyaloseris salicifolia*, E *Stomatochaeta cymbifolia*, F *Duidaea rubriceps*, G *Glossarion rhodanthum*, H, I *Onoseris sylvatica* and single head, J *Mutisia coccinea*, K *Mutisia speciosa*, L *Mutisia campanulata*, M *Mutisia viciaefolia*, N *Mutisia campanulata*, visited by *Leucochloris albicollis*, O *Mutisia kurtzii*, P *Mutisia sinuata* (entomophilous), Q *Mutisia decurrens* (entomophilous). (Photo credits: E Charles Brewer Carias, F Vicki A. Funk, G Charles Brewer Carias, K Marlies Sazima, N Silvana Buzato)



This morphology suggests a change to dichogamy (sequential hermaphroditism). First, the anthers release the pollen, which sticks to the style. By further growth of the style (and contraction of the filaments), the pollen becomes dislodged and freely exposed at the anther tips ('pump mechanism'). At the female stage, the stigmatic branches split. The flowers are usually self-sterile (SAZIMA & MACHADO 1983).

The scarlet colour of the ligules of most taxa of section *Mutisia* is typical for ornithophily. The enormously large capitula of *M. grandiflora* HUMB. & BONPL. were considered by DELPINO (1873–74) and KNUTH (1905) as bird-pollinated. The following species were studied by the author in life (all spp. det. Cuatrecasas): *M. viciifolia* CAV. (Siberia, Bolivia, 3600 m, June; Fig. 2M), *M. coccinea* A.ST.-HIL. (Santa Genebra reserve, near Campinas, São Paulo state, April; Fig. 2J), *M. campanulata* LESS. (near Vila de Leyva, Boyacá province, Colombia; Fig. 2L) and *M. speciosa* AIT. ex HOOK., with pink ray florets (Planalto de Paraná, near Amparo, Brazil, March; Fig. 2K). The heads of all these species are large, robust, always solitary, inclined or pendent on long peduncles, the rays reflexed. This arrangement makes the heads more conspicuous to hummingbirds.

In *M. ochroleuca* CUATREC., of the same section, the long, red ligules of the ray florets (6 cm) tend to converge as a one-sided fan hanging down from the horizontal head, rendering the capitulum zygomorphic. A joint or constriction between the tubes and ligules makes the rays movable. The species was observed in June at 3300 m at Páramo de Cumbal, Nariño province, Colombia, and ornithophily was confirmed independently by W. Barthlott (pers. comm.).

Nectar quantity was analyzed by PERCIVAL (1961) in *M. viciifolia* CAV. and *M. oligodon* POEPP. & ENDL., which revealed the three main sugars, with sucrose predominant.

M. kurtzii R.E.FR., of sect. *Isantha*, a high-mountain plant, is remarkable in lacking ray florets. I observed a dwarf, leathery-leaved shrub in the Argentinian puna; it bore its terminal or axillary heads on short, peripheral, slanting shoots (Humahuaca, Tilcara, Cordillera San Antonia de los Cobres, February, 2000–3500 m). The whole narrowly turbinate flowering head was 38–50 mm long. The inner red and yellow involucre bracts almost completely enveloped the few yellow disc florets, from which only the pollination organs protruded (Fig. 2O). *M. linifolia* HOOK. has similar heads (FUNK et al. 2009: Fig. 14.1E).

Trochilid (*Aglaeactis cupripennis*) visits to *M. microphylla* WILLD. ex DC. (sect. *Mutisia*) were observed by E. Patzelt (pers. comm.) in Ecuador. *Mutisia acuminata* RUIZ & PAV. was considered to be bird-pollinated by KATINAS et al. (2008). *Mutisia campanulata* was seen to be exploited by *Leucochloris albicollis* (Fig. 2N) and *Phaethornis eurynome* (BUZATO, SAZIMA & SAZIMA 2000). SAZIMA, BUZATO & SAZIMA (1996) documented *M. speciosa* as hosting the same species. SAZIMA & MACHADO (1983) and MORELLATO (1992) studied the pollination of *M. coccinea* by

Amazilia lactea; SAZIMA & MACHADO (1983) also saw *Anthracothorax nigricollis*, *Colibri* sp. and *Phaethornis pretrei* in forests near Campinas, Brazil. I also observed a hummingbird visiting *M. clematis* in Colombia, above Vila de Leyva, Boyacá Department, in October.

It is important to note that only part of the genus *Mutisia* is ornithophilous. The entomophilous species are mainly found in the sections *Ovata*, *Guariruma* and *Holophyllum*. The majority of the species attract flies and bees and follow the typical marigold pattern, with smaller and flatter capitula, shorter receptacles, many horizontally spreading narrow rays freely facing the sky and colours other than red. All these taxa are dwarf subshrubs of open savannas of the southern Chilean coastal plains or high mountain slopes, and bear simple tendrils and white, cream or pale pink heads held close to the ground. *Mutisia decurrens* CAV. (sect. *Guariruma*) is a climber living on scrubby slopes in Patagonian steppes (Fig. 2Q), and has erect, deep orange heads (Fortín Chacabuco, Neuquén, Argentina, January). I also found this syndrome in *M. spinosa* RUIZ & PAV. (Quetrihué, Neuquén province), *M. hamata* REICHE (Tres Morros, Purmamarca, Salta province, 3500–4000 m, February), *M. sinuata* CAV. (Valle de Vacas, Mendoza province, Argentina, 1200 m, December; Fig. 2P) and *M. subulata* RUIZ & PAV. (San Felipe de Aconcagua province, Río Blanco, Chile, c. 1000 m, December). KALIN ARROYO, PRIMACK & ARMESTO (1982) recorded several hymenoptera and butterflies on *M. sinuata* and *M. subulata* in the high mountains of central Chile.

Subfam. Mutisioideae, tribe Onoserideae

Onoseris silvatica var. *colombiana* FERREYRA is an ombrophilous, broad- and tender-leaved perennial with narrow leaves. The investigated specimen [from submontane rain forest, 1500 m; Monterredondo near Guayabetal, Cundinamarca province, Colombia (det. Cuatrecasas), January] was 1 m tall and had developed a loose, terminal raceme bearing c. 10 peduncles (paracladia with tiny bracts), each with a solitary, horizontally exposed head. The heads possess a turbinate involucre and ray florets, whose ligular part is hardly longer than the actinomorphic disc florets, with which it forms a tight, straight, deep purple-red bundle, from which the polliniferous styles protrude divergently (Fig. 2H, I).

Compared to entomophilous congeners, such as the (rayed) *O. sagittata* (RUSBY) RUSBY of the 'marigold-type', the form and colour of *O. silvatica* suggest adaptation to trochilid pollination, in that the heads seem to only allow exploitation by hovering pollinators. I interpret the species as ornithophilous, but with some hesitation because of the small size of the heads (23 mm).

Onoseris onoseroides (KUNTH) R.L.ROB., a shrub distributed in central and northern South America, with a similar aspect to the head of the preceding species, can also be considered ornithophilous. Its small heads, exposed in compound inflo-

Fig. 3: Ornithophilous Compositae. A *Cnicothamnus lorentzii*, B *Cnicothamnus azafran*, C *Gochnatia ilicifolia*, D *Dicoma carbonaria*, E, F, G *Echinops ellenbeckii*, H *Cirsium pinetorum*, I *Cirsium mexicanum*, J *Cirsium subcoriaceum*, purple morph, K *C. cf. tolucanum*, L *Cirsium subcoriaceum*, purple morph with a trochilid bird, M *Sinclairia andrieuxii*, N *Hololepis pedunculata*. (Photo credits: D Wilhelm Barthlott, E–G Christian Puff)



rescences, have reddish turbinate involucre, 28 mm long and 5 mm in diameter, each with eight yellow disc florets (1:4 parted limb). These are arranged in a narrow, straight forward-directed bundle. There are no ray florets. A bulb-like stylopodium at the base of the style appears to be a nectary. The species was evaluated on the basis of cultivated plants at the Botanical Garden of Graz (Austria).

Subfam. Gchnatioideae, (only) tribe Gchnatieae

Cnicothamnus lorentzii GRISEB. is a broad-leaved shrub or tree up to 8 m high with alternate leaves; it lives in sub-Andean forests from Bolivia to Argentina. It has very large, terminal, solitary capitula, c. 6 cm long and 4 cm in diameter, which are held erect or erecto-patent (Fig. 3A). The involucre bears many brown, blunt, scaly phyllaries. Many narrow ray florets are present, of vermilion or deep orange colour, including a three-tipped ligule with one small lobe opposite. The florets are hermaphroditic and have a small nectary. The numerous disc florets are hermaphroditic, actinomorphic and five-toothed, and bear a large nectary that fills the corolla-tube with liquid to a depth of 1–1.5 mm. The stiff polliniferous styles emerge 1 cm beyond the limb. It was observed as a cultivar in a Buenos Aires park, October (det. Cuatrecasas).

FRIES (1903–04) wrote a detailed report on this plant, which he saw being exploited by *Chlorostilbon mellisugus* (Trochilidae) in subtropical forests of the Gran Chaco. He found that the birds introduce their beak or tongue repeatedly into the florets during one hovering visit; their plumage revealed pollen dust around the beak and chin.

The second species of the genus, *C. azafran* CABRERA, a 3–4 m tall shrub of the same syndrome, was collected near Comarapa and San Isidro, eastern Bolivia, in a *Gomphrena* steppe at 1900 m, flowering in January (det. Cuatrecasas). The solitary heads are semi-erect, somewhat smaller than in *C. lorentzii* (3.5 cm), with a turbinate, brown involucre; the phyllaries are ochre-felted and bear a long, acute, dark and reflexed tip. The orange-red rays are held erect (Fig. 3B).

Gochnatia ilicifolia LESS. The investigated specimen (collected 30 km north of Jatibonico, Cuba, in fallow ground on serpentine, October 2004) was a monoaxial, c. 1.50 m tall perennial, bearing alternate, glossy, *Ilex*-like leaves and ending with a single, sessile, erect, turbinate capitulum c. 4 cm long. The many phyllaries of the involucre are leaf-like and keeled; there are no ray florets. The bundle of 12 disc florets emerges 1 cm beyond the phyllaries and the polliniferous styles stand straight 1 cm above the disc florets. All parts of the florets are orange-red (Fig. 3C). The assumed visitors are *Mellisuga helenae* or *Chlorostilbon ricordi*, the only trochilids known from Cuba.

Gochnatia enneantha (S.F.BLAKE) ALAIN, from Jamaica, with heads very similar to those of *G. ilicifolia*, can also be considered ornithophilous.

An unidentified entomophilous species with white-flowered, scented capitula, was observed being visited by flies and butterflies near Andalgalá, Tucumán province, Argentina, in December.

Subfam. Carduoideae, tribe Dicomeae

Dicoma carbonaria (S.MOORE) HUMB. (= *Cloiselia carbonaria* S.MOORE) is a much-branched tree of Madagascar, c. 10 m tall, with entire, spatulate, leathery, 3 m long leaves borne in bunches on short shoots (brachyblasts). The flowering shoots bear several solitary, erect heads, terminating the brachyblasts. The involucre is short and green. The two or three scarlet florets are very large and prominent; they show large, somewhat inflated tubes, constricted at the mouth. The florets are exposed separately, and somewhat divergently, and the red styles surmount the anthers and have shortened, hardly spreading stigmatic lobes. Basally, the style is surrounded by a large nectary. At this point, the corolla is enlarged to accommodate the gland (stylopodium). The pappus, well developed at anthesis, takes part in attraction (as in *Stiffia*), sharing its length and red colour with the corolla. W. BARTHOLOTT, who encountered the tree in dry forest near Tsiombe on the road from Cap Sainte Marie to Berenti (western Madagascar) in October, kindly sent me a photograph (Fig. 3D).

As a member of Palaeotropical Compositae, *D. carbonaria* is presumably visited by sunbirds (Nectarinidae), *Zosterops* (Zosteropidae, one species) and *Neodrepanis* (Philepittidae, two species) are also potential pollinators. All these birds exploit and pollinate flowers when perching on the plant.

Out of the five Madagascan species of *Dicoma*, I collected *D. incana* (BAKER) O.HOFFM. in the savanna of the central highlands of Madagascar on the road from Ambalavo to Ihosy, c. 950 m above sea level, in September. It is a low shrub, 1 m high, with many small heads (12 mm diameter) of yellow florets. It can be considered an entomophilous counterpart to *D. carbonaria*.

Subfam. Carduoideae, tribe Cardueae

Echinops is one of the few African genera in which ornithophily occurs, and one of a number of Compositae that have developed flowering heads composed of hundreds of one-floretted capitula, each with its own involucre and subtended by a small bract. The florets are actinomorphic, nectariferous and bisexual, overtopped by a long, initially polliniferous rod-like style. These heads make up a globular unit that flowers in acropetal sequence and is basally subtended by a leafy secondary involucre.

Echinops ellenbeckii O.HOFFM. is a branched shrub or treelet with spiny, pinnatisect leaves up to 45 cm long. Its syncephalia have a diameter of 15–25 cm. Their densely arranged, emergent, 4–4.5 mm long, five-lobed corollas give them a bright red colour. The syncephalia are raised above the foliage by peduncles up to 30 cm long.

HEUGLIN (1869) recorded bird visits to an *Echinops* species growing in the central mountain range of Ethiopia. Later, OSGOOD (1928) observed birds visiting flowers of this genus. I am indebted to Christian Puff (Vienna) for communicating observations he made in Ethiopia. Both sexes of *Nectarinia tacaze* exploited the heads of *E. ellenbeckii* in Shoa province at 2500 m. Like all Old World flower-birds, they perched on the syncephalium or on the subtending internode and took up nectar from one floret after another, getting dusted with pollen on their beaks,

faces and chests (Fig. 3E,F,G). Also noted to visit the heads was a species of *Zosterops* (Zosteropidae).

Echinops amplexicaulis OLIV., an erect, unbranched cryptophyte 1–2 m tall, shares its bird syndrome with *E. ellenbeckii* (above), being also provided with large, scarlet syncephalia. The plant and its bird visitors were observed in lowlands of Gomo-Gofa province, Ethiopia (C. Puff, pers. comm.).

Of the c. 120 known members of this Old World genus *Echinops*, the majority of species are herbaceous and entomophilous, with white, greenish, blue or violet florets.

Cirsium is a large genus of thistles, including around twenty tropical African (TADÉSSE 1997) and American species (PETRAK 1910). They are annual or perennial herbs, and three flower syndromes can be recognised: entomophily (mainly melittophily), ornithophily and chiropterophily (see below). Despite the wide distribution of the genus in the Old World, diversification of the pollination syndrome has only occurred in Central America and California. All the ornithophilous species considered here seem to be members of section *Erythrolaena* (Fig. 3H,I,J,K). As usual in the genus, the leaves are alternate, pinnatisect and spine-toothed. The heads are mostly solitary, terminating the main shoots and branches. The involucre is differentiated into two kinds of phyllaries: the outer ones leafy, green and spinose with their tips curved outward, and the inner ones straw-like, smooth and coloured, forming a cylindrical cover around the body of the numerous disc florets. These are actinomorphic with a long tube, five long segments and stiff, polliniferous styles that are greatly exerted. The base of the style is surrounded by a large cone-like nectary.

Cirsium coulteri HERV. & A. GRAY is an unbranched or little-branched plant, c. 1.5 m tall, with arachnoid-tomentose leaves and a pedunculate head on a long, almost leafless internode. The outer phyllaries are arachnoid-tomentose, spine-tipped and reflexed. In contrast, the inner phyllaries are smooth, entire, scarlet and erect surrounding the orange-red florets which are overtopped by the straight, erect polliniferous styles. The species, which occurs in the Sierra Nevada mountains of California, was studied in the University of California Botanical Garden (Berkeley, CA), where it flowered in August. The curator, Mr. Christ, noted many hummingbirds visiting the heads (pers. comm.).

Cirsium pinetorum GREENM. (= *C. mexicanum* DC., *C. ehrenbergii* SCH.BIP.) is a ramified thistle, 2.3 m high in my samples, similar in overall shape to *C. coulteri* and bearing erect heads 8 cm long and 5 cm in diameter (Fig. 3H). The outer phyllaries are arachnoid-woolly and brownish-crimson, the florets whitish crimson, the florets flesh-coloured, their tube divided into a basal narrow portion and a campanulate distal part, which is wide enough to accommodate a bird's tongue. The nectar fills the floret up to the point where it widens. Hartmut Ern (pers. comm.) saw two species of hummingbird competing for access in a pine forest in Río Grande near Río Frio in the highlands of Mexico (April).

Cirsium mexicanum SCH.BIP. (or possibly a variety of *C. pinetorum*) is an annual herb, c. 1 m tall, with a solitary head terminating each branch. The head is inclined, horizontally exposed and pedunculate; its inner involucre is flesh-coloured and the florets are whitish, their rod-like style bright cardinal red (Fig. 3I). It was common in forests at c. 2000 m near San Felipe,

Oaxaca, Mexico in October. GRANT & GRANT (1965) counted four hummingbird species (*Archilochus alexandri*, *Selasphorus rufus*, *Eugenes fulgens* and *Lampornis clemenciae*) exploiting *C. mexicanum* in California.

Cirsium anartiolepis PETR., seen in the herbarium of the Smithsonian Institution, Washington, is doubtfully interpreted as ornithophilous. The species Tehuacán, Mexico) has heads to similar to those of the earlier species, with bright red inner phyllaries, cream florets and pink styles. In both *Cirsium conspicuum* SCH.BIP. (Tehuacán, Mexico) and *C. cf. tolucanum* PETR. (Fig. 3K), the inner phyllaries are red and orange.

Cirsium subcoriaceum SCH.BIP. is a giant, ramified thistle up to 4 m tall, with spiny-lobed leaves. Its huge heads (10 cm long, 6 cm across) are solitary, terminal and drooping. The form and coloration of the capitula varies to such an extent that the species seems to be diverging into a bird syndrome and a bat syndrome, albeit connected by intermediate forms. Hybridisation with congeners may play a role. The outer phyllaries are dark green and reflexed in both forms, and end in long spines. In the apparently bird-adapted variant, the complex of salmon-pink inner phyllaries (with darker tips) and whitish florets is cylindrically contracted, as is the stiff, red pincushion of polliniferous styles (Fig. 3J). The flowers are scentless. In the páramo of the Cordillera Tamanca, Costa Rica, along the Panamericana on the Cerro de la Muerte at 2500 m and 3000 m, I repeatedly observed unidentified trochilids feeding on the heads (Fig. 3L). This variant also occurs in Mexico on Pico de Orizaba (at 4000–4500 m) (specimens in the US National Herbarium) and I found it also in pine forests and pastures near San Andrés Huayapam between Santa Catarina Ixtepeji and Oaxaca in October.

The entomophilous tropical thistles, at least in Mexico and the US, resemble the European representatives of the genus: they have smaller, purple, pink or cream heads and less rigid, moderately exerted rod-like styles, often accompanied by an agreeable scent. The relevant species include *C. jorullense* SPRENG. and an unidentified species I found in Shenandoah, Virginia. Further insect-adapted taxa in Mexico include *C. texanum* BUCKLEY, *C. neomexicanum* A. GRAY and *C. pumilum* SPRENG. CLUTE (1892) records, along with insect visits, visits by the trochilid *Selasphorus rufus* in *Cirsium muticum* MICHX. in New Jersey (USA).

Subfam. Cichorioideae, tribe Vernoniae

Vernonia fulva GRISEB., from Argentina, is cited by KNUTH (fide FRIES 1903) as being pollinated by the trochilids *Chlorostilbon lucidus*, *Chlorostilbon mellisugus*, *Sappho sparganura* and *Microstilbon burmeisteri*. Considering its small, lilac heads (1 × 1.5 cm), this shrub clearly exhibits an entomophilous syndrome. I believe that the activity of hummingbirds has been motivated to hunt the plant's true pollinators.

Hesperomannia arbuscula HILLEBR. is a shrub or tree up to 10 m high, with alternate, elliptic, entire leaves and heads 4.5–5.5 cm long in terminal, inclined position, solitary or in clusters of 2–4. The involucre consists of numerous papery phyllaries, of which the outer are green, the inner brownish red. There are no ray florets. The c. 25 yellow, actinomorphic disc florets are 2.5–3 cm long, and their linear, erect segments exceed the involucre by more than half and are themselves overtopped by their

stiff, whitish polliniferous styles. The styles form a pincushion (Fig. 4D), and their stigmatic lobes are almost absent; the plant is considered to be apomictic (ANDERBERG et al. 2007).

All five species of *Hesperomannia* are Hawaiian endemics, native to the islands of Oahu and Maui. The capitula are similar to ornithophilous taxa in Mutisieae, a tribe to which *Hesperomannia* was formerly assigned. Molecular evidence led KIM et al. (1998) to the surprising conclusion that *Hesperomannia* is instead closely related to African Vernoniae, and that its arrival in the Hawaiian Islands must date back to the mid-Tertiary. This probably occurred through long-distance dispersal, and probably by birds, because the cypselas are not adapted to dispersal by wind or water. They probably arrived on islands that are now submerged. Their apomixis may indicate that establishment is still incomplete. Because no comparable design of the syndrome exists among its African relatives, *Hesperomannia* represents a striking example of convergence, with its bird-pollination syndrome probably acquired independently of any predecessors.

The ornithophily of *Hesperomannia* was recognised by PORSCHE (1930), apparently on the basis of photographs published by ROCK (1913), although Rock made no comments on the subject. The genus is quite rare, and no direct observations of bird visits seem to have been made so far. As members of the rich bird-pollinated Hawaiian flora, the plants must be nectar-hosts of the endemic family Drepanididae (which may be related to American Coerebidae), several genera of which feed on nectar, as do some endemic Meliphagidae.

Chresta speciosa GARDNER [= *Glaziioanthus speciosus* (GARDNER) MACLEISH] is a perennial herb with a basal rosette of entire leaves that dry up when the single, c. 40 cm tall, ebracteate shaft develops its terminal, spherical syncephalium, 6 cm in diameter. This 'glomerule' consists of 8–12 heads, the whole being subtended by numerous small bracts. The heads open simultaneously, and each has an imbricate, cylindrical involucre of 8–10 reddish, acute phyllaries. The heads usually contain only one floret, but occasionally 2–3. The florets are complete, elongate, freely projecting with their cylindrically dilated upper tube and five 11 mm long, linear, patent lobes c. 15 mm above the involucre. The mouth opens c. 2.5 mm wide. The scarlet corolla is adorned with an orange guidemark both inside and outside the mouth; the freely exposed filaments are also inserted on the corolla. The filaments' bases are sufficiently separated to allow free access to the tube, and the cylindrical nectary is voluminous (Fig. 6H) (FUNK et al. 2009: p. 801). The form of the inflorescence is uncommon within the family Compositae, in that the florets appear to be 'individualised', resembling a bunch of single, euanthic, ornithophilous flowers (Fig. 4A, B, C). I observed no bird visits. Specimens were collected in grassy gallery forest of the campo rupestre on the Chapada dos Pirineus, Goiás state, central Brazil in August, 800 m (det. H. Robertson, Washington).

Hololepis pedunculata DC. is a low, poorly-ramified shrub 2 m high with several axillary, solitary, horizontally exposed heads. Only some older leaf axils bear mature inflorescences. These are long-pedunculate, laterally spreading and end in a solitary head. The head and its involucre are enclosed in a group of large, dark purplish-green foliar bracts, and emerges horizontally, escaping the shadow of the foliage. Ray florets are absent. The actinomorphic florets are purple, have tubes

16 mm long and 1 mm wide with erect lobes, and an emergent 14 mm long polliniferous style of the same colour. Collectively, the rod-like styles form a dense bundle. The dark violet stigmatic branches curl back in the receptive phase (Fig. 3N), and all florets enter anthesis at the same time. Samples were collected in Minas Gerais, near São Roque de Minas in the Serra da Canastra, campo rupestre, 1100 m.

Although no animals were seen exploring the florets, and the flower colour is uncommon in ornithophilous taxa, I regard the long tubes and their elongate rod-like styles, collectively forming a stiff brush, and the large nectaries as indicative of bird-pollination.

Subfam. Cichorioideae, tribe Liabeae

Sinclairia andrieuxii (DC.) H.ROB. & BRETTELL [= *Megaliabum andrieuxii* (DC.) RYDB.] is a 2–3 m high ramified, lactiferous shrub with broad, entire leaves, which are arachnoid-tomentose below. Its handsome heads, measuring 5 × 5 cm, are solitary and terminal, on a fistulose peduncle exposed in an inclined position. The phyllaries are green and apically reflexed. The ray florets are yellow to orange, rather short and semi-erect. In the c. 35 yellow disc florets, each with a tube 1.5 mm in diameter, nectar rises up to the throat; polliniferous styles with short, divergent stigmatic arms emerge 15 mm above the mouth, forming a stiff pincushion (Fig. 3M). I assume that this species is ornithophilous, albeit with hesitation, as no bird visits were observed but a bumblebee collecting pollen was noted. Strong indications of the bird syndrome are large heads, reduced rays, wide tubes, elongate style rods and copious nectar. It was observed in October at 900 m in sloped rain forest on the road between Tuxtla Gutiérrez and La Ventosa in the Sierra Madre de Chiapas, Mexico.

Sinclairia pringlei (GREENM.) H.ROB. & BRETTELL is like *S. andrieuxii* in sect. *Megaliabum* (TURNER 1989) and is home to Mexico. It has a similar habit, except that the ray florets are completely absent (see Fig. 27.4 G in FUNK et al. 2009). I assume it to be bird-pollinated.

Subfam. Cichorioideae, tribe Cichorieae

The genus *Dendroseris* comprises 11 species, all of them endemic to the Juan Fernández Islands, 670 km off the Chilean coast.

Dendroseris litoralis SKOTTSB. has the repute of being one of the rarest angiosperms in the world and, without being able to examine this plant by dissection, I refer mainly to the recent detailed account of HIND & JOHNSON (2006). The species grows on coastal cliffs, and represents a usually single-stemmed tree up to 4.5 m tall, which develops a dense, branched crown with rosettes of large (> 40 cm), cabbage-like, lactiferous leaves and, at times, several axillary, ramified inflorescences descending below the crown. Each of their paracladia ends in a single pendent flowering head. These, including up to a dozen buds per bunch, open sequentially, with 3–6 heads in anthesis at any time. Flowering heads tend to be largely arranged in one horizontal plane and so, with free space below the crown, facilitate the approach of flying birds. The head has a campanulate or

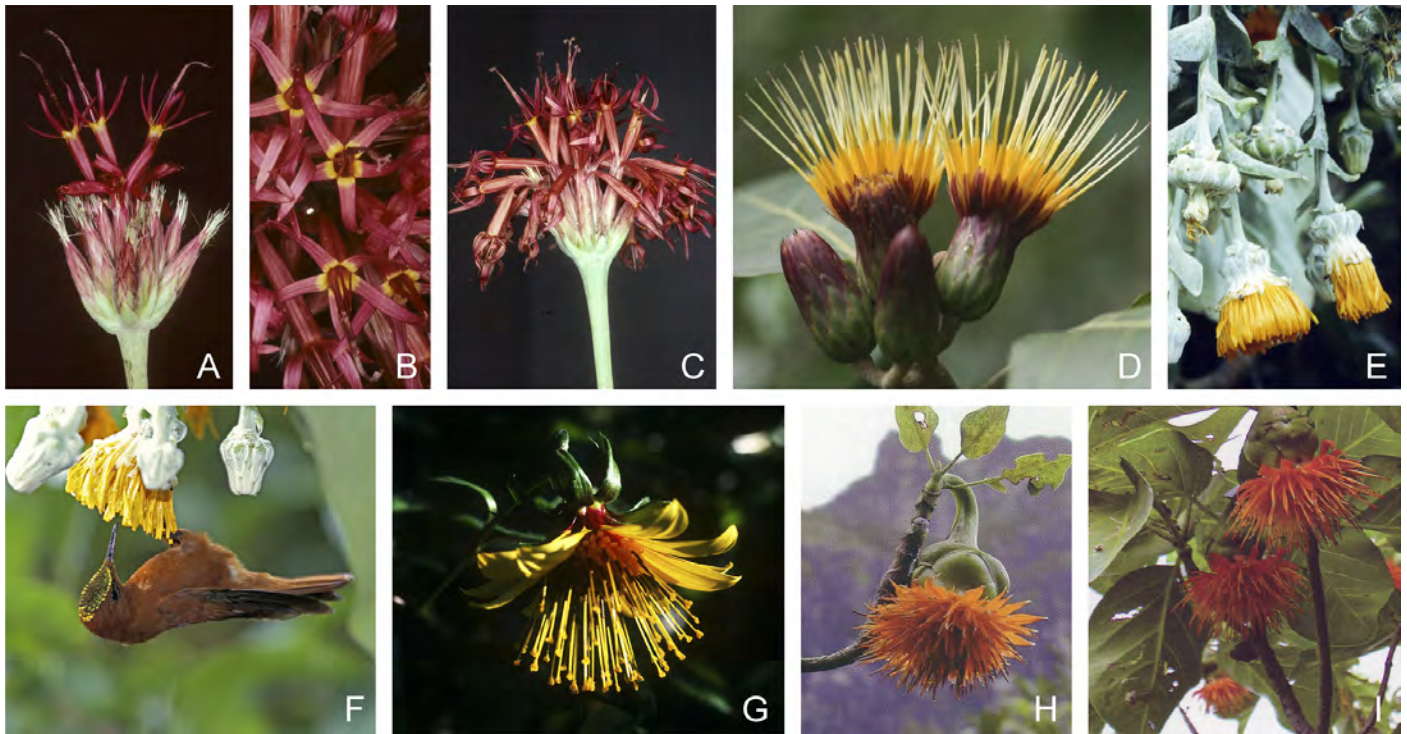


Fig. 4: Ornithophilous Compositae. A–C *Chresta speciosa*, syncephalium, D *Hesperomannia arbuscula*, E *Dendroseris litoralis*, F same, visited by *Sephanoides fernandensis*, G *Bidens cosmoides*, H–I *Fitchia nutans*. (Photo credits: D William Weaver, E Georg Zizka, F Greg W. Lasley, G Fred Ganders, H, I Ken R. Wood)

almost globular receptacle 1.5 cm in diameter. All the c. 100 florets are ligulate, of the Cichorieae type, spreading jointly from an inverted 6–6.5 cm cone with a bare, funnel-shaped surface behind the involucre. The centre is initially occupied by immature florets, because the florets open sequentially. The ligules (2.3–2.7 cm long), the tube (10–11 mm) and the rod-like styles are bright orange (Fig. 4E, F). The styles hardly project, their long stigmatic arms curling backwards. The shape and large size of the nectaries are not mentioned in the diagnoses, but a longitudinal section is depicted by MANI & SARAVANAN (1999). Nectaries are obviously present and secrete huge quantities of nectar, as studied by BERNARDELLO, GALETTO & ANDERSON (2000) and ANDERSON et al. (2001); their analyses yielded 73.5% sucrose, 15.6% fructose and 10.9% glucose – a sucrose dominance typically seen in ornithophilous flowers (BAKER 1979; ANDERSON et al. 2001).

Bird visits to *D. litoralis* were first recorded by SKOTTSBERG (1922). The endemic *Sephanoides fernandensis*, the only trochilid native to the archipelago, visits the plants (Fig. 4F) and also feeds on a few other bird-flower species on another island. Later observers have confirmed Skottsberg's reports: ANDERSON et al. (2001) and G. Zizka (Frankfurt am Main, pers. comm.), witnessed the pollination event on Isla Robinson Crusoe. A second trochilid species, *S. sephaniodes*, a recent immigrant from Chile, was also seen to visit the plant.

An ornithophilous syndrome can be attributed also to *D. macrophylla* D.DON, which has similar capitula.

Dendroseris neriifolia (DECNE.) HOOK. & ARN., *D. micrantha* HOOK. & ARN. and *D. pruinata* SKOTTSB. show much smaller, white heads, which are certainly entomophilous, showing that the local radiation of the taxon also incorporated changes in the floral syndrome.

Subfam. Asteroideae, tribe Madieae

Dubautia ciliolata (DC.) D.D.KECK. belongs to a Hawaiian endemic genus of 24 described species (GIVNISH & SYTSMA 1997). A stiff, erect shrub that inhabits the island of Hawaii, *D. ciliolata* develops panicles of drooping heads with a green or purplish involucre and yellow disc florets. In his *Quellenstudien*, PORSCH (1919) qualified the plant as ornithophilous, albeit without explanation. He apparently relied on the notes of ROCK (1913), but I have not been able to trace Rock's statement.

Subfam. Asteroideae, tribe Coreopsiadeae

Bidens cosmoides (A. GRAY) SHERFF, another composite with isolated occurrence of the ornithophilous syndrome, and so far unique in this genus of over 200 species, was described as ornithophilous by GANDERS & NAGATA (1983), whose detailed account forms the basis of the following description. The species is native to Kauai, representing one of 19 Hawaiian endemic

species in the genus, and the sole member of sect. *Degeneria*; the other 18, in sect. *Campylotheca*, are entomophilous.

The large, pendent heads of *B. cosmoides* are borne on thick peduncles on cymose lateral branches. The outer phyllaries of the dimorphic involucre are leafy and recurved, whereas the inner ones are papery and erect. The yellow rays are sterile and form a campanulate wreath around the disc florets. The radial disc florets have a red-orange tube and deep yellow lobes. The pollen/stigma region is extremely exposed, overtopping the style c. 20 mm above the level of the disc florets (Fig. 4G). The styles jointly form a stiff brush or pincushion, which is c. 20–30 mm longer than the styles, as in section *Campylotheca*. The growing style, acting as a piston, transports the sticky pollen through the anther tube on the tip of the style, where the pollen mass is exposed for 3–4 days. The stigma lobes below it then diverge and become receptive. The process resembles that in taxa such as *Mutisia*. The two subsequent sexual phases proceed synchronously. The heads are facultatively self-fertile. An individual disc floret produces 12–15 µl of dilute nectar with a sugar concentration of 30% (GANDERS & NAGATA 1983), 35 times higher than that measured in other Hawaiian species of *Bidens*. Because of the greater volume, the sugar concentration is only half of that seen in its congeners – both typical features of bird-flower nectar. The pollinators, which have not yet been directly observed, are probably species of Drepaniidae. The analysis of GANDERS & NAGATA (1983) convinces me that the species is ornithophilous.

This example illustrates the rise of a new floral syndrome among a distinct interrelated assemblage of species that still hybridise. According to multiple lines of evidence given by GANDERS & NAGATA (1983), the arrival of *Bidens* in Hawaii occurred in a single event. This ancestral species, probably stemming from North America, experienced an (unbalanced) adaptive radiation in floral characters and underwent a drastic metamorphosis.

Fitchia speciosa CHEESEMAN is a bushy tree up to 7.5 m tall (CARLQUIST 1957; WORTLEY et al. 2007), developing prop-roots; its leaves are opposite, oval and entire. The solitary heads, 65 mm long, 50 mm in diameter (CARLQUIST 1957), hang inverted on c. 10 cm long, thick, recurved peduncles beneath the upper foliage (Fig. 4H). Arched, green, coriaceous phyllaries make up the receptacle. Only disc florets are present (43–47 mm long) and they form a spectacular, deep orange bunch spreading far beyond the rim of the receptacle.

The florets are ligulate, with five long segments and a rather wide tube. The styles are extricate with reduced stigmatic arms. I found no mention of the presence of a nectary at the base of the tube, but nectar is secreted: CHEESEMAN (1903) reports that ‘in the flowering-season the natives make numerous expeditions to the hills in order to collect the honey from the flowers, which is secreted in large quantities’. I found no information about bird visits; species of Meliphagidae are likely to be the principal visitors. *Fitchia speciosa* occurs on Rarotonga in the south-western Pacific Ocean. It is one of five similar species, each found on a different island in the region, including the Society Islands and Tahiti. In the past, the closest relative of these species was thought to be another bird-pollinated island endemic, *Dendroseseris* (ENGLER & PRANTL 1897). It is now placed near the genus *Oparanthus* of Heliantheae subtribe Coreopsidinae (KIMBALL & CRAFFORD 2004)

Subfam. Asteroideae, tribe Millerieae

Espeletia is a genus of 85 species of caulirostrate, woolly treelets, producing axillary or terminal, multi-headed inflorescences. The plants are characteristic elements of the páramos of the northern Andes and Venezuela. Their heads are rather large, yellow, rayed (of the marigold type) or rayless. *E. schultzei* WEDD. and *E. moritziana* SCH. BIP. ex WEDD. were occasionally observed to be visited by the trochilid *Oxyphaps guerinii* at altitudes of 3900 and 4250 m (BERRY & CALVO 1994). The birds were seen to perch on the edge of the capitulum – allegedly – for nectar-feeding and were dusted with pollen on their breast, neck or bill. However, these observations do not provide sufficient evidence that these two or any other *Espeletia* species are bird-pollinated. There is not a single morphological-functional trait indicating ornithophily. SNOW (1983) watched *Espeletias* in the Colombian Andes and saw several trochilids visiting the plants. He denies the florets to offer nectar and arrived at the conclusion, that the birds merely hunt insects and collect the “wool”, which covers the disc, for nest construction. In conclusion, the species of *Espeletia* have – apart from some anemophiles – to be categorised as entomophilous (allotropous), with bumblebees, beetles and flies being the effective pollinators.

Other (doubtful) taxa

PORSCH (1929), in an uncommented list, presented a series of composites he assessed as ornithophilous on the basis of published illustrations (with sources indicated). Those not discussed above include:

- Mutisieae: *Seris discoidea* LESS. (= *Richterago discoidea* (LESS.) KUNTZE), *Trichocline macrorhiza* CABRERA, *Trichocline maxima* LESS., *Trixis bowmanii* BAKER, *Trixis divaricata* SPRENG., and *Trixis gigas* WAWRA
- Vernoniaceae: *Piptocarpha pyrifolia* BAKER, *Lychnophora staavioides* MART., and *Eremanthus bicolor* BAKER
- Moquinieae: *Moquinia paniculata* DC.

I do not consider the sources cited by PORSCH (1929) to provide sufficient evidence to infer ornithophily in these species.

CHIROPTEROPHILY

In the Compositae, the syndrome of chiropterophily, suggesting pollination by bats, is much rarer than the ornithophilous syndrome. As shown below, evidence by observations of bat visits is available only in a single case (*Gongylepis jauaensis*). Nonetheless, I am convinced that pollination by bats plays a more important role in the family than hitherto believed.

Subfam. Barnadesioideae, (only) tribe Barnadesieae

Dasyphyllum latifolium (GARDNER) CABRERA is a spiny, stiffly erect shrub of 1.5 m, with lanceolate, leathery leaves. The species has pedunculate capitula very similar to those of *Wunderlichia* in shape and colour, albeit measuring only 30 mm in

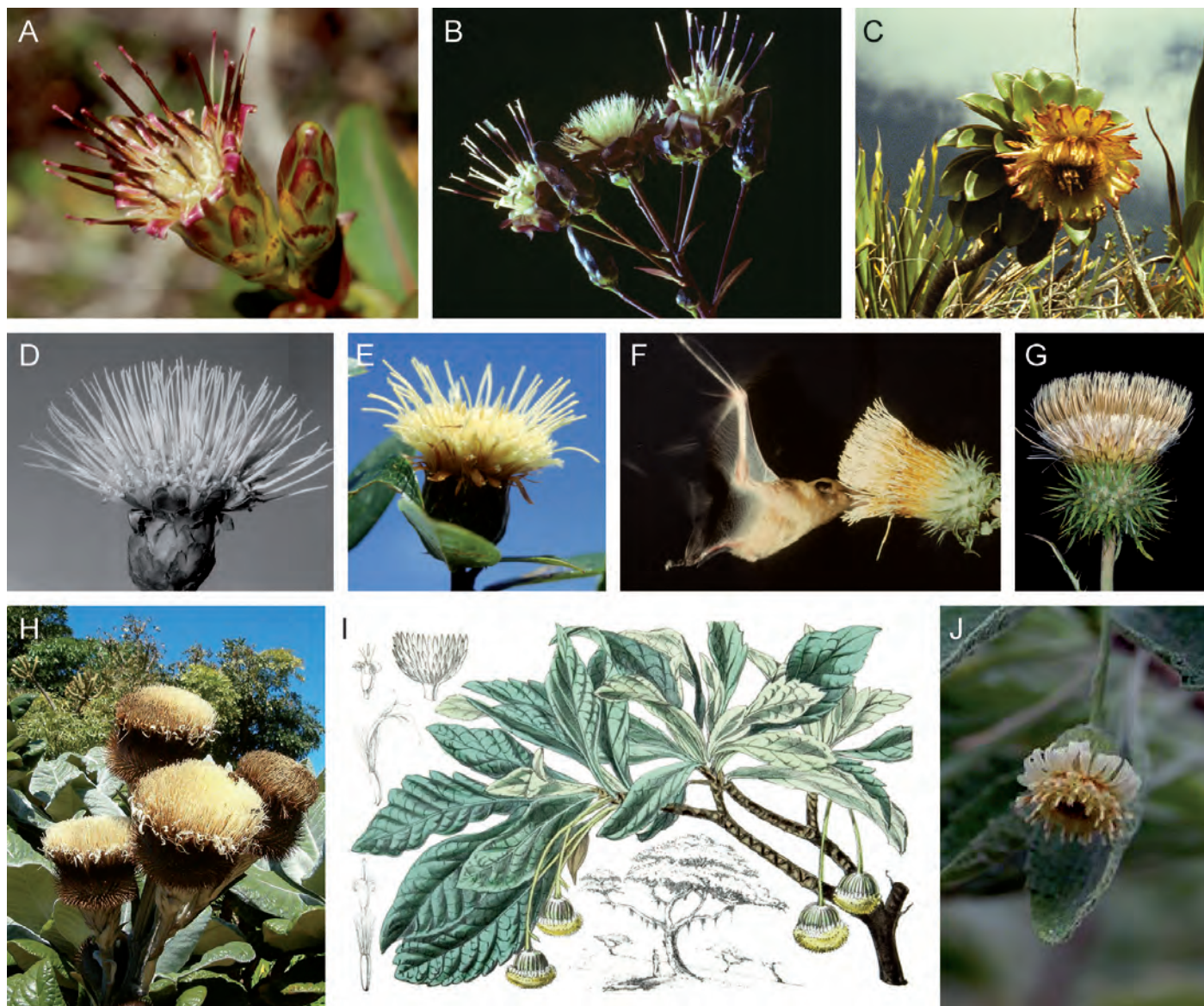


Fig. 5: Chiropterophilous Compositae observed resp. discussed. A *Gongylolepis benthamiana*, B *Gongylolepis huachamacari*, C *Gongylolepis jauaensis*, D *Wunderlichia crulsiana*, E *Dasyphyllum latifolium*, F *Cirsium subcoriaceum*, white morph, visited by *Chaeronycteris mexicana*, G *Cirsium subcoriaceum*, white morph, H *Oldenburgia grandis*, I, J *Commidendrum robustum*. (Photo credits: A Fabian Michelangeli, B, C Vicki A. Funk, F Otto v. Helversen, H Günter Fuchs, I from Curtis Botanical Magazine, J Marcella Corcoran)

diameter (Fig. 5E). Despite the striking similarity to *Wunderlichia*, *Dasyphyllum* belongs to a different subfamily (Barnadesioidae). The phyllaries are appressed and shiny green; the disc florets are wide-mouthed, abaxially unilinguate and five-dentate. The flowers possess a large nectary with plentiful nectar. The scent is said to be agreeable. One trochilid species, *Colibri serrirostris*, was seen taking up nectar (see below), but the character syndrome suggests that this was an opportunistic action, and that the plant is pollinated by bats. I studied the plant in April at 1300 m in campo rupestre on sandstone in the Serra do Cipó, Minas Gerais, Brazil.

Dasyphyllum cryptocephalum (BAKER) CABRERA and *D. sprengelianum* (GARDNER) CABRERA (sect. *Macrocephala*), both with large, yellowish-white heads similar to those of *D. latifolium*, can be assumed to be bat-pollinated. Most of the 40 species of this South American genus, have small, entomophilous flower heads, and make up sect. *Dasyphyllum* (CABRERA 1959).

Subfam. Stifftioideae, (only) tribe Stifftieae

The species of the genus *Gongylolepis* inhabit the Guyanese tepui plateaus. Not having seen plants in life, I rely on the

taxonomic descriptions by PRUSKI (1989b, 1997) and ANDERBERG et al. (2007) and on photographs by Otto Huber published in GEORGE (1988).

Gongyolepis jauaensis (ARISTEG., MAGUIRE & STEYERM.) V.M.BADILLO is a dwarf, woody plant with dense rosettes of large, coriaceous, broadly lanceolate leaves and a large terminal capitulum on an inclined to pendent peduncle. The involucre is hemispherical, c. 10 cm long and 4 cm in diameter. There are about 150 cream-coloured disc florets, which are bilabiate with an outer three-pointed lip tightly curled backwards and with two long, inner, recurved lobes (Fig. 5C). The tube is 20 mm long and contains a large nectary. PRUSKI (1997) reports Otto Huber's observations in the Cerro de la Neblina (Venezuela): 'at night, bats visit these large white-flowered capitula and eat some florets and outer phyllaries. This species may prove to be the first member of the Compositae to be bat-pollinated'. Despite Huber's indication of florivory, the behaviour of the bats (presumably phyllostomid flower-bats) cannot be interpreted as phytophagous. The damage appears to be caused by the bat's vigorous activities. There is little doubt that the bats take up nectar, as strongly indicated by the form of the capitulum. The position of the head close to the ground would also allow access for non-flying mammals.

Gongyolepis benthamiana R.H.SCHOMB. is a sub-shrub of the tepuis of the Guiana Shield, with an inflorescence containing several capitula. The 3 cm long involucre is green and brown, and is overtopped by the limbs of the c. 30 curled, dull red outer lips of the bilabiate disc florets, which collectively form a funnel-shaped entrance to the head. They bear long, stiff rod-like styles and free, blackish anthers. The head's appearance unequivocally suggests pollination by bats (Fig. 5A).

Gongyolepis huachamacari MAGUIRE from the Cerro de la Neblina, Venezuela (900–2700 m), shares the floral aspect of the other *Gongyolepis* species. According to the label on a herbarium specimen at Bogotá, the involucre is 'deep reddish'. The polliniferous styles are exerted about 10 mm above the corolla lobes (Fig. 5B). RENNER (1989), who encountered this plant on a tepui of the Cerro de la Neblina (at c. 2100 m), cites a person named Bellerophon, who has seen the hummingbird *Campylopterus duidae* visiting the flowers and making contact with the styles. However, I believe that this visitation was an opportunistic action, rather than legitimate bird-pollination. The floral syndrome is clearly in favour of bat-pollination.

I suspect that also other species of *Gongyolepis* and related genera, nearly all from the Guyana highlands or adjacent parts of Colombia, are bat-pollinated. The chiropterophilous syndrome is apparent in specimens consulted at the Herbarium of Bogotá, and shown in illustrations in PRUSKI (1997) and STEYERMARK et al. (1997): *G. oblanceolata* PRUSKI, *G. martiana* (BAKER) STEYERM. & CUATREC., *G. colombiana* (CUATREC.) CUATREC. (= *Neocaldasia colombiana* CUATREC.), *Stenopadus kunhardtii* MAGUIRE, and *Chimantaea lanocaulis* MAGUIRE, STEYERM. & WURDACK. In contrast, the features of the related genera *Duidaea* and *Glossarion* suggest bird-pollination (see above).

Subfam. Wunderlichioideae, tribe Wunderlichieae

Wunderlichia crulsiana TAUB. is a 3–4 m tall tree that is leafless in the flowering period. Several of the woody branches are crowned by one or two large capitula and are then reminiscent of

flowering in columnar cacti. The heads are terminal and upright. The involucre (3 cm in diameter) is globose, its outer phyllaries are light green or brownish, dry at the margins and tightly appressed, the inner \pm erect and as long as the c. 80 disc florets. The disc florets are actinomorphic, ivory-coloured, and their five linear lobes are coiled backwards. The tube is 20 mm long, relatively wide and contains a large nectary. The nectar (dilute, 19%) rises up to the mouth when slight pressure is exerted on the involucre. The polliniferous styles are extremely long (40 mm in total) and stout, with short, bifid stigmatic lobes on top. Anthetic styles spread apart to form a brush-like bunch four times wider than the involucre, recalling the androecium of a bombacaceous bat-flower (Fig. 5D). Nocturnal observation was not possible, but there was an odour of pollen in the day-time. The plant examined was collected in October at c. 200 m, in campo rupestre on Pai Inácio near Lençóis, Chapada Diamantina, Bahia, Brazil.

Judging from herbarium material (at COL, specimen from Minas Gerais), the same chiropterophilous syndrome is present in at least *W. mirabilis* RIEDEL & BAKER, a tree up to 10 m with even larger cream-coloured heads, woolly phyllaries and round, petiolate leaves.

Subfam. Carduoideae, tribe Cardueae

As noted above, *Cirsium subcoriaceum* SCH.BIP. appears to be diverging into two morphs, one exhibiting the ornithophilous and the other the chiropterophilous syndrome, connected by intermediates. Both morphs have large heads, long and stiff polliniferous styles and large quantities of nectar. The bird syndrome is characterised by red florets, which, together with the styles, show a broadly parallel arrangement, forming a tight, straight bundle that applies pollen to the beak and face of hummingbirds. The bat syndrome is characterised by robust and diverging polliniferous styles and cream-white florets that both tend to diverge (Fig. 5G), thereby contacting larger areas of a bat and its wings. Scent is released, but it is not typically chiropterophilous, rather recalling that of pollen. The periodicity of flowering was not determined; anthesis lasts for several days. The highly exposed, terminal heads (up to 4 m above the ground) facilitate approach by bats. I made no attempt to observe bat visits, but v. Helversen (in litt.) predicted this type of interaction in Mexico and documented the process bat visitation by bringing the plants and bats together in captivity (Fig. 5F).

Note on the origin of Fig. 5F: This photograph, apparently taken in a flight cage in Freiburg (Germany) was donated to me by Prof. Otto von Helversen. He had encountered *Cirsium subcoriaceum* in the field in Mexico in 1988. He assumed it to be bat-pollinated, but had no opportunity to verify this because highway robbers killed one of his students. However, he was able to collect seeds and raised plants successfully to flowering in a glasshouse at the University of Freiburg (Germany). Here he also introduced glossophagine bats, including *Choeronycteris mexicana*. Unfortunately, no further details could be found after his death in 2009.

Subfam. Asteroideae, tribe Astereae

The genus *Commidendrum*, comprising four rather disparate species, is endemic to the subtropical South Atlantic island

of St. Helena, an island that arose 14 million years ago in the late Miocene. According to CRONK (1987, 2000) and EASTWOOD et al. (2004), *C. robustum* (ROXB.) DC. reaches 10 m in height and has a broad, umbrella-shaped crown. It used to form forests, but is now rare. Its oval, leathery leaves are clustered at the tips of the branches. The capitula, 15 mm across, are solitary on long, pendent peduncles, hanging head-first below the crown (Fig. 5I, J). The involucre is hemispherical, with many green phyllaries. There are c. 30 short, whitish-green, reflexed pistillate ray florets and c. 180 complete, actinomorphic, greenish-yellow disc florets. Their polliniferous styles are only slightly exerted.

The almost perpendicular position of the heads on long, bare pedicels (penduliflory) is characteristic of a number of bat-pollinated (non-asteraceous) trees of the New World and Old World tropics, including West Africa (nearest to St. Helena), as is the flower's greenish hue. However, other factors are not in favour of chiropterophily: the head is too small, nectar data are lacking, and molecular evidence shows ancestorship near that of the entomophilous shrubby South African *Felicia* (EASTWOOD et al. 2004). Today, there are no bats on the island (NAGEL 2006), and only syrphids have been seen on the heads (CRONK 2000). It is conceivable that this relictual, self-compatible, polyploid plant is an ancient component of a tropical community which is incompletely adapted to pollination by bats.

Mammal-pollination can be tentatively also predicted for *Urmenetea atacamensis* PHIL. from Chile and Argentina, and *Dicoma capensis* LESS. from South Africa. Both are prostrate desert perennials with heads held close to the ground, paralleling the yellowish-white, mouse-pollinated flowers of *Protea* species (FUNK et al. 2009, REBELO & BREYTENBACH 1987).

THEROPHILY

Pollination by mammals other than bats – that is by terrestrial or arbicolous mammals such as rodents, insectivores and marsupials – has come to general knowledge only in the last decennia (see REBELO & BREYTENBACH 1987). If occurring at all, it seems to be extremely rare in the Compositae and only one genus can be quoted to be potentially pollinated by non-flying mammals.

Subfam. Carduoideae, tribe Oldenburgieae

Oldenburgia. This is a South African genus with four species. Most of the characters mentioned below are taken from the revision of the genus by BOND (1987). The species are either trees up to 5 m or dwarf, thick-stemmed shrubs. They bear tufts of large, oval to broadly lanceolate, leathery leaves and pedunculate or sessile heads, which are either solitary or borne in groups of 2–3. The urn- or cup-shaped involucre contains many narrow phyllaries. The florets are differentiated into more than 60 pistillate rays – reflexed, whitish in all species and in 2:3 arrangement – and up to 800 actinomorphic, 5-lobed, yellowish or white disc florets. The polliniferous styles emerge somewhat above the level of the disc florets. Bond emphasises a striking similarity of the inflorescences of *Oldenburgia* to those of South African

Protea species – especially to those pollinated by feral mice (REBELO & BREYTENBACH 1987). I also have the impression that the heads are much nearer to the therophilous syndrome than to the ornithophilous one. This is substantiated by the fact that two species bear their heads close to the ground: *O. intermedia* BOND, and the curious *O. paradoxa* LESS., a cushion-forming shrub that develops rosettes with a single, terminal head at a height of 5 cm above the ground (BOND 1987).

BOND (1987) did not mention nectaries, but the presence of plentiful nectar (17% ± 3% in the morning) was reported for *O. grandis* BAILL. (Fig. 5H) by REBELO (1987). This author also observed frequent visits of this species by the Cape sugarbird, *Promerops cafer* (Promeropidae), in the Kirstenbosch National Botanical Garden. This seems to contradict my suspicion that *Oldenburgia* is pollinated by non-flying mammals (bats can be excluded, as there are no flower-visiting bats in South Africa). However, the birds perhaps do not represent the legitimate pollinators, but only side pollinators. It is not uncommon that flower-birds sip nectar from non-bird flowers. Moreover, it is well known that mice and other small mammals are able to climb up to shrubs and small trees, and this may also apply to *O. grandis*.

The fourth species, *O. papionum* DC., prefers rocky habitats and exposes its capitula on top of a tuft of leaves on upright shafts almost 1 m long. I could not find out whether the specific epithet, meaning baboons, was an allusion by the first collector (J.F. Drège, 1794–1881) to the plant's association with baboons and it remains dubious whether these animals have something to do with pollination. In summary, there are reasons to believe that the species of *Oldenburgia* are pollinated by non-flying mammals, and this specially applies for *O. intermedia* and *O. paradoxa*, with their heads held close to the ground.

BOND (1987) suggests that *Oldenburgia* is most closely related to the South American genus *Cnicothamnus*, and proposes a Gondwanan origin. Unlike *Oldenburgia*, *Cnicothamnus* clearly exhibits the bird pollination syndrome (see above).

DISCUSSION

Ornithophily. More than 60 species of Compositae, out of 27 genera, are listed above to exhibit the bird-pollination syndrome. Actual bird visitations are reported (based on literature data and personal observations) for c. 20 taxa (albeit almost exclusively representing casual observations), while the rest are predictions from the floral syndrome analysed. The ornithophilous syndrome is present in a well-marked guild, which but forms a very small minority in the large family of Compositae. The syndrome is present in members of 8 subfamilies (out of 12 presently recognised in the Compositae) and 13 tribes, respectively: Barnadesioideae (with only tribe Barnadesieae), Stiffioideae (with only tribe Stifftieae), Wunderlichioideae (tribe Wunderlichieae), Mutisioideae (tribes Mutisieae and Onoserideae), Gnochatioideae (with only tribe Gnochatieae), Carduoideae (tribes Dicomeae and Cardueae), Cichorioideae (tribes Vernoniae, Liabeae and Cichorieae), and Asteroideae (tribes Madiaceae and Coreopsidae). Many taxa belong to the subfamilies Barnadesioideae, Stiffioideae and Mutisioideae. Due to their basal positions in the family's phylogeny, it has been argued that the ornithophilous syndrome might be the ancestral condition. This

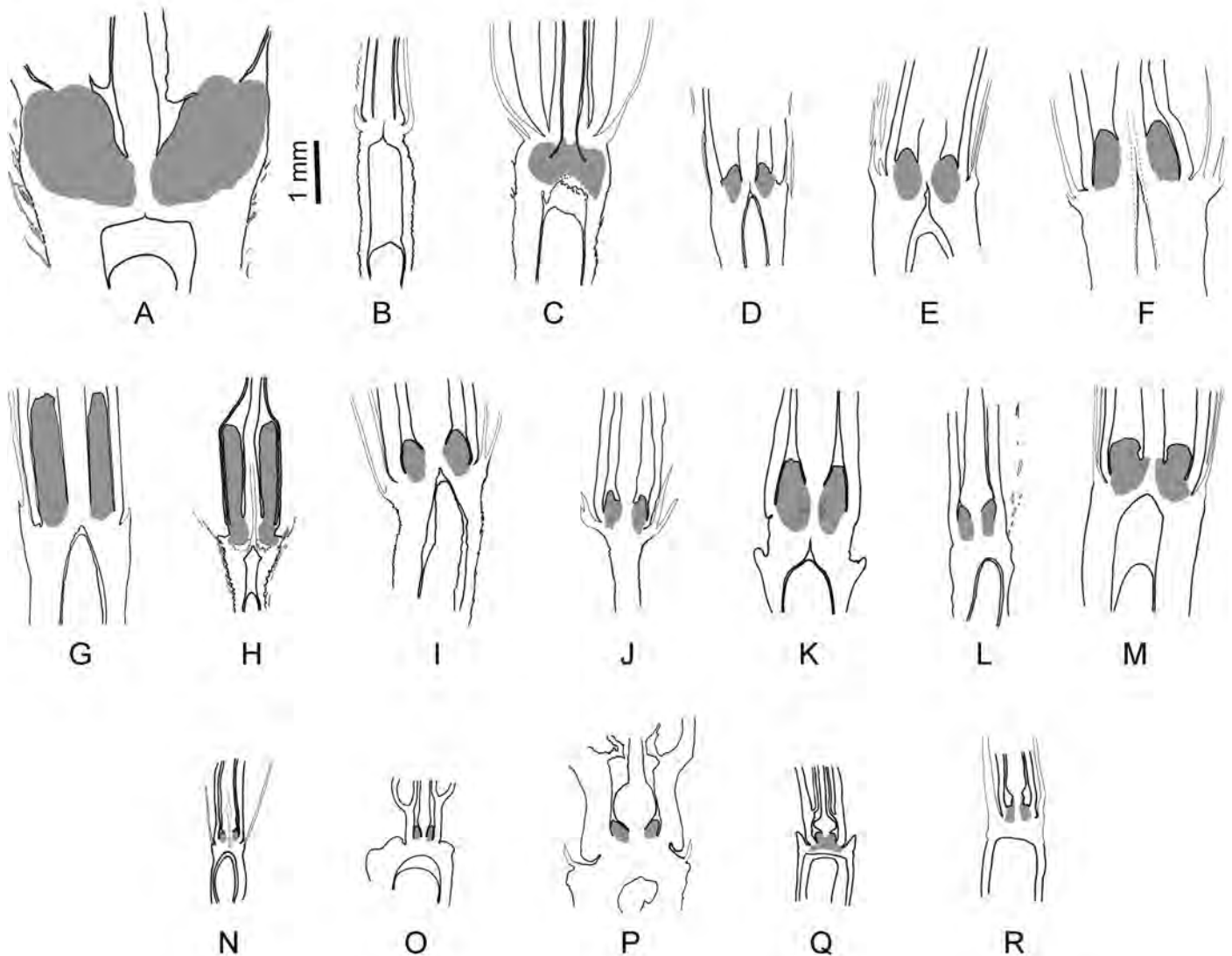


Fig. 6: Nectary sizes and positions (shaded): A–L of several ornithophilous Compositae, M–Q (for comparison) those of entomophilous species, all at same scale. A *Barnadesia spinosa*, nectariferous disk floret, B same species, nectarless ray floret, C *Chuquiraga longiflora*, D *Hyaloseris rubicunda*, E *Hyaloseris salicifolia*, F *Stiffia chrysantha*, G *Mutisia coccinea*, H *Chresta speciosa*, I *Cnicothamnus lorenzii*, J *Cnicothamnus* sp., K *Cirsium subcoriaceum*, L *Dendroseris litoralis*, M *Hololepis pedunculata*, N *Aster ageratoides*, O *Zinnia elegans*, P *Tithonia rotundifolia*, Q *Rudbeckia fulvida*, R *Tagetes patula*.

view may be supported by the fact that 70% of our cases are trees and shrubs, a trait TAKHTAJAN (1959) regarded as plesiomorphic. In the opinion of EZCURRA (2002) and GRUENSTAEUDL et al. (2009) the inference that avian visitors were the first pollinators in this family is a step too far. Almost all of the genera in the groups regarded as basal in Asteraceae exhibit the bird-pollination syndrome alongside with entomophilous clades, and the families closest to Asteraceae are not bird-pollinated. At any rate, ornithophily apparently arose early in the family's evolution, probably in the Oligocene.

Ornithophilous Compositae are distributed over four continents with tropical or subtropical climates: North and South America, Africa, Australia and some oceanic islands. Centre of

diversity is in the Andes and the Guiana Shield. The apparent absence from Asia, especially the Indian and Malesian regions, where bird- and bat-pollination occurs in many non-asteraceous families, is remarkable and unexplained.

Birds that visit Compositae belong to different families in different areas: Meliphagidae in South Asia, Australia, Melanesia and Hawaii; Nectarinidae and Promeropidae in Africa and Madagascar; Drepanididae in Hawaii; Trochilidae, with Coerebidae co-occurring in most areas, in America (Tab. 1). As a rule, the pollinating birds are generalists, visiting all available ornithophilous plants in a given area, habitat and season, although geographical vicariants of visitor species often occur. The near-absence of members of the subfamily Phaethornithinae from the list is striking. Possible ex-

Tab. 1: Birds that have been observed to pollinate ornithophilous Compositae.

Trochilidae-Trochilinae	<i>Lampornis clementiae</i>	<i>Sephanoides fernandensis</i>
<i>Aglaiactis cupripennis</i>	<i>Lesbia sparganura</i>	<i>Thalaurania glaucopis</i>
<i>Amazilia fimbriata</i>	<i>Leucochloris albicollis</i>	
<i>Amazilia lactea</i>	<i>Oreotrochilus chimborazo</i>	Trochilidae-Phaetornithinae
<i>Anthracothorax nigricollis</i>	<i>Oreotrochilus estella</i>	<i>Phaethornis eurynome</i>
<i>Archilochus alexandri</i>	<i>Oreotrochilus pichincha</i>	<i>Phaethornis pretrei</i>
<i>Chaerocercus burmeisteri</i>	<i>Oxygogon guerinii</i>	
<i>Chlorostilbon aureoventris</i>	<i>Petalofora iolata</i>	Nectarinidae
<i>Chlorostilbon prasinus</i>	<i>Rhamphomicron stanleyi</i>	<i>Nectarinia tacazze</i>
<i>Colibri coruscans</i>	<i>Sapho sparganura</i>	
<i>Colibri serrirostris</i>	<i>Selasphorus rufus</i>	Zosteropidae
<i>Eugenes fulvens</i>	<i>Sephanoides sephaniodes</i>	<i>Zosterops spp.</i>

planations are the preference of these hummingbirds for the forest interior, which is poor in ornithophilous Compositae, or their curved bill, which is less suitable for accessing the disc florets.

Ornithophily includes certain features dictated by the morphological organisation of the capitulum. The flower heads are voluminous, up to 6 cm in diameter and never less than 2–3 cm across, solitary, robust, actinomorphic and mostly exposed in terminal, upright or transverse position. The form of their reproductive structures implies obligatory dichogamy and herkogamy with secondary pollen exposure (being mostly via a drag mechanism) with bundled, jointly exerted, stiff (partly lignified) polliniferous styles, spacious corolla tubes, voluminous nectaries with copious nectar (Fig. 6) and no scent. The prevailing colours of disc and ray florets – and often of the involucre – are scarlet, magenta and carmine, often combined with dark yellow, and plain yellow. The involucre is reflexed, forward-pointing or absent. These features facilitate approach and exploitation by birds, which sip nectar while perching or hovering and become dusted with pollen on their beak and surrounding plumage, on the chin or belly. Hummingbirds are able to switch rapidly from forward to backward flight when systematically screening the disc florets. Topics such as whether there are pronounced diurnal periods of activity, how long the capitula are in anthesis, the amounts of nectar production, the nectar quality etc. remain largely unknown. Flower-birds often try to exploit pseudanthia with the ‘wrong’ syndrome or hunt for insects in them, if no other ornithophilous plants are flowering locally. Migrant birds cross wide areas that lack their genuine hosts – for example hummingbirds returning from their summer territory in Canada, to overwinter in South America. As an example, Ruby-throated hummingbirds (*Archilochus colubris*) were observed to probe marigolds (*Calendula*) while resting in Indiana (HINE 1894).

The polliniferous style, an essential floral part in the Compositae, is characteristically modified in the ornithophilous representatives. In most species, they extend far beyond the limb of the florets and are often conspicuously coloured. They are stiffened through sclerotisation of the anthers or style (CARLQUIST 1957; PESACRETA & STUESSY 1996). The drag mode of proterandrous secondary pollen exposition is by far the most frequent (YEO 1993). Pollen is deposited on the distal part of the style in the bud and exposed by subsequent growth of the style out of the filament tube, enabling this complex to be used for

both pollen dispersal and acquisition. There is a tendency for flowers to keep their own pollen as far as possible away from the nectar. The tongues of birds (and bats) are moist and sticky, and thus unsuitable for pollen transport. Tight bunching of the long rod-like styles is typical for bird-pollinated Compositae: whereas insects will get trapped between them and remain out of reach of the nectar, birds can straddle the rods and reach the reward with their beak and tongue, thereby effecting pollination. The styles are often capable of negative geotropism to compensate for the skewed head positions. The change between male and female phases in a head (the latter by exposing the stigma lobes) often proceeds simultaneously in ornithophilous capitula. The common view is that capitula in the female phase do not secrete nectar, but this seems implausible, because it would reduce the number of visits and the amount of remnant pollen dispersed from such a head.

Exceptions to the predominant red and yellow signal colours include the purple *Barnadesia* and *Hololepis*. Signal colours are not restricted to the ray florets (as in *Mutisia*) or disc florets (as in *Echinops*, *Chresta*, *Cirsium* and *Sinclairia*), but often include the phyllaries, especially the inner ones (*Cnicothamnus*, *Chiquiraga*, *Glossarion*, *Stomatochaeta*, *Hyaloseris* and *Cirsium*), or the styles and stigmas (*Barnadesia*, *Arnaldoa*, *Stiffia* and *Mutisia*). In the heads of entomophilous Compositae the ligules of the ray florets are typically spread horizontally to help insects to alight. In bird-flowered Compositae, they do not serve this function; they are typically erect, recurved or absent. Many species live at high altitudes, especially in the Andes, where birds, including hummingbirds, can continue feeding during adverse weather conditions, but insect pollinators are scarce.

Nearly all evidence on the biology of the birds that pollinate Asteraceae remains anecdotal, and good luck remains indispensable for discovering new cases of ornithophily in the family or to study the behaviour of the floral visitors. A number of topics, however – such as the periodicity nectar secretion, nectar composition, the sequence of floret unfolding etc. – require thoroughly planned and patient investigations.

Chiropterophily. It seems that, until recently, no-one has asked whether any Compositae are pollinated by bats or other mammals. Bat-pollination and its association with a distinct floral syndrome was recognised much later than bird-pollination,

becoming evident only in the middle and late 20th century. In previous lists of bat-pollinated plants (e.g. VOGEL 1958 a,b; 1968 1969 a,b; DOBAT & PEIKERT-HOLLE 1985) the Asteraceae are missing. As shown above, the chiropterophilous syndrome does occur in the Compositae, although it is much rarer than the ornithophilous one. Historically, a first hint for bat-pollination was supplied by ALVAREZ & GONZÁLEZ-QUINTERO (1970) who screened the stomach contents of the flower bat *Anoura geoffroyi* and found 28% Compositae pollen.

17 species out of 9 genera are quoted above to be potentially pollinated by bats. They belong to 4 subfamilies and 5 tribes, respectively: Barnadesioideae (with the only tribe Barnadesieae), Stiffioideae (with the only tribe Stiffieae), Wunderlichioideae (tribe Wunderlichieae), Carduoideae (tribe Cardueae) and Asteroideae (tribe Astereae). Observations of bat visits relate to a single species only: *Gongylolepis jauaensis*.

The aggregate nature of the Compositae capitulum limits the plants' evolution to a rather narrow subset of the features seen in other (non-asteraceous) bat-pollinated plants. Above all, the 'gullet' type of flowers is absent, and the 'pincushion' type is predominant. The polliniferous styles are greatly elongated and take part in attraction. They are stiff, often being lignified, and negatively geotropic. Unlike in ornithophilous flowers, they are not tightly bundled but spread apart to form a more or less bouquet-like 'super-flower'. This arrangement intensifies and broadens the contact of the reproductive organs, either with the body's ventral surface in animals that crawl over the capitulum surface, or with the wings when hovering to feed. The ray florets are either absent or their ligules are reduced or upright. The floret tubes tend to be wide enough to accommodate the visitor's tongue. Dilute but plentiful nectar is produced in accordingly large nectaries, alongside sour, yeasty, musty or fruity odours – traits shared with other mammal-pollinated plants (see below). Bat-adapted composites have several traits in common with bird-flowers, such as head exposure, head size, robustness, nectar quantity and elongation of the polliniferous styles. It is therefore not surprising that some genera have evolved both the ornithophilous and the chiropterophilous syndromes or show transitions between the two.

Therophily. Mammals known to visit and pollinate flowers, either regularly or occasionally, include not only bats, but also terrestrial and tree-dwelling, non-flying groups such as rodents, insectivores and marsupials. The general mammal-pollination syndrome has been characterised more recently by REBELO & BREYTENBACH (1987). Despite their taxonomic diversity, the flying and terrestrial mammals share a small, mouse-like body, and their floral diet is usually nectar. The corresponding floral syndrome fulfils the animals' requirements and constitutes a fairly uniform biological pattern. It only varies in matching the airborne approach of bats and the terrestrial approach of the others.

Although this unity of floral traits allows us to group the taxa under a single syndrome, the recently recognised terrestrial visitors cannot be subsumed under 'chiropterophily', the term long used for bat-pollination. Therefore, some decennia ago the term 'therophily' has been proposed for the syndrome of pollination by non-flying mammals. Though the term is imprecise (as 'Theria' includes the Chiroptera in mammal classification) it is adopted here, as no term for non-chiropteran mammals is available and difficult to coin.

Pollination by non-flying mammals seems to be extremely rare in the Compositae. At present, only the genus *Oldenburgia* can be quoted to be potentially therophilous, and this even may apply only for two of the four species. Present knowledge is poor because mammal pollination takes place in the dark and is often much more fleeting than other modes of flower visits. Confirmation of predictions on the basis of the therophilous syndrome requires all the necessary equipment, an appropriate locality and extreme patience.

FINAL REMARKS

Examination of the colour plates should convince the reader that the presented examples of apparently bird-, bat- and non-flying-mammal-pollinated Compositae each reveal strong similarities despite their different taxonomic positions. Such a suite of floral similarities is known as a floral syndrome, with morphological and functional characters such as specific shape, size, colour, scent, nectar quality, accessibility, spatial position, activity period etc. These syndromes can be well characterised based on recurring combinations of characters and are unambiguously related to specific groups of pollinators, known as guilds. The syndromes are clearly based on functional traits, and possess significant predictive power. There are at least seven floral syndromes that recur, through convergent evolution, in taxa scattered all over the angiosperms, independently of the floral *bauplan* of the respective groups ('floral styles' in VOGEL 1954; 'floral modes' in ENDRESS 1994). They have been known for a long time and represent well-established concepts in floral ecology, although their nature and origin are still a matter of debate. The predominant current explanation is that they are the exclusive result of non-directional variation and natural selection. I have, however, raised fundamental arguments against the idea that the floral signatures have evolved solely through extrinsic forces. These arguments are summarised in VOGEL (1954, 2012) and should be considered in the context of the present paper.

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Autor(en)/Author(s): Vogel Stefan

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