Those flowers, also, which had their stamens and pistils placed, in relation to the size and habits of the particular insects which visited them, so as to favour in any degree the transport of their pollen from flower to flower, would likewise be favoured or selected.

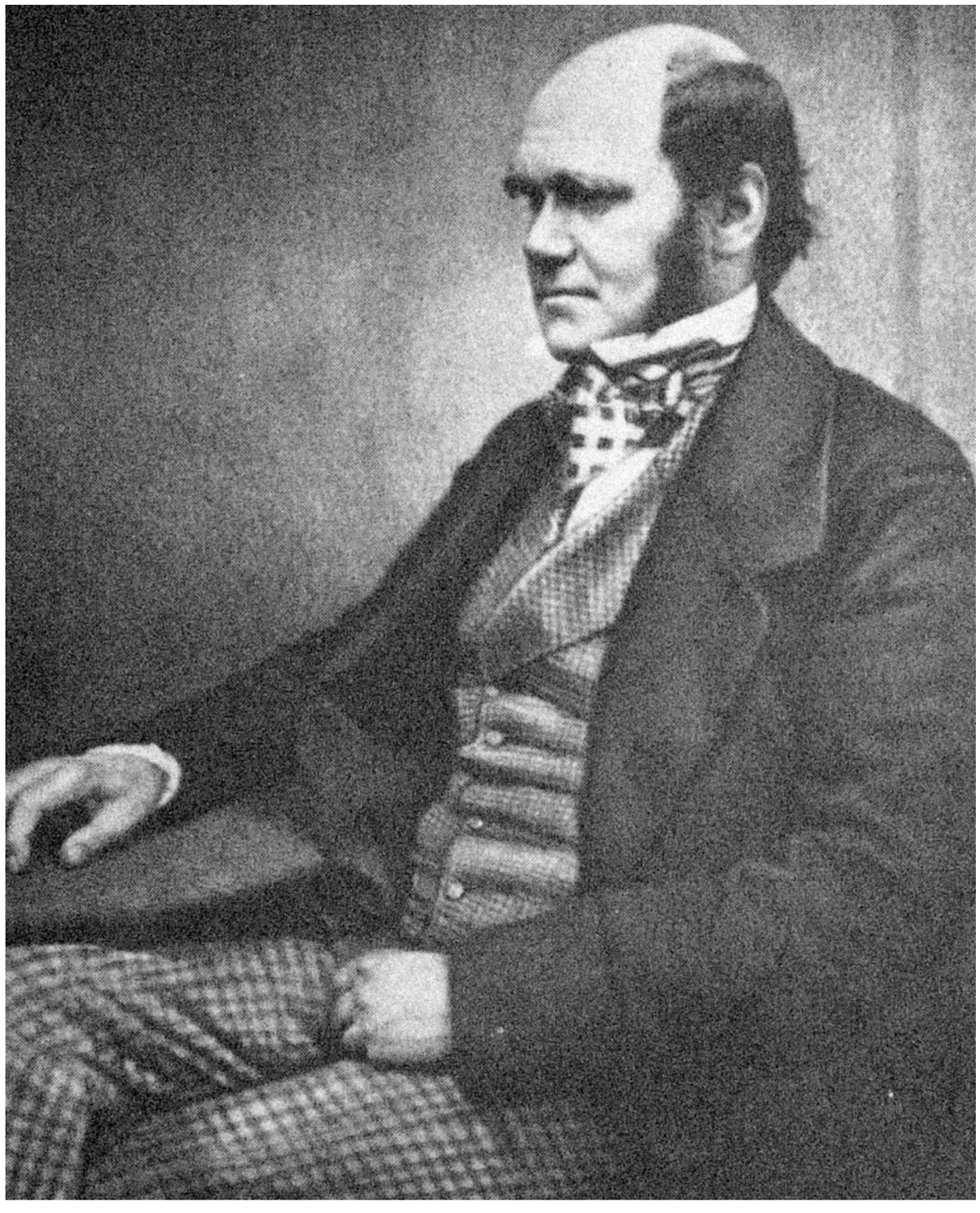
Charles Darwin (**1859**) The Origin of Species

Wednesday 8th Week Hilary Term

Organisms

timothy.walker@obg.ox.ac.uk

Angraecum sesquipedale whose pollinator was described by Darwin 20 years before it was discovered



BIOLOGICAL POLLINATION

i.e. animals

I can see no reason to doubt that an accidental deviation in the size and form of the body, or in the curvature and length of the proboscis, etc, far too slight to be appreciated by us, might profit a bee or other insect, so that an individual so characterised would be able to obtain its food more quickly, and so have a better chance of leaving descendants

Thus was born Pollination Biology and in particular Pollination Syndromes

Charles Darwin (**1859**)

Relationship between flower type & pollinator

Blossom type / **Function**	**DISH** (Tulip)	**BELL or FUNNEL** (Gentiana)	**BRUSH** (Proteaceae)	**FLAG** ((Pelargonium)	**GULLET** (Acanthus)	**TRUMPET** (Lonicera)	**TUBE** (Aloe)
Origin of the visual attraction	All perianth segments	Corolla or other parts of perianth	All perianth segments	Standard petal	Lips	Margins of the perianth segments	Perianth segments plus the tube
Alighting point	Anywhere	Central	Anywhere	Horizontal lower petals	Lower lip	Anywhere around the edge	None
Guiding devices for pollinator	None	Some lines	None	Symmetrical marks on vertical petal	Structure of the lower lip	Lines into the centre of the tube	Only one route
Display of the attractant	Open to all comers	Half hidden but central	Open to all comers	Well hidden	Well hidden	Hidden	Deeply hidden
Pollen deposition	Randomly inside flower	Centrally inside flower	Randomly outside the inflorescence	Accurately in side the flower	Accurately in side the flower	Centrally inside flower	Accurately Inside the flower
ADAPTED FOR WHAT?	**BEETLES & other primitive**	**BEES & other crawlers**	**BEES, BIRDS BUTTERFLIES *Et al* with long mouth parts**	**BEES who can alight & force an entry**	**BEES who can alight & force an entry**	**BUTTERFLIES**	**MOTHS, BIRDS & hoverers**

BEETLE POLLINATION

open, disk shaped flower (clockwise) *Magnolia acuminata*, *Calycanthus floridus* & *Cistus ladanifer*. A robust flower because beetles are clumsy

Cycad gorge in central Australia

Cycad gorge in central Australia

Female cones of *Macrozamia reildleri* being pollinated by weevils

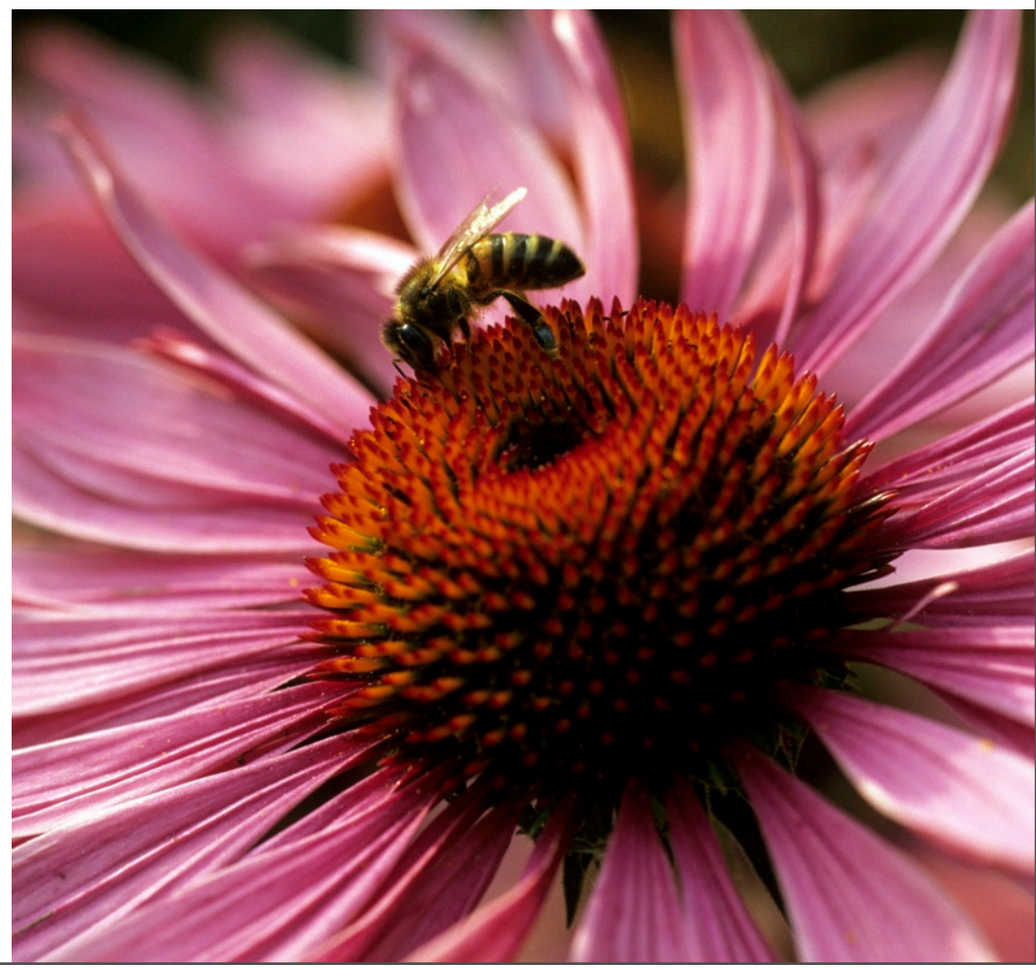
Biting midges –
Ceratopogonidae

BEES

BEE POLLINATION

many & varied flower types (clockwise)

Allium, *Echinacea* & *Eryngium*



Bees often pollinate flowers that are bell shaped or gullet-shaped e.g. *Acanthus* (right) & *Gentiana sino-ornata*

BEE POLLINATION at Cape St Vincent (clockwise) *Antirrhinum*, *Coronilla* & *Lithodora*. In all of these some form of forced entry is required

MOTHS Night flowering cactus *Selenocereus grandiflorus* (left) & night scented *Brugmasia knightii* (below)

British native honeysuckle (*Lonicera periclymenum*) is heavy scented at night to attract night flying moths

Butterflies visiting *Erysimum* (above) & *Ageritina*

A visit from an animal may not result in pollination

Comparing moth & butterfly pollinated flowers

Butterflies	***Butterfly flowers***	***Moths***	***Moth flowers***
Active during the daytime	Pollen released during the day and no closure of the flowers at night	Nocturnal	Pollen released at night, flowers often closed during the day or lasting just one night
Weak olfactory sense	Weak odour and agreeable	Strong olfactory sense with instinctive preference	Strong heavy-sweet perfume at night
Well developed visual sense for shape & colours including red	Vividly coloured, including pure red	Visually sensitive to colours at night	Mostly white or pale colours, but may be red, drab or insignificant
Do not perceive deeply dissected contours	Rim of perianth segments not dissected	Visually sensitive to dissected outlines	Deeply dissected, notched, grooved or fringed perianth segments
Land on the flower prior to pollination	Flowers held erect with the rim generally flat but narrow. Flowers actinomorphic & anthers fixed in position.	Hover in front of the flower during pollination	Flowers held horizontally or pendent without a rim or if present bent back. Flowers sometimes zygomorphic due to bending back of lowest petal and anthers versatile
Long & thin proboscis	Nectar at the base of a long, narrow tube or spur	Very long, thin proboscis	Nectar at the base of very long, narrow tubes or spurs (narrower than those on bird pollinated flowers)
Metabolic rate not very high and a less active flier	Ample nectar	Very high metabolic rate and active fliers	More nectar than butterfly or bee pollinated flowers
Prefer some guidance of the proboscis	Groove on petal acts as mechanical tongue guide, or simple lines	Prefer some guidance of the proboscis	Petals contoured to give guidance

BIRDS – Bird pollinated flowers are often red, tubular and full of nectar e.g. *Tecoma stans* (top right); *Erythrina crista-galli* (bottom right) produces more an 1cc of nectar per flower

Birds are very delicate pollinators

Anigozanthos manglesii state flower of Western Australia. After one flower has been pollinated it bends to the side to clear the path to the next flower

Duabanga taylori (top right) pollinated by **BATS.** Robust flowers with a musty smell, held of the edge of the tree or on a very long stalk such as *Agave* (below)

This *Agave ferox* as the Botanic Garden was planted in 1894 and flowered in 1996.

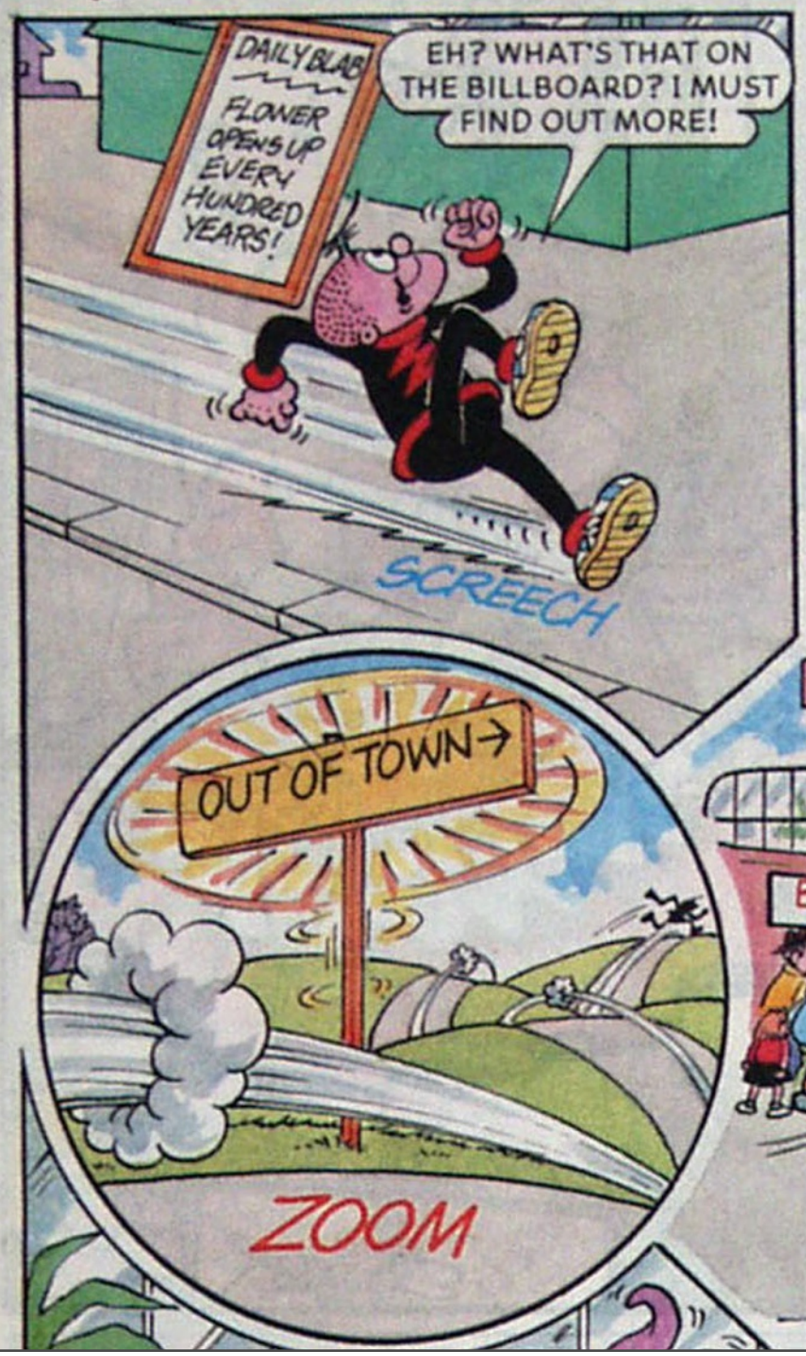
The queue to view the *Agave ferox* in flower

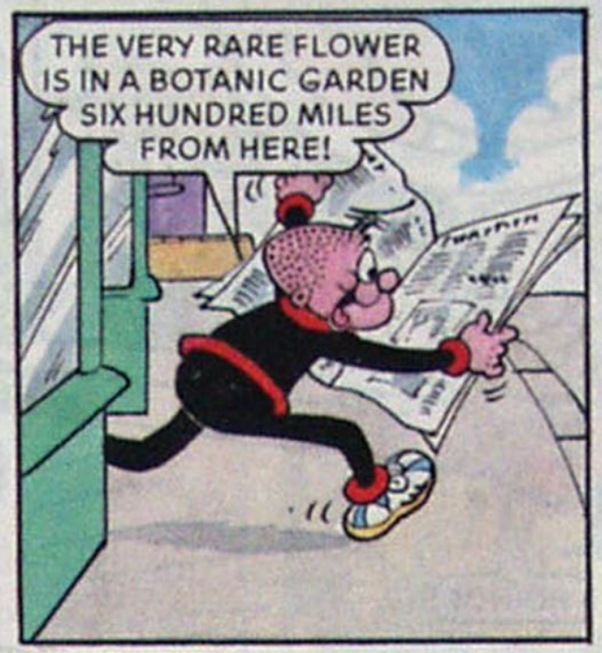
Tuesday, 16 April 2013

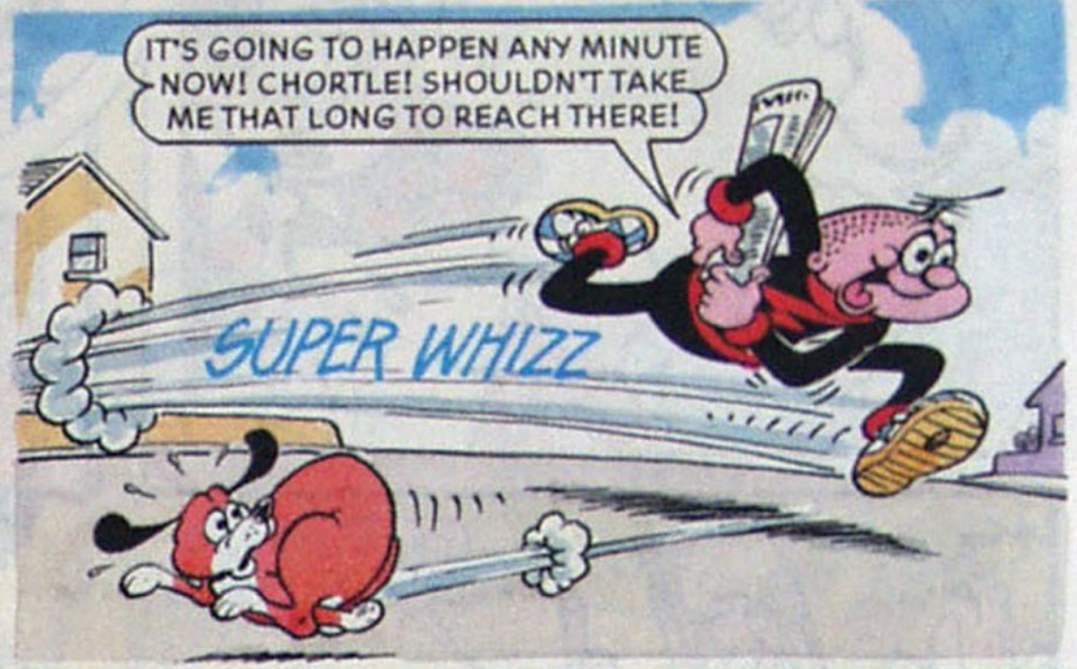
It even made the Beano

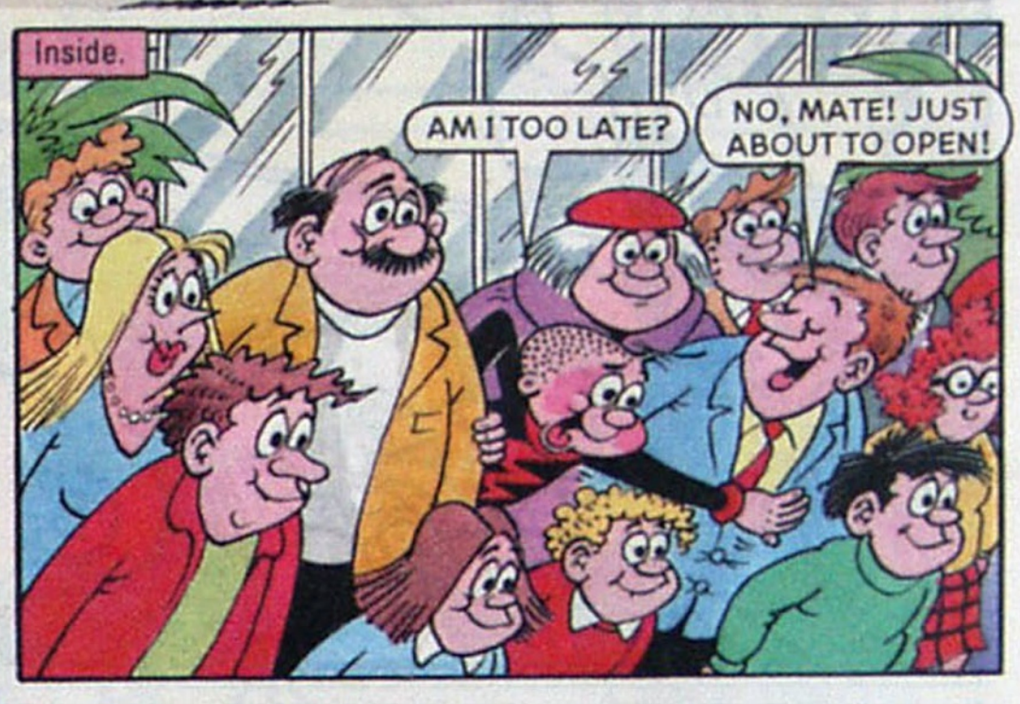
EVERY THURSDAY ★ ★ ★ ★ THE BEANO ◆◆◆◆ JANUARY 11th, 1997

BILLY WHIZZ









Bird pollination compared to bat pollination

Birds that pollinate	*Bird flowers*	*Bats that pollinate*	*Bat flowers*
Active during the daytime	Pollen released during the day and no closure of the flowers at night	Nocturnal	Pollen released at night, flowers often lasting just one night
Weak olfactory sense	Odours absent	Strong long-distance olfactory sense with preference for stale odours	Strongly scented at night with a stale smell similar to a brewery
Well developed visual sense especially for red but not UV	Vividly coloured and often scarlet or reminiscent of a parrot with contrasting stripes	Visually sensitive for near orientation but colour blind	Sometimes white or creamy but often drab, greenish or purplish
Large for a pollinator and great consumers of food	Nectar very abundant with a capillary system that brings the nectar to a drinkable position but preventing it from flowing out of the flower	Relatively large pollinators with a strong metabolism and pollen as the bats' sole source of protein	Exceedingly large volumes of nectar plus large quantities of pollen from large & numerous anthers
Too heavy to land on the flower prior to pollination and with a hard, long bill	Flowers without a lip or if present bent back. Flowers tubular sometime pendent Hard flower with united filaments and well-protected ovaries. Flower tube or spur wider than in butterfly flowers	Land animals that cling with thumb claws. Short nose & tongue	Large mouthed, robust single flowers often in strong inflorescences with many flowers
Nectar guides absent	Intelligent & good at finding access to nectaries	Sonar system makes flight in foliage difficult	Flowers held outside the foliage or on bare stems

POSSUMS often pollinate the flowers of banksias in Australia

FLIES – flies are unspecialised pollinators

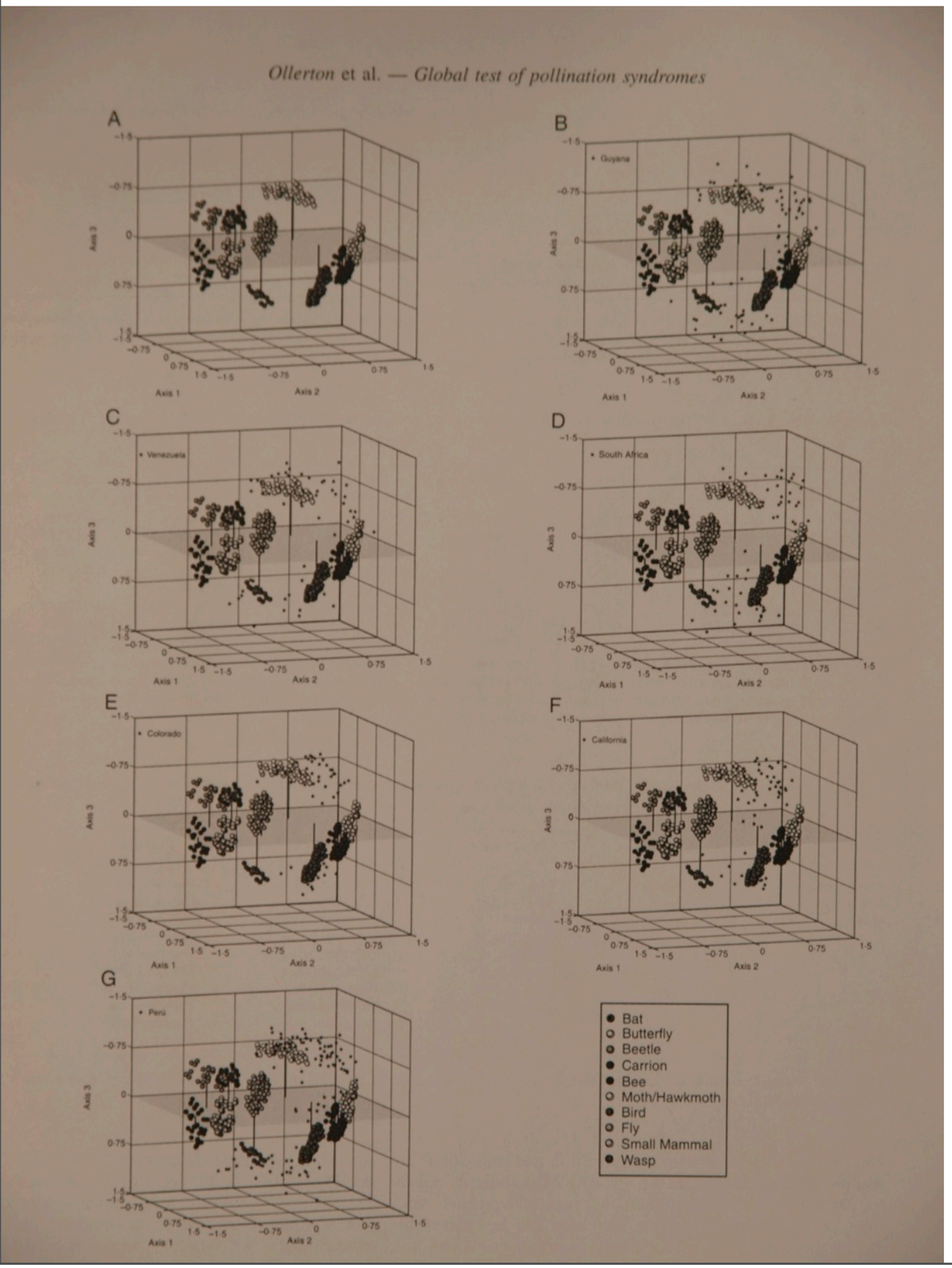
Thalictrum (below) is typical of the unspecialised flowers pollinated by flies

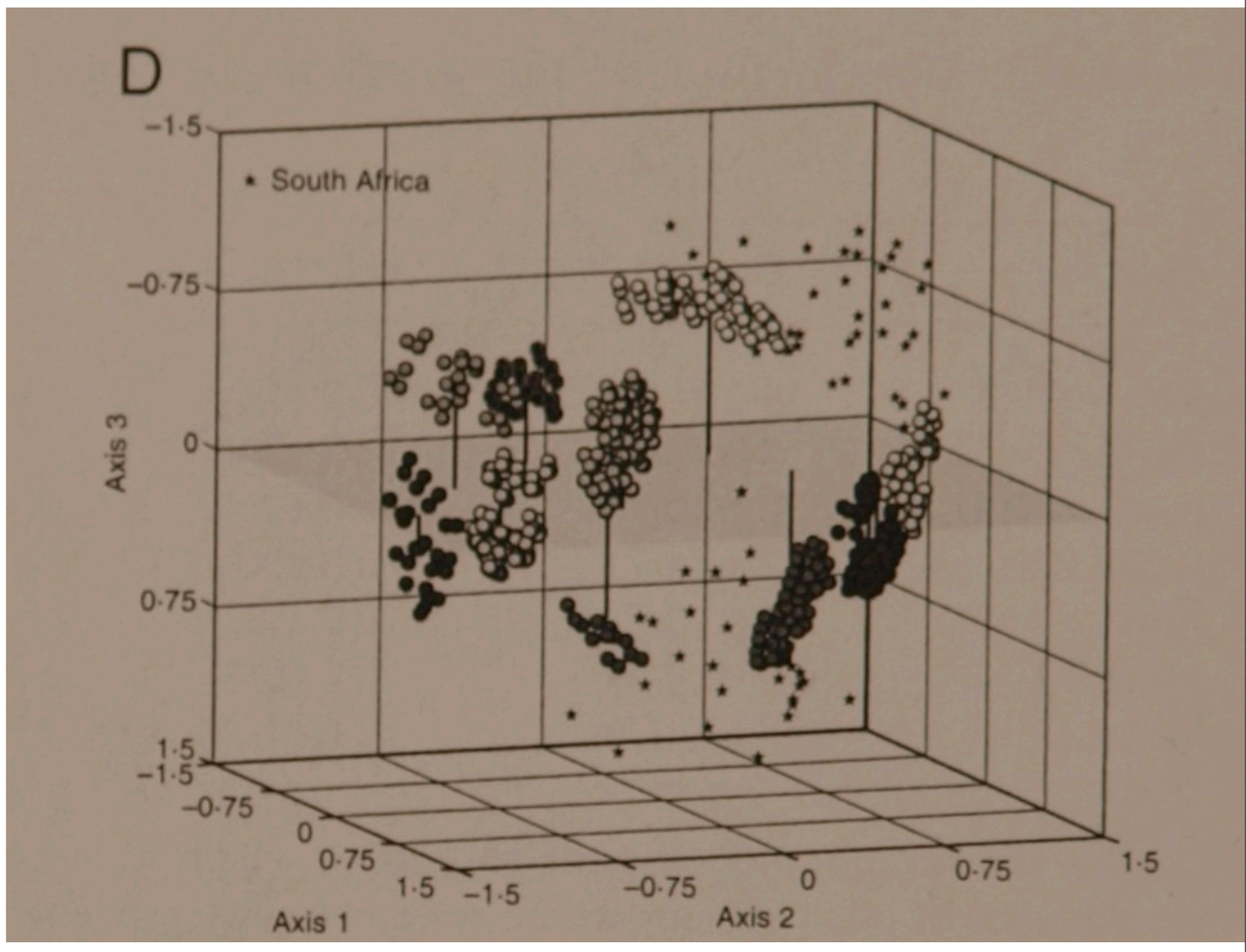
MOLLUSCS – not the fastest method of pollination and sometimes maybe only visitors

Hakea being pollinated by a bird in central Australia

Do pollination syndromes really exist?

Ollerton et al (2009)





And yet *Barnadesia caryophylla* - a member of the daisy family (Asteraceae) flowering at the Botanic Garden today is pollinated by .....?

Thus I can understand how a flower and a bee might slowly become, either simultaneously or one after the other, modified and adapted in the most perfect manner to each other, by the continued preservation of individuals presenting mutual and slightly favourable deviations of structure.

Charles Darwin (1859)

So does pollinator behaviour drive speciation?

Not always:

Ollerton et al (2009) showed rapid diversification in *Ceropegia* without evolutionary shifts in pollinator functional specialization. These flowers are visited by a wide range of small Dipteran flies

Can generalist (unspecialised) flowers actually be selective? (Ollerton 2007)

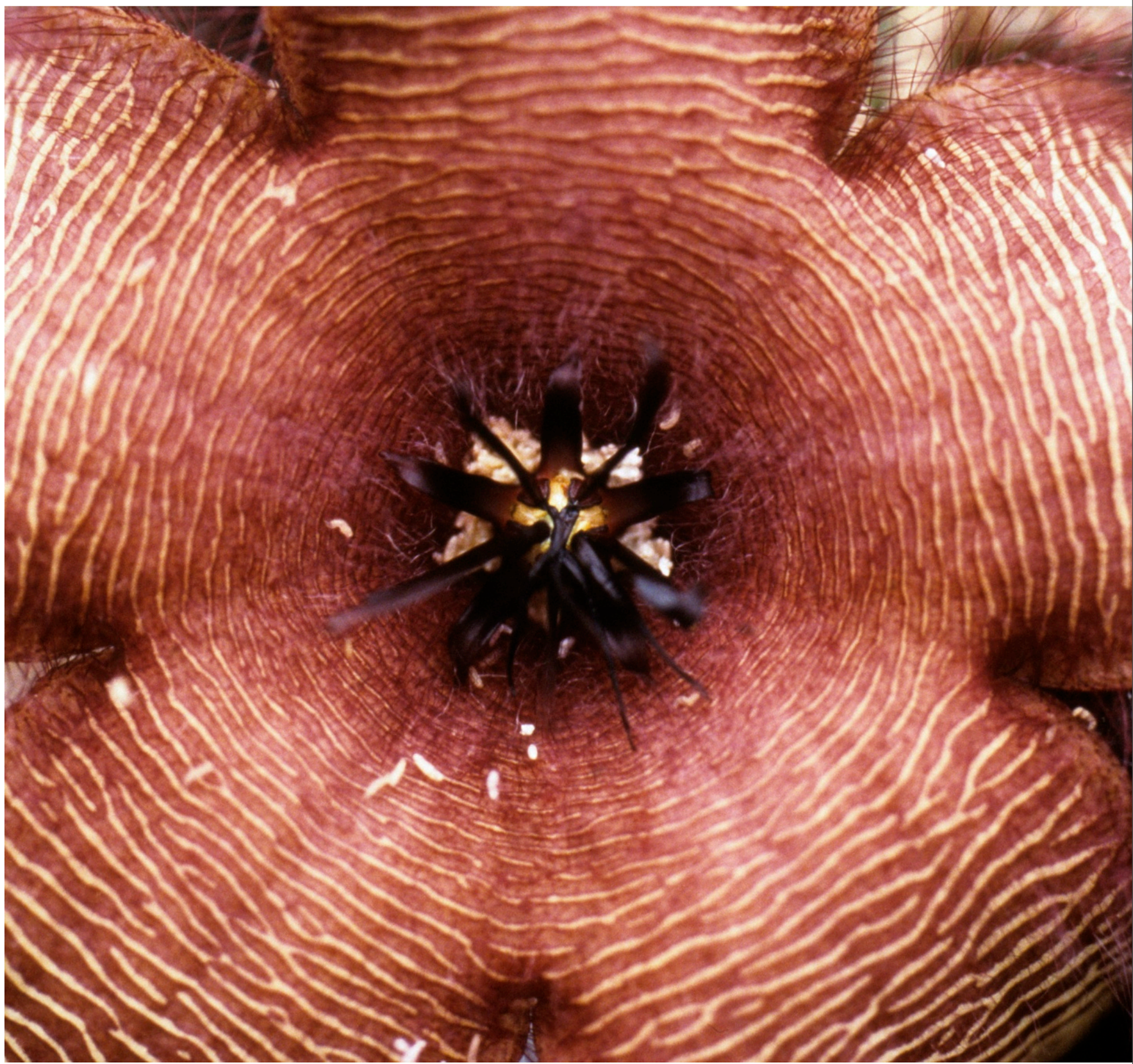
- Some open access flowers **are** in fact visited & pollinated by a wide range of animals
- Some open access flowers actually **only** attract a narrow range of pollinators
- Some flowers attract a wide range of pollinators but are only pollinated by a few of the visitors
- Some flowers appear to display a pollination syndrome but are in fact visited by a wide variety of animals
- Some species have flowers that are visited by different pollinators in different parts of their ranges.
- **"the relationships between flowers and pollinators are much more ecologically and phylogenetically complex than previously imagined"**

ATTRACTION & REWARD

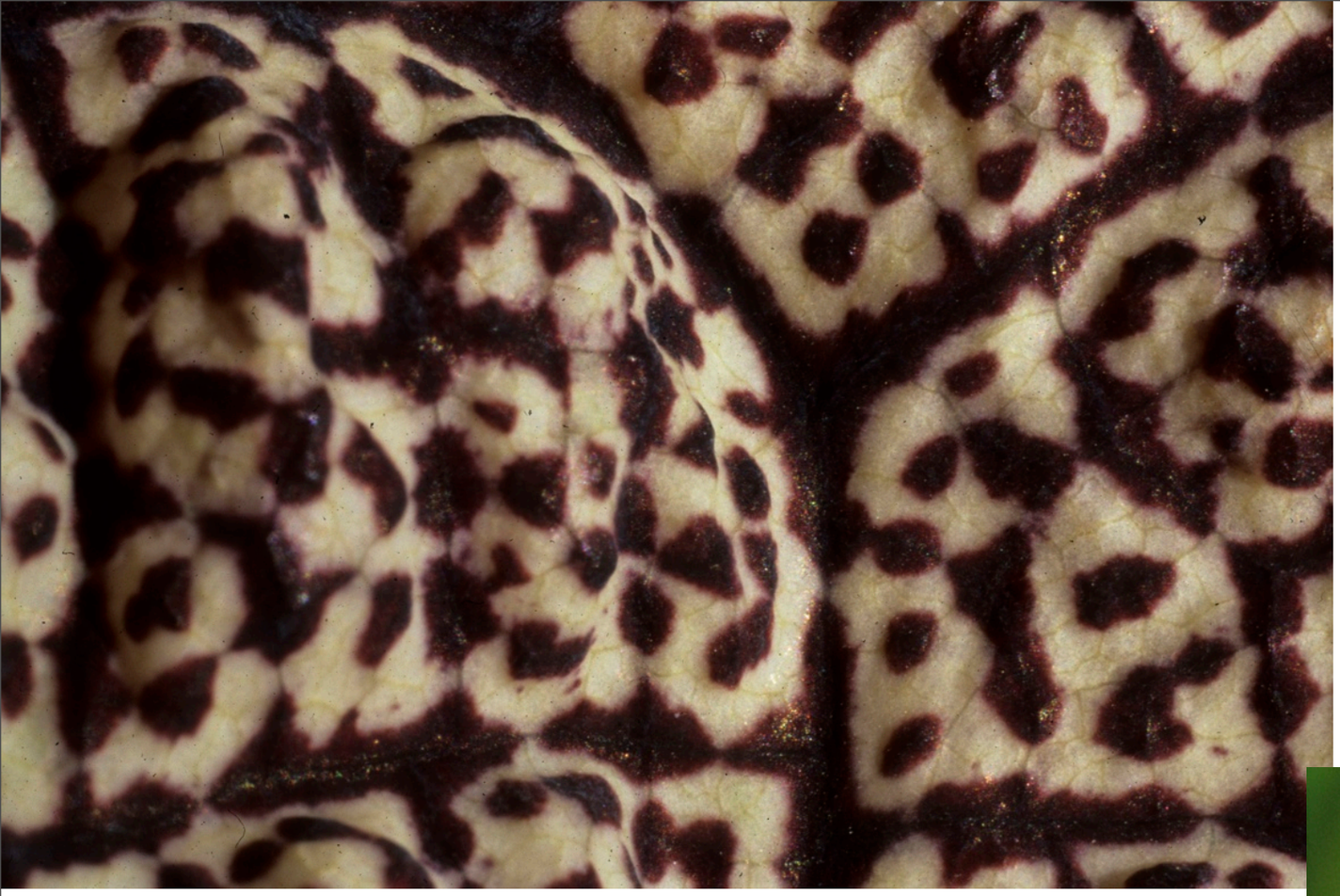
ATTRACTING A POLLINATOR

Hoodia has flowers that smell like a festering nappy. Attraction & reward is a strategy that is open to abuse as a result of mimicry and no reward.

Maggots in the flower of *Stapelia* laid by the pollinating fly



Attraction may be through visual signals and/or scent



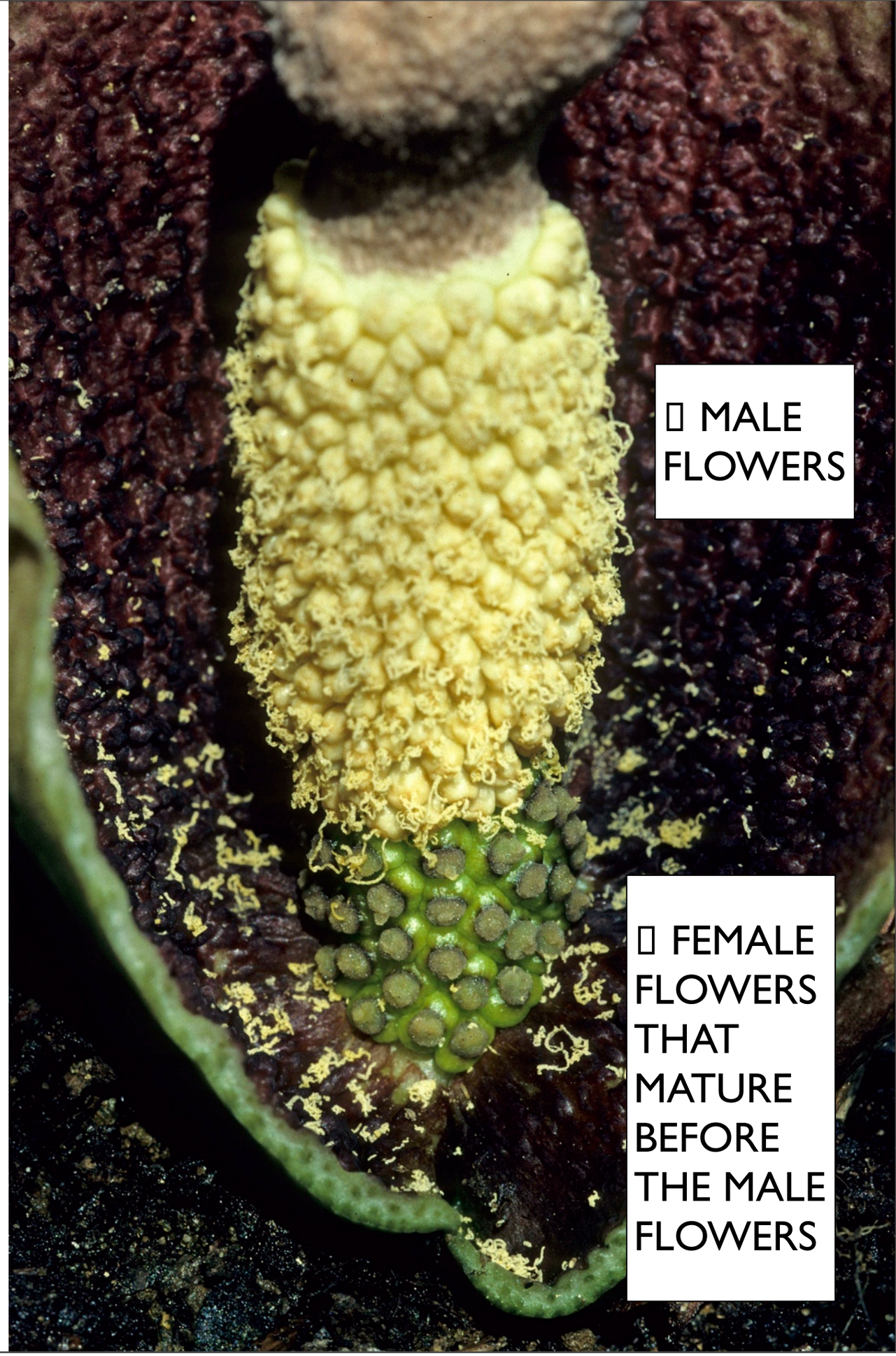
Some *Aristolochia* species (above) use both scent & visual signals. If the attraction is purely visible then the pollinator approaches in a straight line but visual stimuli may not always be visible to the human eye e.g. bees see UV colours

When the attraction is scent then the pollinator approaches in a zig-zag path.

Scents do not have to appeal to humans – this is *Helicosideros muscivorous* a.k.a. the dead horse arum

Dracunculus vulgaris
with a purple, petaloid
spathe & shiny spadix
at the base of which
are the flowers

Flies are attracted to the inflorescence by the foetid scent. This scent is amplified by the burning of lipid to raise the temperature by up to 20ºC above ambient. The flies bring pollen from another plant that the deposit on the receptive female flowers. They often find a mate inside the warm spathe. When the scent is turned off by the plant the flies leave and a dusted with pollen from the now mature male flowers



REWARDS

Brood chamber e.g. *Yucca*: night flying moths are attracted by scent. The female moth scales the stamen & collects the putty-like pollen. She lays eggs only in locules that are developed to right stage and between laying each egg she climbs up the style and it puts some pollen on the stigma to ensure that the flower does not abort & thereby ensuring that the fruit grows. The egg is sustained by a gall-like growth. Larvae emerge with the uneaten seed. Yuccas are protogynous so out breeding is more likely.

Each species of fig is pollinated by a specific wasp whose life cycle is intimately integrated with the syconium

Winter: the syconium has male flowers near the ostiole and neuter flowers at the base. A female wasp lays eggs in the neuter flowers & dies. The concentration of CO_2, O_2 & ethylene stimulates the emergence of male flies (wingless, blind & legless) that bore into the neuter flowers containing the female wasps. The male dies after mating. The young females emerge from flowers through holes bored by males and leave the syconium past male flowers collecting the pollen as they exit

June: now the syconium has no male flowers but fertile female flowers with long styles & neuter flowers with short styles. The now mature female wasps lay eggs in neuter flowers only because the length of the styles of the fertile flowers prevents the ovipositor reaching the ovules. Again the concentration of CO_2, O_2 & ethylene stimulate the emergence of male (wingless, blind & legless) that bore into the neuter flowers that contain the female wasps. The male dies after mating but the females emerge & fly away.

Autumn: The syconium now has just just neuter flowers. The female wasp lays eggs that hatch into only females that fly. These then force entry into the winter syconium. During the struggle to enter they loose their wings & legs but this enables the fig to select the right species of wasp

Nectar is a common reward for a wide variety of pollinators
e.g. *Brownea & Mahonia*

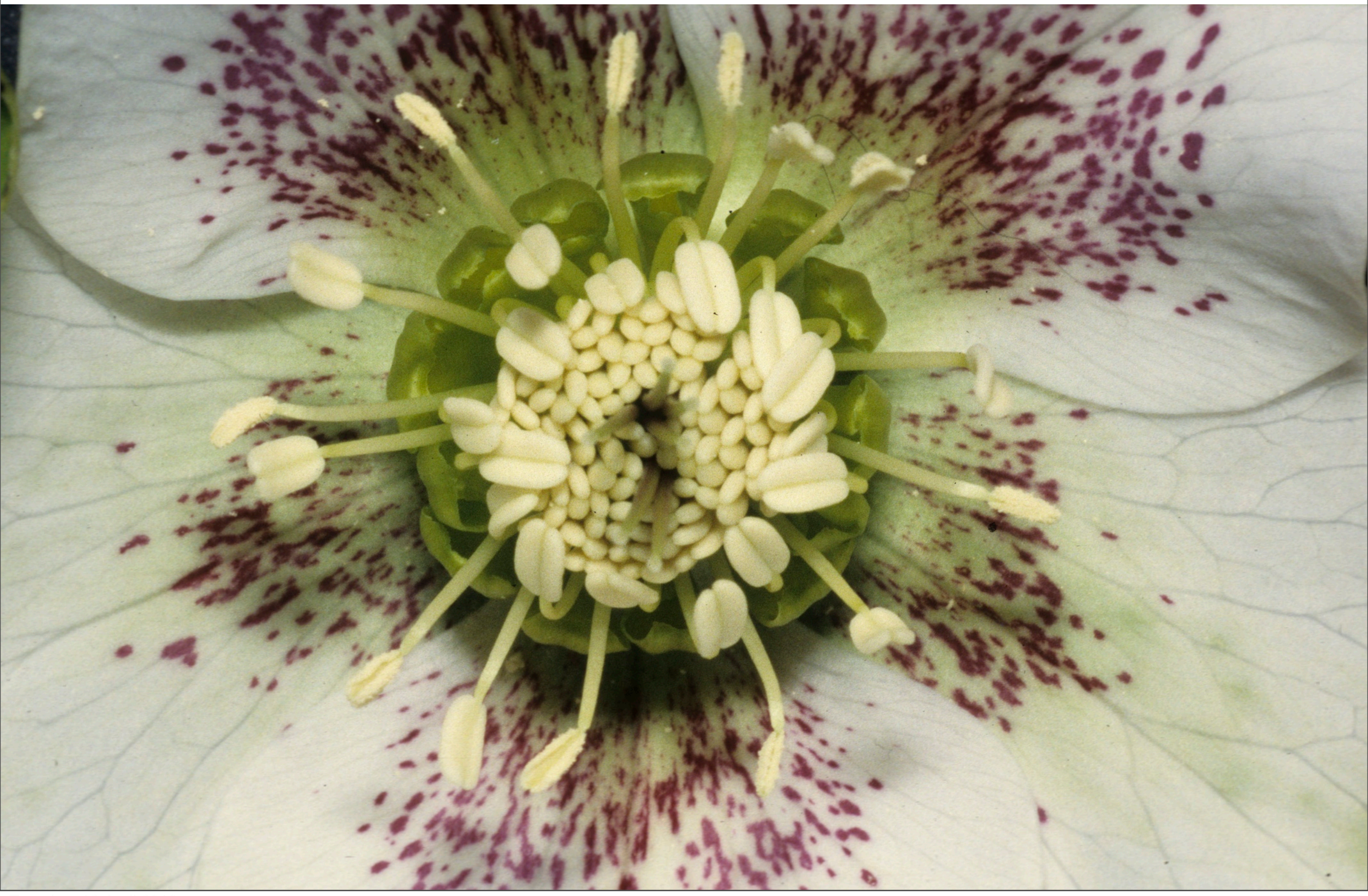
Tuesday, 16 April 2013

Tuesday, 16 April 2013

Tuesday, 16 April 2013

Romneya coulteri provides pollen as a reward because pollen is very nutritious 30% protein, 15% sugar, 10% fat & 7% starch

Helleborus orientalis provides both **nectar & pollen** as reward



Victoria amazonica Day One flower when the stigma is receptive (protogyny): it is scented with rewards of **nectar, starch bodies & brood chamber**

Victoria amazonica
Day Two flower when the stigma is no longer receptive but the stamens are shedding their pollen.

Graham Stone et al. carder bee watching in the Botanic Garden. *Stachys byzantina* hairs are eaten by male solitary carder bees but the flowers are pollinated by female solitary carder bees

ENTRAPMENT –
Coryanthes macrantha

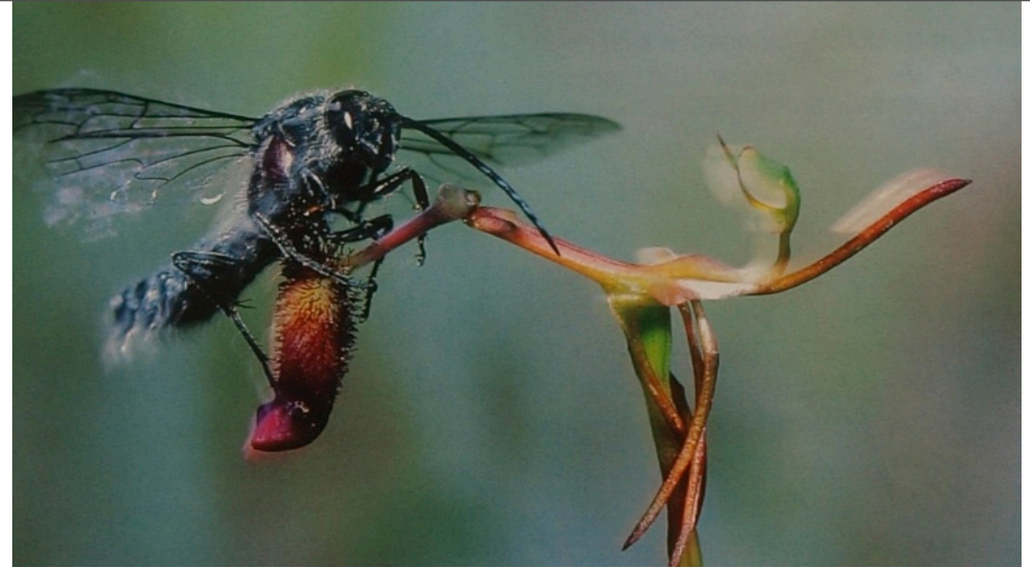
PSEUDO-COPULATION The mirror orchid (*Ophrys speculum*)

Tuesday, 16 April 2013

The mirror orchid flower is preferred over a female bee by 9 out of 10 male bees

Drakea gracilis from Western Australia

Drakea gracilis from Western Australia



Drakea gracilis from Western Australia

MIMICRY

Bellevalia forniculata (left) produces a scent and nectar as a reward.

Dactylorhiza umbrosa (right) just produces the scent.

These facts alone incline me to believe that it is a general law of nature (utterly ignorant though we be of the meaning of that law) that **no organic being self-fertilises itself for an eternity of generations.**

Charles Darwin (**1859**)

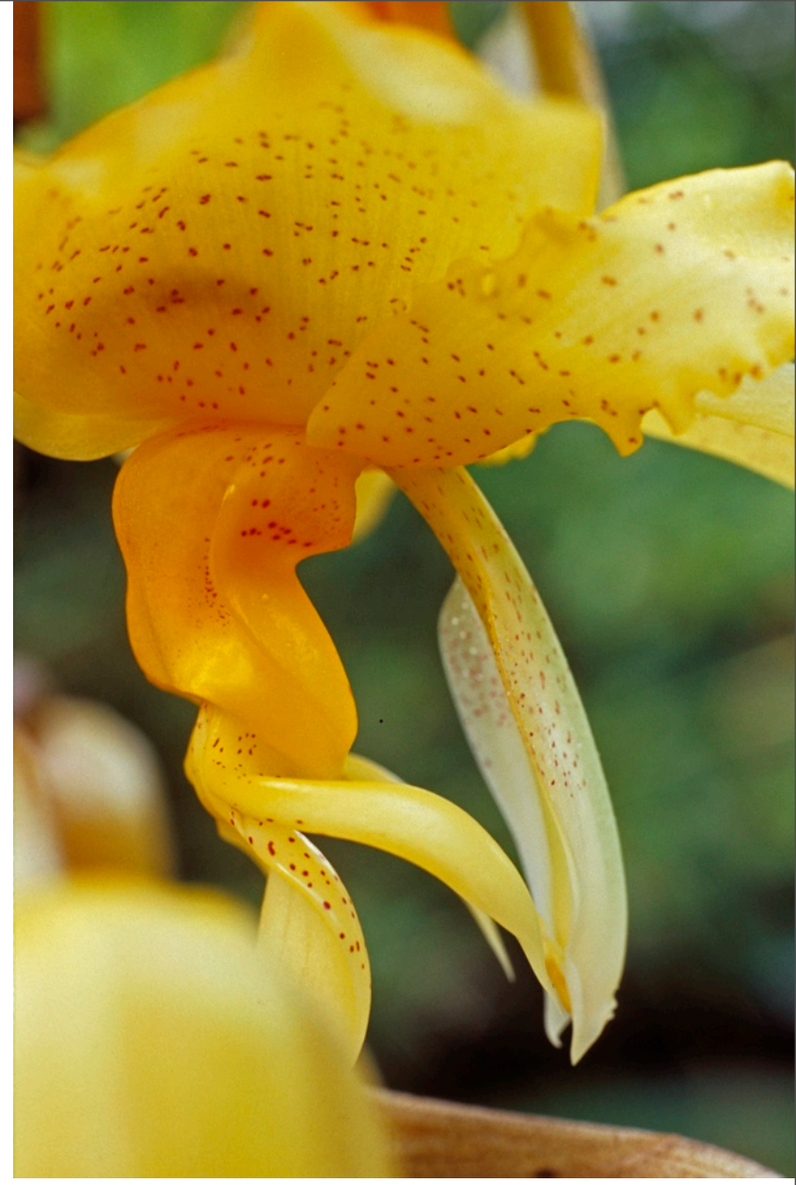
So most plants go to a lot of trouble to promote out breeding but reproductive assurance is Good Strategy

Clianthus puniceus from New Zealand has a protective sheath on its stigmatic surface for the first part of the flowering season. This prevents self pollination but it is rubbed away by a visiting, pollinating bird. If no birds visit the flower then the sheath dries and sloughs off towards the end of flowering to facilitate self pollination.

SO WHAT?

ECONOMIC reasons for understanding pollination. One-in-six crops is pollinated by bees with implications for the application of pesticides.

Cotton is genetically modified to provide systemic resistance to stem boring caterpillars reducing the need to spray pesticides



Brazil nuts are pollinated by the same bees that require other species. *Stanhopea* is the alternative food source for this euglossine bee that pollinate brazil nut trees

Despite being wind pollinated maize has pollen that does not travel far and GM pollen is unlikely to fly more than a mile

PLANT CONSERVATION requires an understanding of the needs of endangered species.

Serapias lingua is pollinated by a species of bee that sleeps in the flowers over night.

Banksia gardneri is pollinated by ground dwelling possums that are threatened by introduced rats, cats & foxes

Platanthera a threatened species of orchid from the USA that is pollinated by hawkmoths that have disappeared

Encephalartos ferox

Tuesday, 16 April 2013

Tuesday, 16 April 2013

Tuesday, 16 April 2013

Successful alien, invasive weed species often have unspecialised pollination syndromes e.g. *Clematis vitalba*