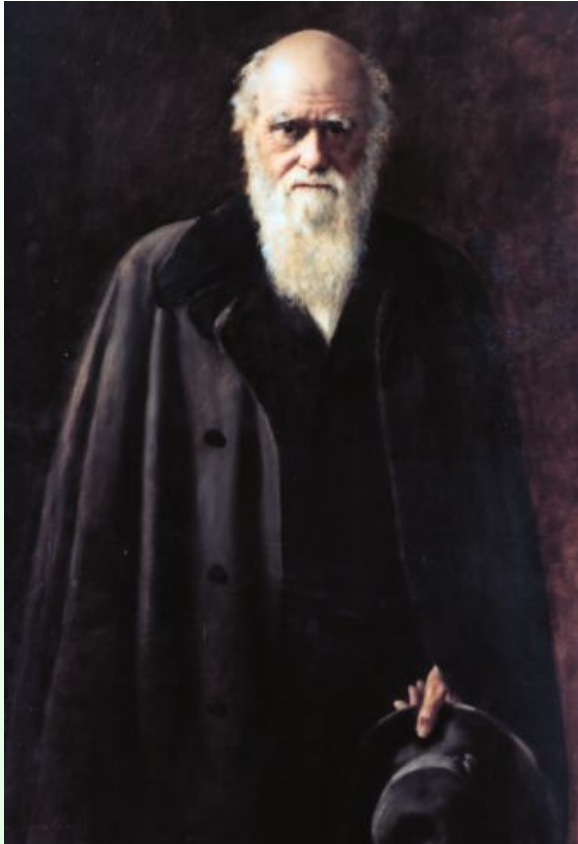




***Darwin's legacy: the
form and function
of flowers***





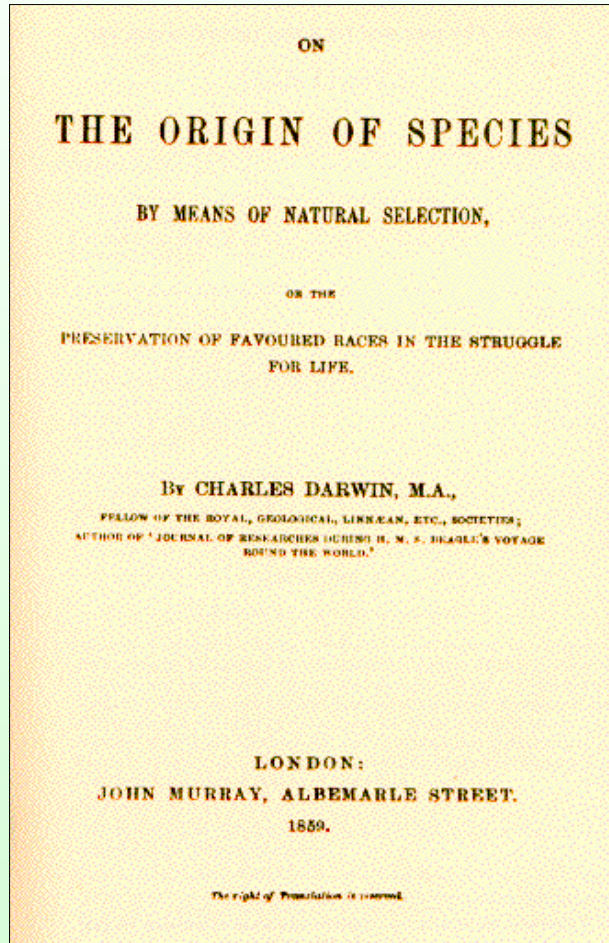
Darwin



Wallace

- First comprehensive theory of evolution
- Co-discoverer with A.R. Wallace of the chief mechanism of evolution - **Natural selection**

The Origin of Species (1859)



Two basic ideas

- All organisms have descended with modification from common ancestors
- The major agent of modification is natural selection operating on variation among individuals within populations

Darwin the Reluctant Botanist



‘Flowers are not only delightful for their beauty and fragrance, but display most wonderful adaptations for various purposes’

Darwin 1878



Darwin's Botanical Works

After '*The Origin of Species*' Darwin wrote six books on botanical topics

- 1862 '*On the Variances Contrivances by which British and Foreign Orchids are Fertilised by Insects*'
- 1865 '*The Movements and Habits of Climbing Plants*'
- 1875 '*Insectivorous Plants*'
- 1876 '*The Effects of Cross and Self Fertilisation in the Vegetable Kingdom*'
- 1877 '*The Different Forms of Flowers on Plants of the Same Species*'
- 1880 '*The Power of Movement of Plants*'

Plants were also covered extensively in:

- 1868 '*The Variation of Animals and Plants Under Domestication*'

Darwin's Botanical Mentor - Rev J.S. Henslow



- Darwin took courses from Henslow at Cambridge
- Henslow recommended Darwin to Fitzroy for HMS Beagle
- Darwin sent all plant specimens he collected on voyage to Henslow
- Henslow emphasized importance of sampling variation within species
- Darwin collected more than 7000 plant specimens





Charles Darwin at 31

Darwin turns to plant sex

- 1836 Beagle returns
- 1839 marries Emma Wedgwood
- 1842 moves to Down House, Kent

“During the summer of 1839...I was led to attend to the cross-fertilisation of flowers by the aid of insects”

A photograph of Down House, a large white Georgian-style mansion with a blue roof and two chimneys, set in a lush green lawn with large trees. A person is visible running on the lawn in the foreground.

***'Plant Reproductive
Biology Central'***

Darwin's Home - Down House (1842 - 1882)

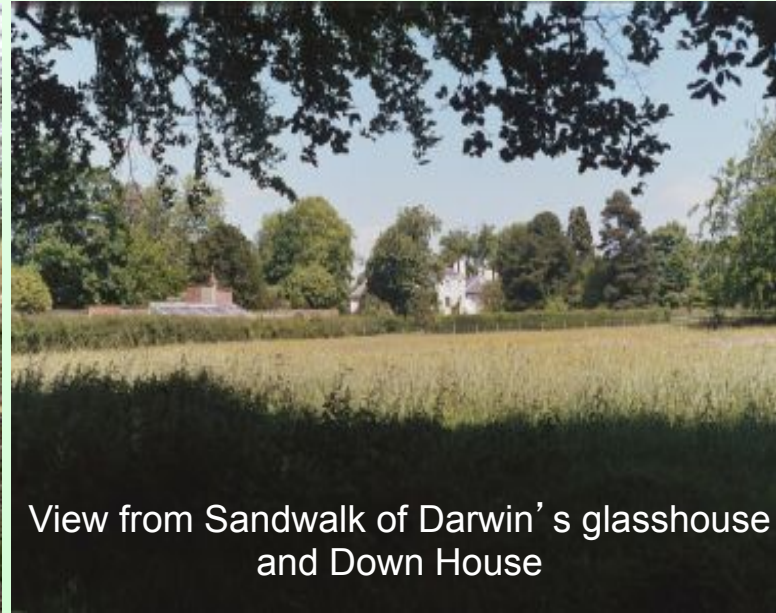




Darwin's study



The Sandwalk – Darwin's thinking walk



View from Sandwalk of Darwin's glasshouse and Down House

Why did Darwin devote more of his life to studying plants than any other group of organisms?

- Family interest and influential mentors John S. Henslow and Joseph D. Hooker
- Easy to observe at Down House, able to obtain seeds & preserved flowers from his many correspondents
- Plants easy to grow and manipulate, facilitating experimental tests of his adaptive hypotheses
- Not just curiosity, appealed to Darwin's practical side - numerous early articles in *Gardener's Chronicle*

Geissorhiza radians Iridaceae
Western Cape, South Africa



*Genetic variation within
populations*

Coevolution of Orchid Flowers and their Pollinators



- Orchid from Madagascar with exceptionally long (30cm) floral tube
- Darwin predicts its pollinator should have proboscis long enough to reach nectar
- Prediction correct - hawk moth discovered 41 years later in 1903



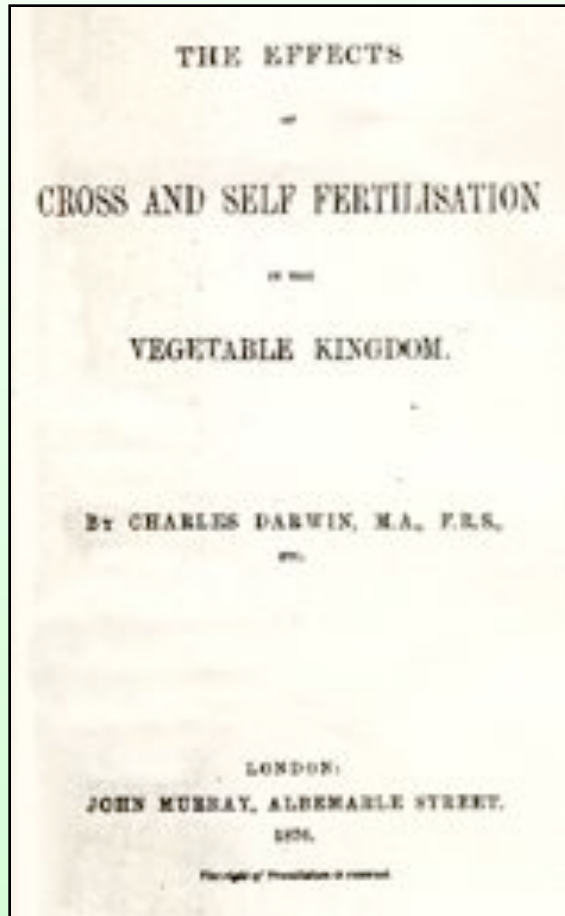
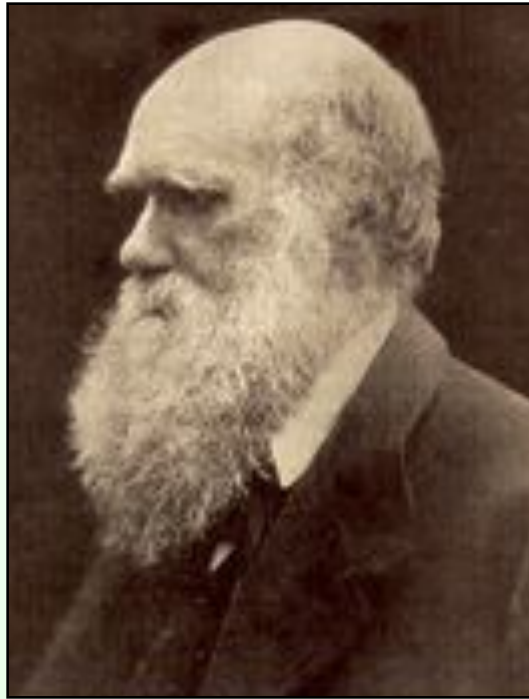
Darwin's Dilemma - Most flowering plants are hermaphroditic but 'nature abhors perpetual self-fertilization'

Female

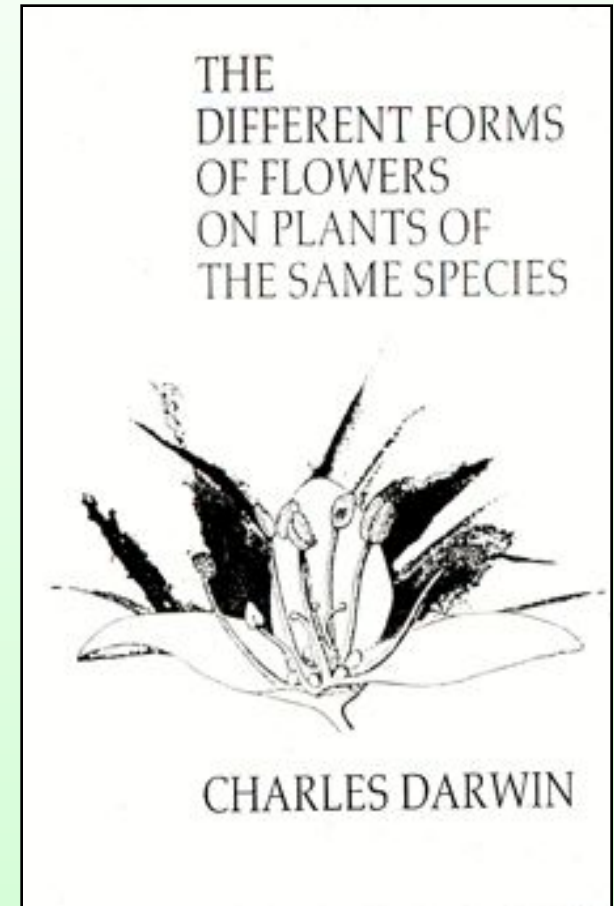
Male

Lilium humboldtii



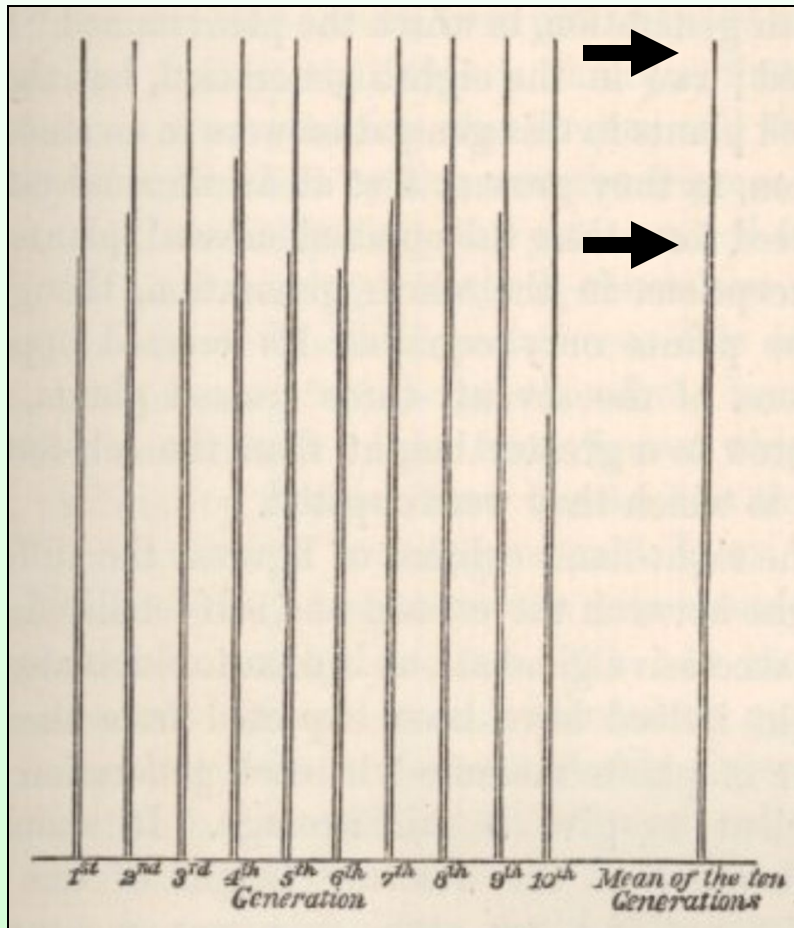


***Darwin's
fascination
with inbreeding
& outbreeding
in plants***





Darwin the Experimentalist : Long Term Study of Inbreeding in Morning Glory (Ipomoea)



- Conducted 10 generations of controlled cross- and self-pollinations
- Compared the height of plants from the two pollination treatments
- Obtained clear evidence that selfed offspring performed less well

First comprehensive analysis of inbreeding depression in plants

The genetic consequences of inbreeding

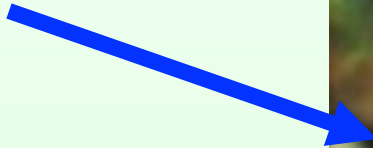
- Genotypic frequencies changed
- Allele frequencies unchanged
- Heterozygosity reduced by 50% per generation with self-fertilization
- Homozygosity for deleterious recessive alleles results in inbreeding depression

Inbreeding depression

- The reduction in fitness of inbred offspring in comparison with outcrossed offspring
- Manifested by reductions in viability (survival) and fertility (reproductive output)
- Strong inbreeding depression favours survival of outbred offspring thus favouring outcrossed mating systems

Evolution of Separate Sexes - Dioecy

Female



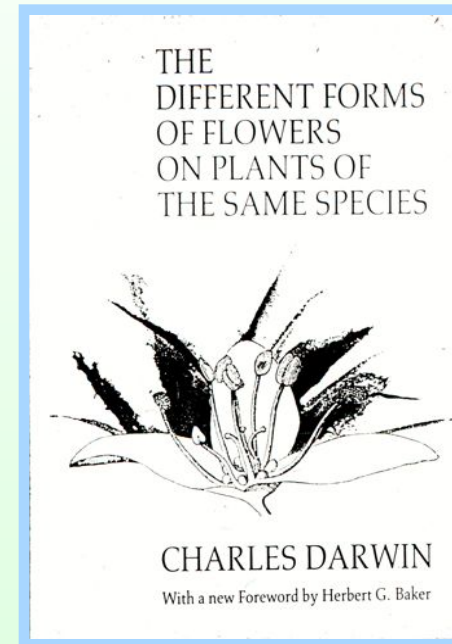
Wurmbea dioica

Male



But dioecy rare in flowering plants ~ 6-7% species

Outcrossing Mechanisms and Floral Function



“I do not think anything in my scientific life has given me so much satisfaction as making out the meaning of the structure of heterostylous flowers” Darwin 1876

***Heterostyly originated independently
in diverse insect-pollinated families***



Primulaceae



Linaceae



Lythraceae



Turneraceae



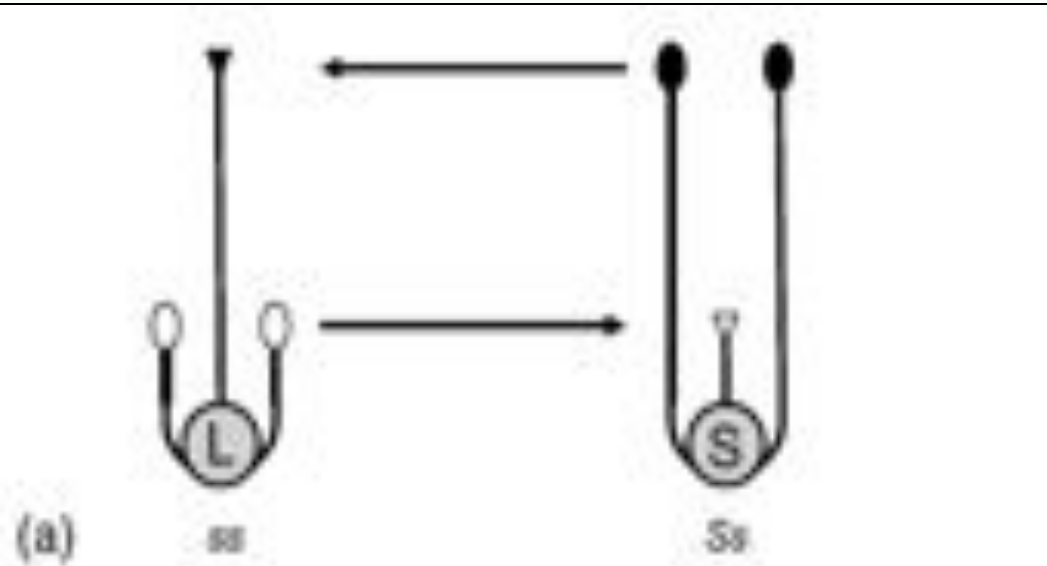
Erythroxyllaceae



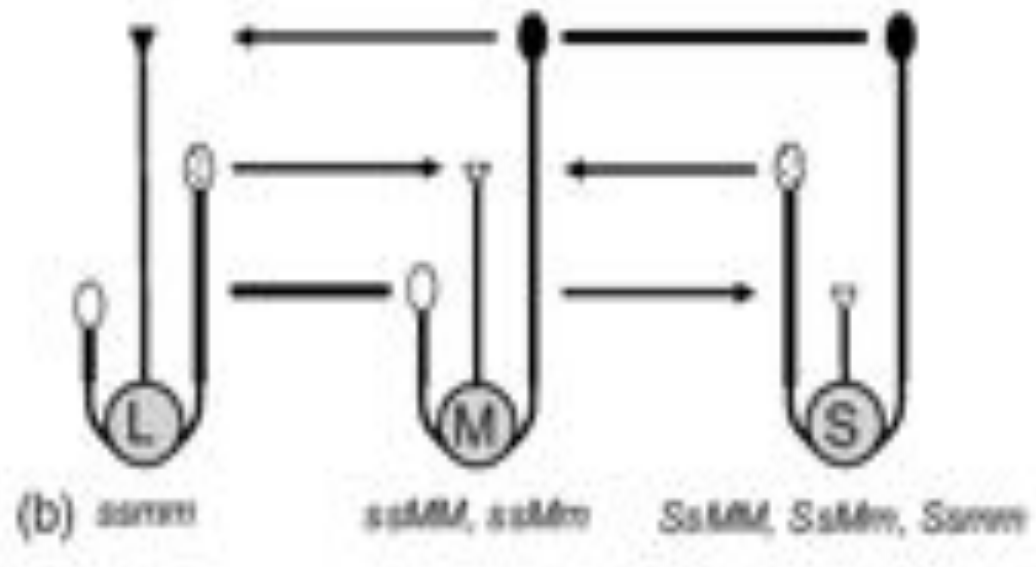
Iridaceae

What is Heterostyly?

distyly



tristyly



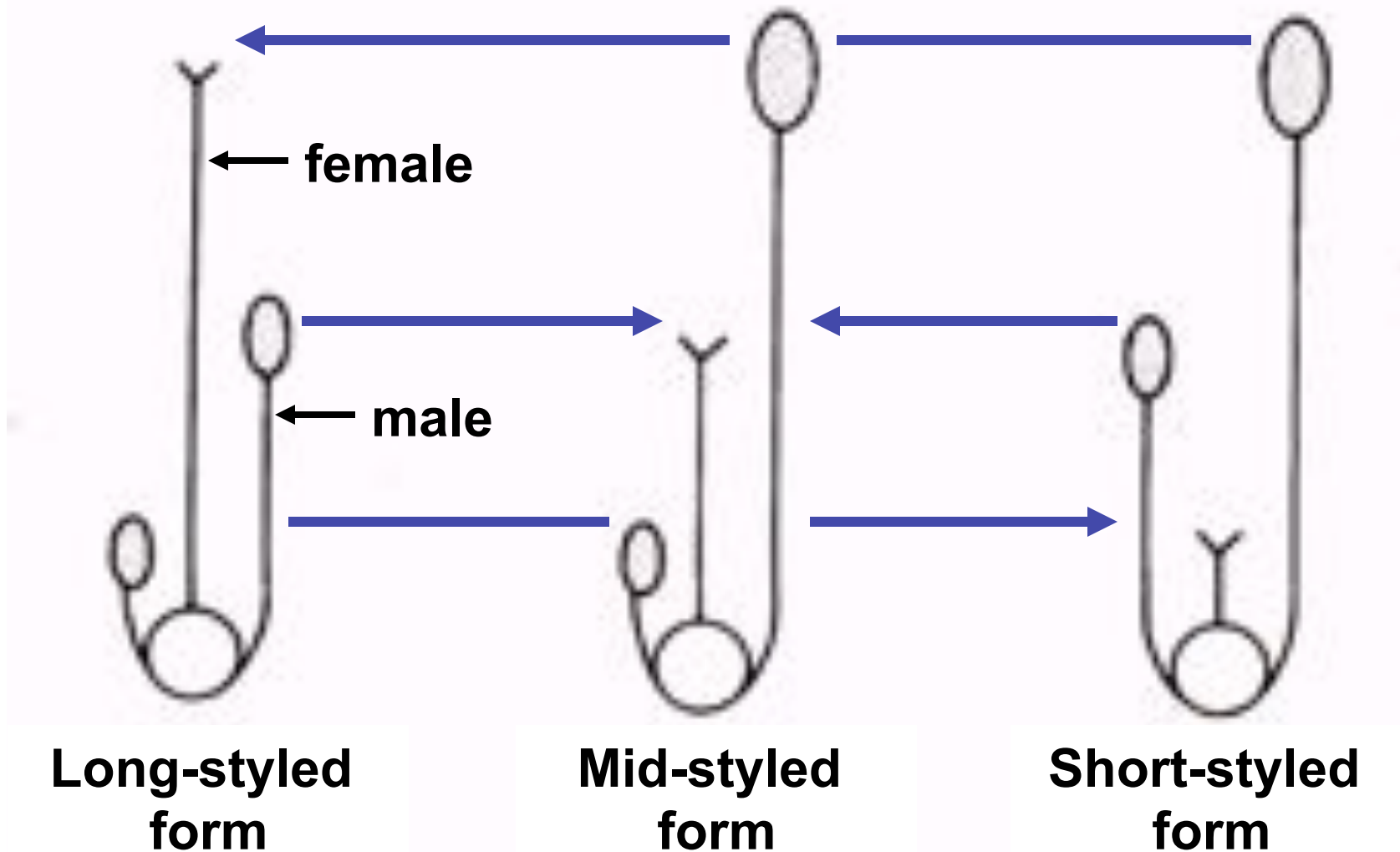


‘In their manner of fertilization a more remarkable case than can, perhaps, be found in any other plant or animal ... nature has ordained a most complex marriage-arrangement, namely a triple union between three hermaphrodites’

Darwin 1877



Darwin's adaptive hypothesis for the function of tristylly



Testing Darwin's hypothesis using Pickerel Weed



Pontederia cordata
Paugh Lake, Ontario



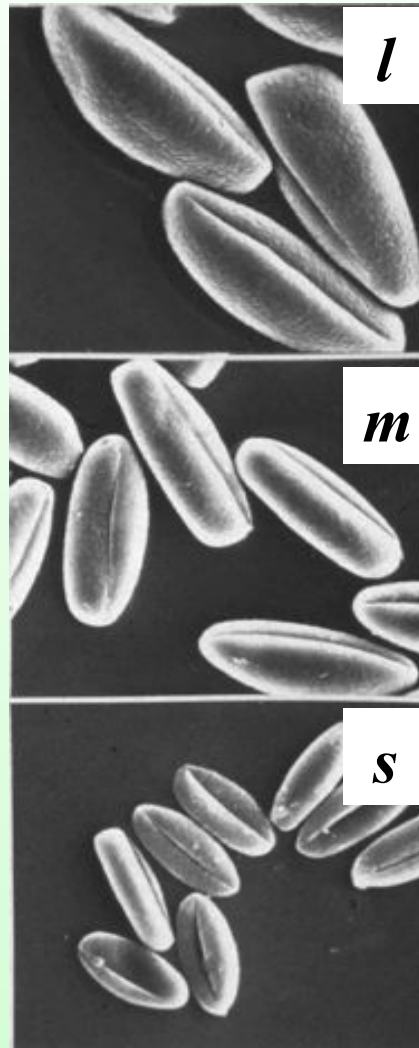
Steven Price

Pickereel Weed Team



Deborah Glover & Lorne Wolfe

Pollen-size trimorphism allow tests of Darwin's hypothesis



Prediction

- preferential pollen transfer between anthers and stigmas of equivalent height

Result

- studies of pollen deposition on bees and flowers support Darwin's adaptive hypothesis

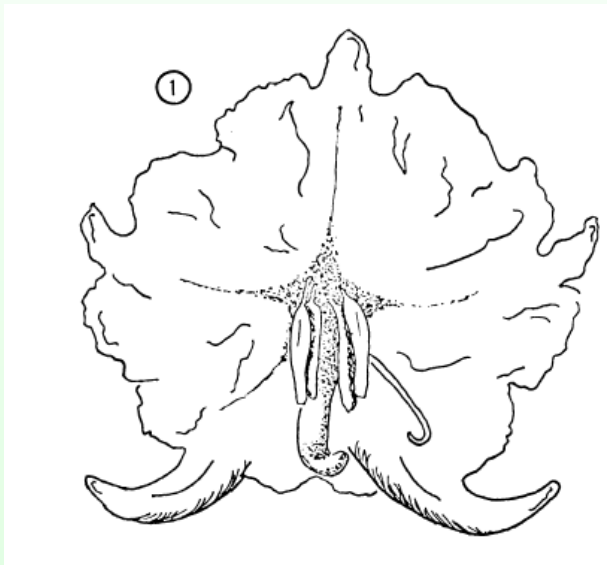
BJLS (1984) 21: 315-329

Evolution (1985) 39: 766-774

BJLS (1989) 36: 317-329

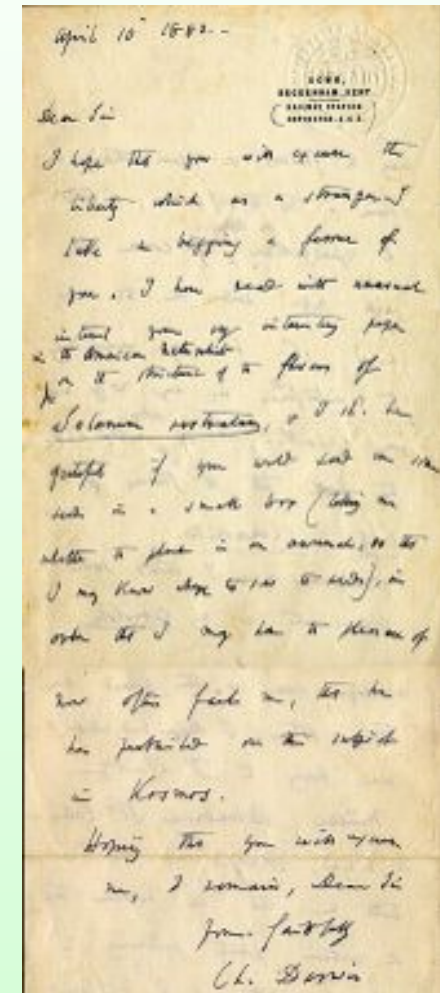
Mirror-image flowers and heteranthery

Darwin misses out



“ ...[I] have wasted enormous labour over them and cannot yet get a glimpse of the meaning of the parts.”

Letter to JD Hooker, October 14 1862



Letter to JE Todd, Darwin's last scientific correspondence
9 days before his death

Function of Mirror-Image Flowers and Heteranthery*



L



R

*enantiostyly

Cyanella alba

Heteranthy

Anther differentiation within flowers



Solanum



Cyanea



Monochoria



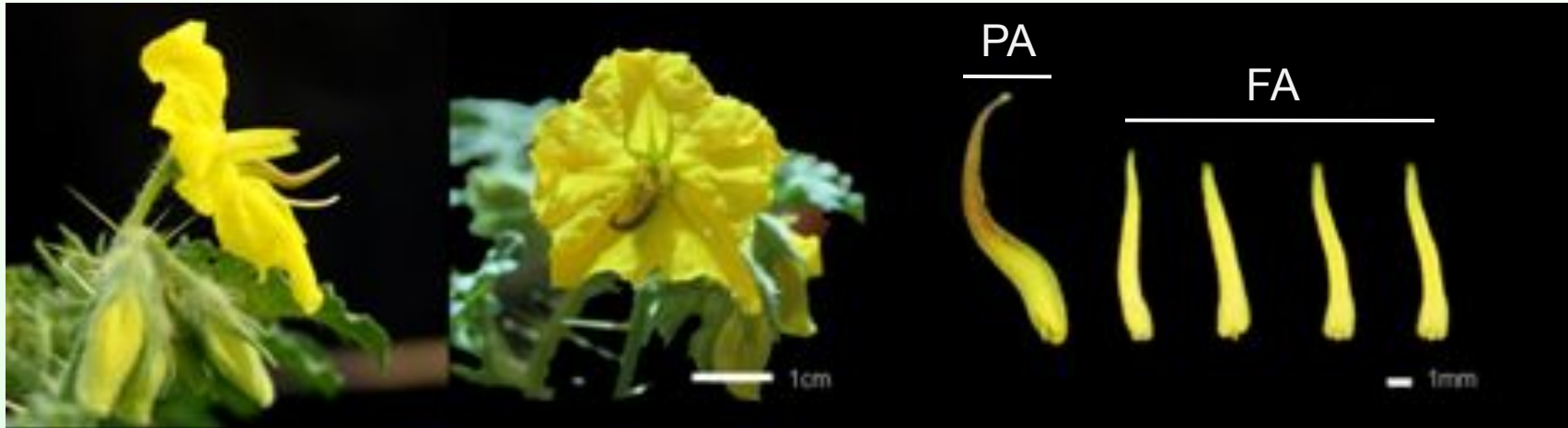
Cassia

- Differences in position, size and colour of anthers

- Occurs in ~ 23 families

- associated with enantiostyly, bee pollination and nectarless flowers

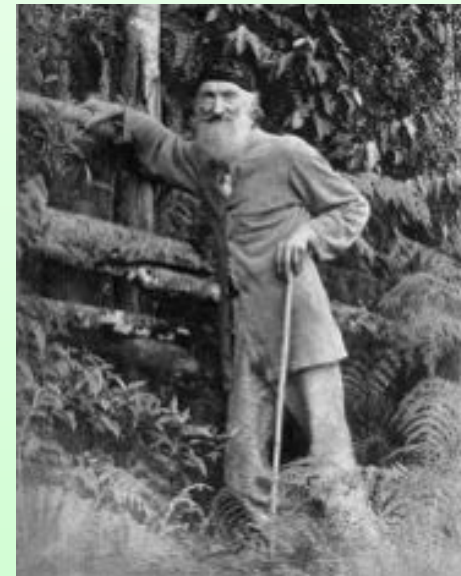
Fritz Müller's Division of Labour Hypothesis



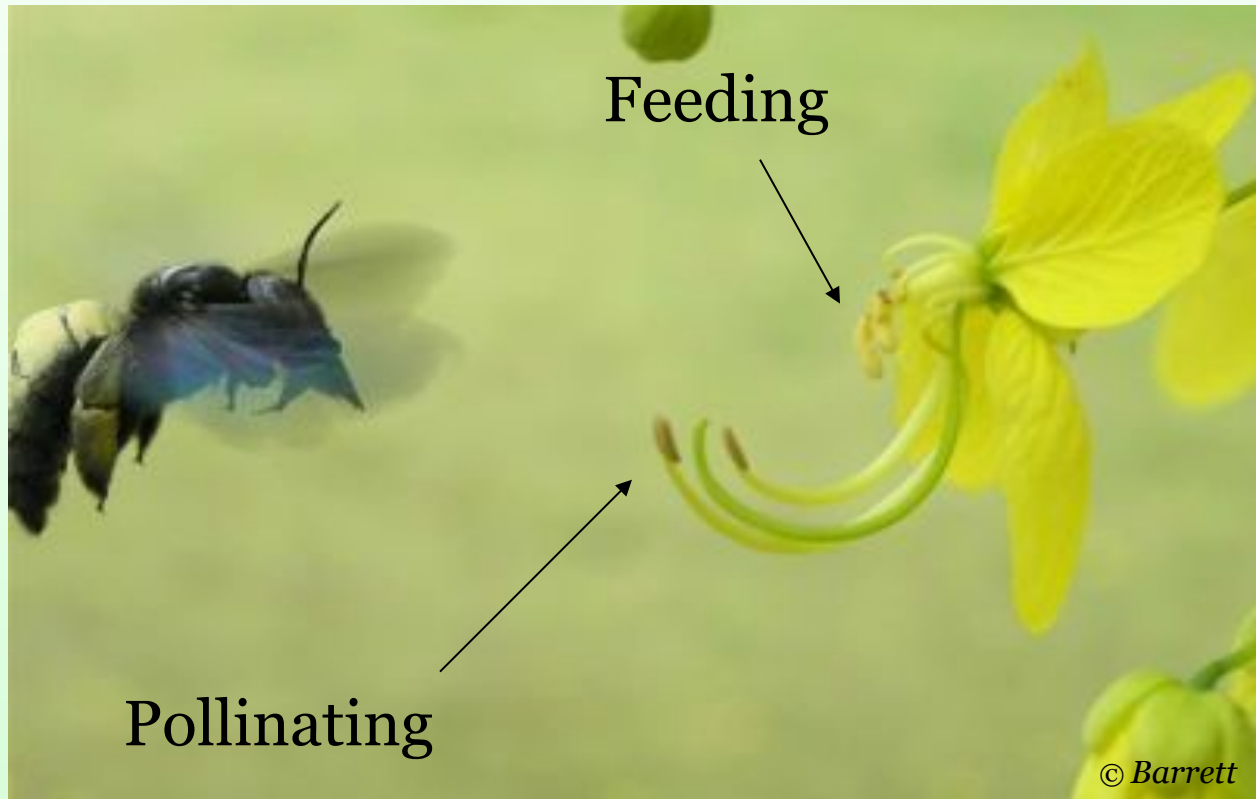
- **Small anthers attract and feed pollinators (feeding anthers, FA)**
- **Large anthers export pollen to other plants (pollinating anthers, PA)**

F. Müller 1883 *Nature*

***J. Evolutionary Biology* (2009) 22: 828-839**



***Heteranthery* resolves conflict of using pollen as food for pollinators and as gametes**



***Xylocopa* (Carpenter bee) visiting *Cassia fistula* - Caesalpinaceae**



Do mirror-image flowers promote cross-pollination?

***Experiments on Solanum rostratum
by Linley Jesson***



N	N	N	N
N	N	N	N
N	N	N	N
N	N	N	N

Straight-styled

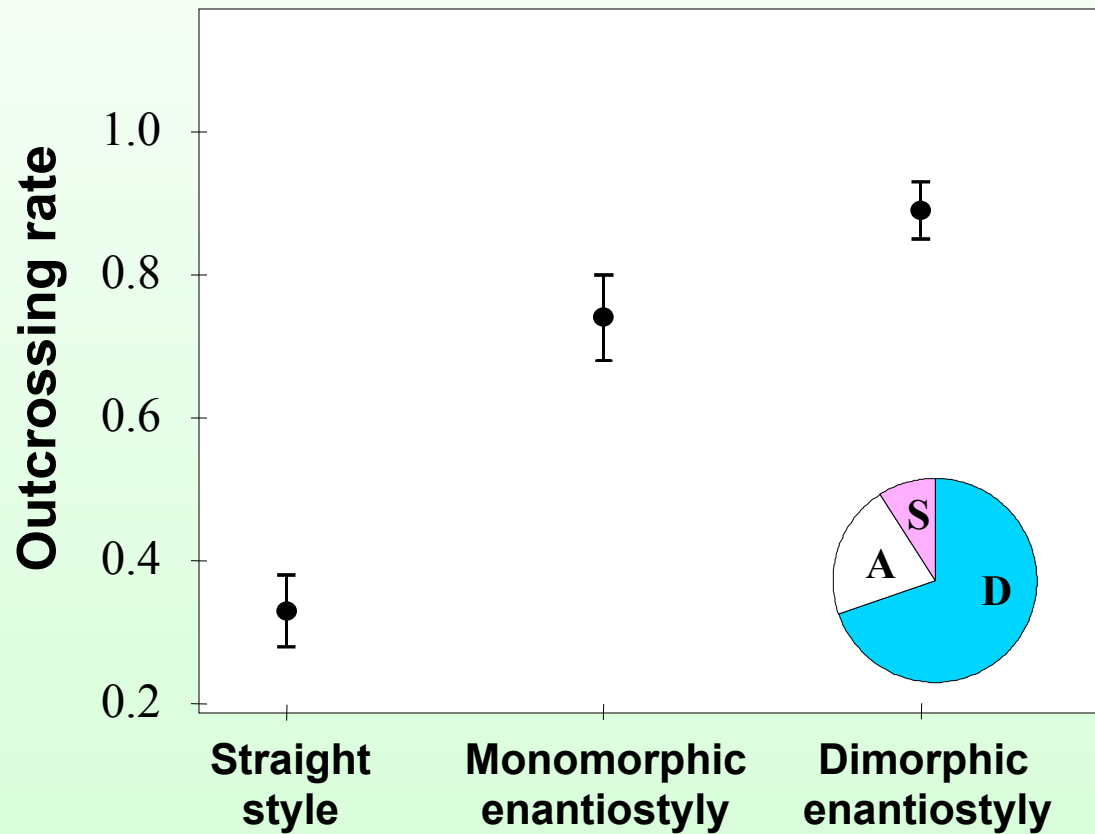
L/R	L/R	L/R	L/R
L/R	L/R	L/R	L/R
L/R	L/R	L/R	L/R
L/R	L/R	L/R	L/R

M-enantiostyly

L	R	L	R
R	L	R	L
L	R	L	R
R	L	R	L

D-enantiostyly

Mirror-image flowers promote more proficient cross-pollination



Nature (2002) 417: 707

D = intermorph mating
A = intramorph mating
S = selfing

Darwin's Selective Forces and the Reproductive Diversification of Flowering Plants

- **Divergence of pollination systems**
floral radiations associated with animal, wind & water pollination
- **Anti-selfing mechanisms**
reproductive traits that function to limit selfing and inbreeding depression (maternal fitness)
- **Pollen dispersal mechanisms**
reproductive traits that function to promote cross-pollen transfer (paternal fitness)

Today's General Messages

- Darwin not the 'botanical ignoramus' he claimed to be
- Darwin an experimentalist
- Darwin a functional biologist
- Lots more to discover about floral evolution following Darwin's lead


Further Reading

**PHILOSOPHICAL
TRANSACTIONS**
— OF —
**THE ROYAL
SOCIETY**

B
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*Papers of a Discussion meeting issue edited by Peter R. Crane, Elze Marie Friis
and William C. Chaloner*



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