Pollination Biology

Peter G. Kevan

(With assistance from Carlos F. Greco, Franco DiGiovanni, Carlos Vergara, and many students)

International Network of Expertise for Sustainable Pollination
Departament of Environmental Biology, University of Guelph, Guelph, ON,
Canada N1G 2W1

International Pollination Course 2007
Presented by:

Professor Peter G. Kevan
International Network of Expertise for Sustainable Pollination
Departament of Environmental Biology, University of Guelph, Guelph, ON,
Canada N1G 2W1

Professor Blandina Felipe Viana
Universidade Federal da Bahia, Instituto de Biologia, Departamento de
Zoologia, Laboratório de Biologia e Ecologia de Abelhas – LABEA, *Campus*
Universitário de Ondina, Salvador, Bahia, Brasil, 40170-290

Chapada Diamantina
Bahia, Brasil

Index

First edition of this manual was prepared for the field course in pollination biology co-sponsored by the University of Guelph and by the Jardin Botanico, Estacion de Biologia Chamela y Los Tuxtlas of the National Autonomus University of Mexico (UNAM) from 1990 on. The course has also been presented in the National University, Heredia in Costa Rica (2001) at St. Louis University, the Missouri Botanical Garden (2001) and National Parque of Chapada Diamantina, Lençóis, Bahia, Brazil (2003 and 2005).

Introduction

Introduction

The mandate of this course is to provide a general framework for the study of plant pollination systems. Through integration of both lecture and field exercises, *Pollination Biology* will promote the student to critically examine the mating dynamics of plants as well as how and why plant pollination systems have become evolutionarily stable.

Pollination is simply the transfer of pollen from an anther to a stigma (Fig. 01). However, owing to plant immobility, hermaphroditism and reliance on vectors for pollination transfer, this basic process is manifest through a range of mating patterns which vary widely in their degree of the adaptive complexity.

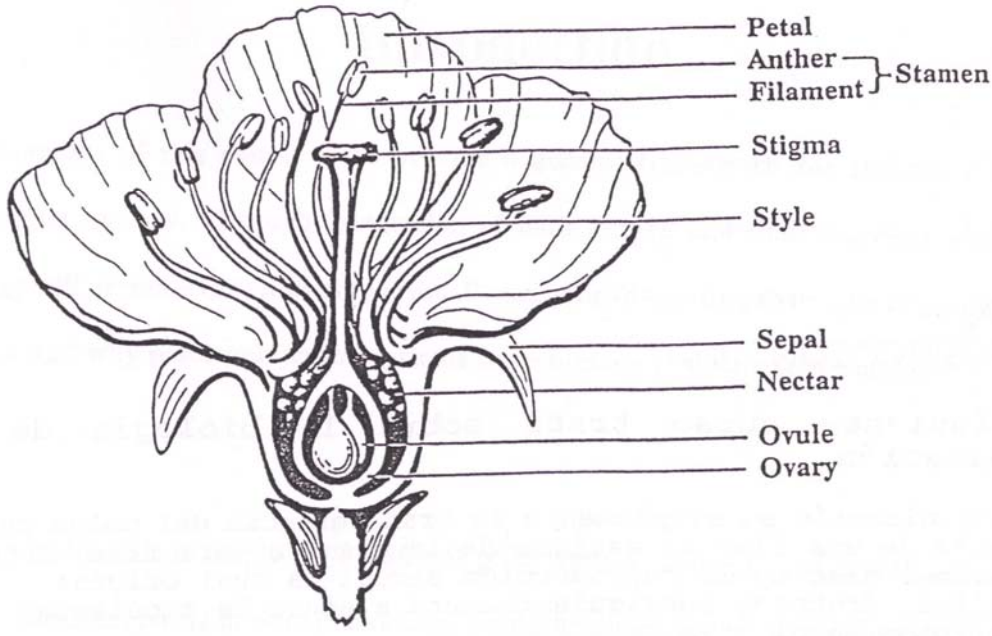


Figure 01: The parts of a flower.

Notwithstanding a high degree of variability, some fundamental principles are common to all pollination systems. The student, at the outset of this course, is encouraged to familiarize themselves with basic plant phenology and the concept of an alternation of generations.

Because of vector-mediated gamete transfer and elaborate sexual systems, plant mating can be highly promiscuous, with individuals mating with many sexual partners including themselves (Fig. 02).

Note that self-pollination is likely to occur regularly but will not necessarily result in fertilization unless the plant is a self-fertile species or variety.

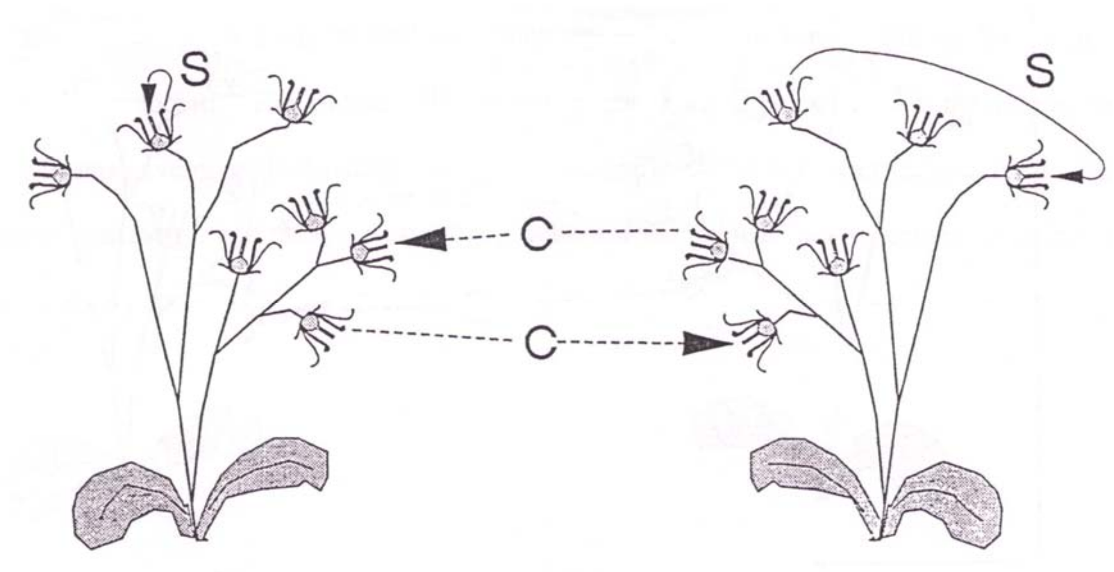


Figure 02: Cross and self-pollination.

Both biotic and abiotic vectors may me employed by plants for pollen transfer. Abiotic vectors, such as wind and water are the general rule among the Gymnosperms. Most plants species, however, employ animals as pollen vectors because the behavioral flexibility of animals disposes them to be manipulated by plant characteristics. Biotic vectors, by contrast, are common among the Angiosperms.

In this course we are going to explore pollination biology from a botanical, zoological and physical standpoint. The course will attempt to foster an appreciation for the proximate mechanisms governing plant mating, the functional significance of floral architecture, measuring mating complexity, and understanding the genetic and evolutionary consequences of different mating strategies.

Botanic Aspects of Pollination Biology

Botanic Aspects of Pollination Biology

Problem of classifying flowers according to their pollination systems

Various schemes designed:
- based on attractant (nectar, pollen, both, others)
- based on mode of pollination (wind, water, insects, birds, etc.)
- based on functional structure (how the flower works)

Leppik produced a system of classifying blossoms based on functional structure and presumed evolutionary levels:
- level 1: amorphic
- level 2: haplomorphic
- level 3: actinomorphic
- level 4: pleomorphic (with form numerals)
- level 5: stereomorphic
- level 6: zygomorphic

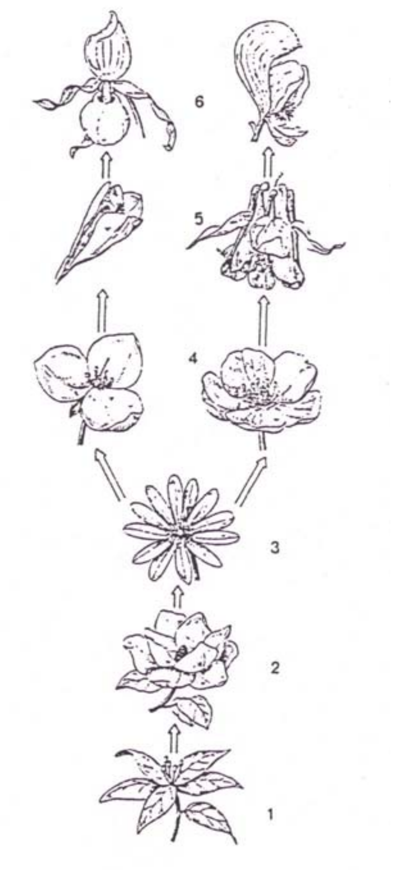


Figure 03: Important trends in the evolution of flower shape over a span of 100 million years. (1) Most primitive amorphous flower without clearly discernible shape or symmetry. (2) Flower of open hemispherical shape with no clear symmetry (like the magnolia flower). (3) Typical open radially symmetrical flower (like the yellow adonis). Subsequent divergence into different lines of development, such as flowers of the monocotyledonous plants shown here on the left, and those of the buttercup family (right). (4) Flowers with reduced but fixed number of petals (like those of the spiderwort, left, and buttercup, right). (5) Flowers with tubes (Steromorphic). (6) Bilaterally symmetric flowers. APAGADO NO ORIGINAL

Faegri & van der Pijl “The Principles of Pollination Ecology” use a blossom classification which includes function of the inflorescences as units as well as individual flowers.

The functional units sometimes called “anthia” place. Levels 1 to 4 above are all in category “dish-to bowl-shaped blossoms” below.

They start from a different place:
- I. Blossoms open during anthesis
- II. Blossoms closed during anthesis (cleitopetalous)
- III. Trap blossoms

Relatively few examples of II and III are specialized forms of I. Type III are specialized on their own (Araceae etc.)

Type I subdivided:

- I.1. Blossoms inconspicuous
  - A. Mostly abiotically pollinated (wind, water)
  - B. Some autogamous (self-pollinating) flowers
  - C. Possibly some insect-pollinated flowers, but scent or other attractant may make the flowers conspicuous to pollinators.

- I.2. Blossoms conspicuous
  - A. Dish-to Bowl-shaped blossoms
    - a. Sexual organs diffuse to concentric in flower e.g. *Rosa*, Compositae, umbels, *Magnolia*, *Passiflora*
    - b. Choripetalous

  - B. Bell-to Funnel-shaped blossoms (Stereomorphic)
    - a. Sexual organs centric
    - b. *Campanula*, Tulip and Lilies, daffodils
    - c. *Ficus syconium* as an inflorescence
    - d. Choripetalous and Sympetalous

  - C. Head-to Brush-shaped blossoms (Rhopalomorphic)
    - a. Sexual organs diffuse
    - b. *Thalictrum*, *Calliandra* and *Salix*, Proteaceae
    - c. Transitions to Anemophily: Salicaceae, *Salix* to *Populus*
    - d. Fagaceae: *Castanea* to *Lithocarpus* to *Quercus*, within *Thalictrum*
    - e. Choripetalous and Sympetalous and Apetalous

  - D. Gullet-shaped blossoms (Zygomorphic)
    - a. Sexual organs excentric and in upper part of the flower
    - b. Labiatae, Scrophulariaceae, *Iris*
    - c. Pollen is deposited on the back of the pollinators = “nototribic”

    d. No multiflowered inflorescences act as Gullet anthia
    e. Generally sympetalous, some choripetalous

E. Flag-shaped blossoms (Zygomorphic)
    a. Sexual organs excentric and lower part of the flower
    b. Pollen deposited on underside of pollinator = “sternotribic”
    c. Papilionaceae, *Fumaria*, *Discentra*
    d. Generally choripetalous, some sympetalous

F. Tube-shaped blossoms (Stereomorphic and Zygomorphic)
    a. Sexual organs centric or excentric, the tube is the important feature as it restricts pollinators’ abilities to obtain reward

Question: Is F really distinctive classes, or does it depend on how the human observer sees the blossom?

Tube-shaped flowers are also included in D and E:

e.g. Gullet flower (D) with a Flag (E), is Zygomorphic and Nototribic and with Nectar Spur or Tube as in *Linaria*, *Delphinium*, or Sternotribic with deep corolla Tube as in many Leguminosae.

e.g. Bell-and funnel-shaped flowers (B) may be so deep as to form tubes in *Primula*, *Gentiana* etc., *Phlox* etc.

The category is, nonetheless, useful as a structural class. Summary Table (below) is a highly generalized, with many exceptions, but is useful.

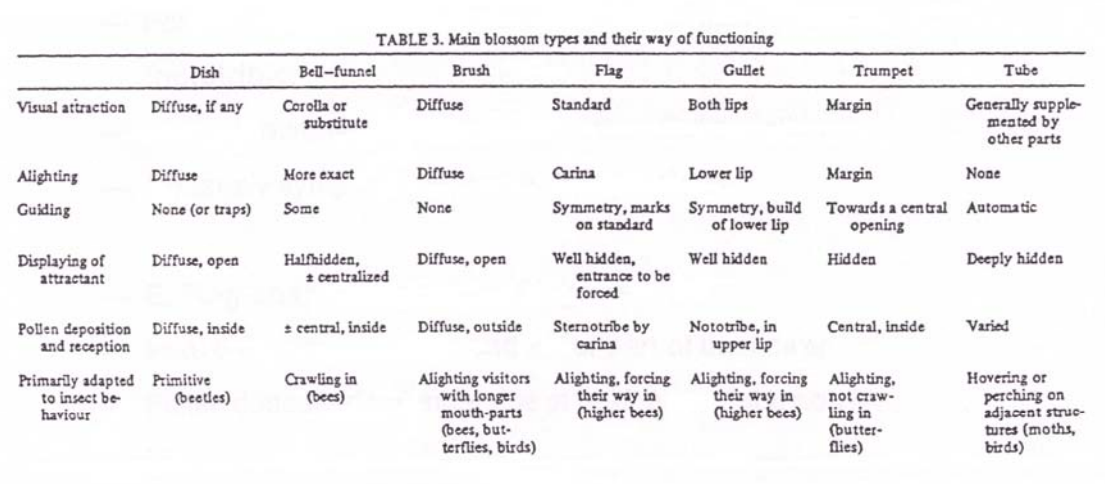


TABLE 3. Main blossom types and their way of functioning

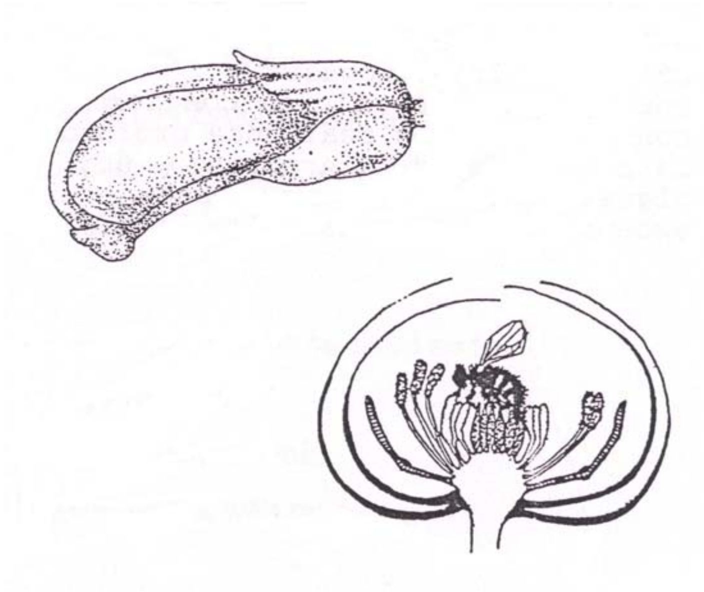
	Dish	Bell–funnel	Brush	Flag	Gullet	Trumpet	Tube
Visual attraction	Diffuse, if any	Corolla or substitute	Diffuse	Standard	Both lips	Margin	Generally supplemented by other parts
Alighting	Diffuse	More exact	Diffuse	Carina	Lower lip	Margin	None
Guiding	None (or traps)	Some	None	Symmetry, marks on standard	Symmetry, build of lower lip	Towards a central opening	Automatic
Displaying of attractant	Diffuse, open	Halfhidden, ± centralized	Diffuse, open	Well hidden, entrance to be forced	Well hidden	Hidden	Deeply hidden
Pollen deposition and reception	Diffuse, inside	± central, inside	Diffuse, outside	Sternotribe by carina	Nototribe, in upper lip	Central, inside	Varied
Primarily adapted to insect behaviour	Primitive (beetles)	Crawling in (bees)	Alighting visitors with longer mouth-parts (bees, butterflies, birds)	Alighting, forcing their way in (higher bees)	Alighting, forcing their way in (higher bees)	Alighting, not crawling in (butterflies)	Hovering or perching on adjacent structures (moths, birds)

II. Cleistopetalous flowers
- A. Form a parallel series in Group I
- B. Some are flowers are cleistogamous (i.e. self-pollinating in the bud) but these are usually excluded from this group by convention
- C. e.g. of cleistopetalous insect pollinated flowers

Bottle gentian by bumblebess,

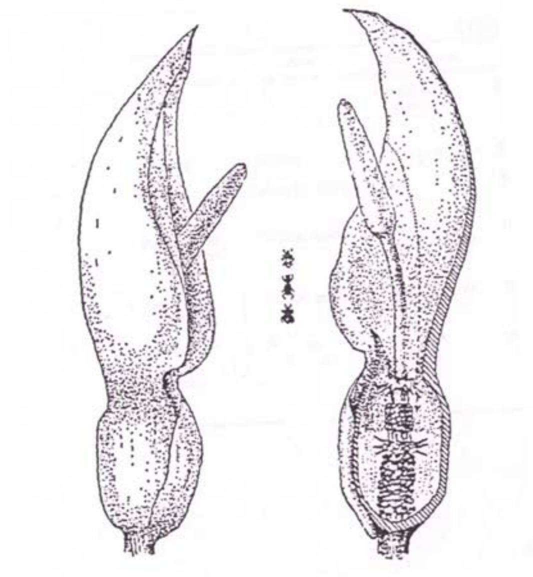
Pedicularis sceptrum-carolinium by bumblebees

Trollius europaeus by beetles



III. Trap blossoms
- A. Full trap blossoms
    - i. Blossoms act by deceit
    - ii. Mimetic colours or scents or both
    - iii. e.g. Araceae, Nymphaea and Nuphar

Pollinators are trapped for a definite period of time.
Time of release dictated by the flower or inflorenscence.



B. Semi-trap blossoms
   i. Blossoms may act by deceit or not
   ii. Pollinators can find their way out any time
   iii. Some blossoms have slippery surfaces, pollinators repeatedly fall back, but eventually escape.
   iv. Some blossoms have organs which turn over or fold when pollinator clings to it.
   v. Lots of specialized examples in Orchids.

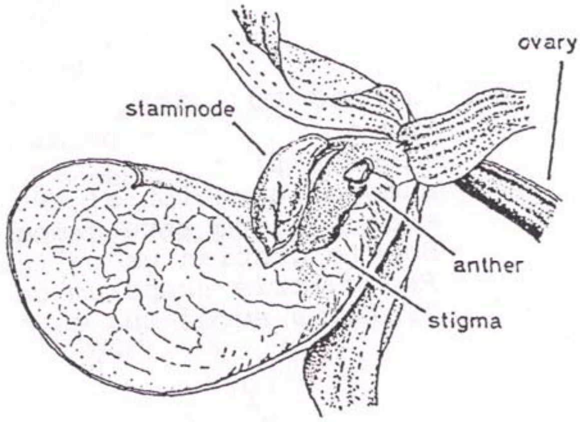


FIG. 75. Lady's Slipper (*Cypripedium calceolus*). Flower with half of lip removed to show details of the column and the path taken by a visiting insect.

Classification of Pollination Mechanisms

Blossoms can be classified accordingly:

- Abiotic pollination
- Anemophily (wind)
- Hydrophily (water)
- Ephydrophily (water surface)
- Hyphydrophily (under water)
- Ombrophily (rain)?
- Pollination by gravity
- Biotic pollination
- Zoophily
- Entomophily (insects)
- Cantharophily (beetles)
- Miophily (flies)
- Sacromyophily (flies)
- (Wasps)
- Myrmecophily (ants)
- Melitophily (bees)
- Psychophily (butterflies)
- Phalaenophily (moths)
- Malacophily (slugs and snails)?

… etc. inventing terms

- Ornithophily (birds)
- Chiropterophily (bats)
- By scansorial mammals (rodents, marsupials, primates, etc.)

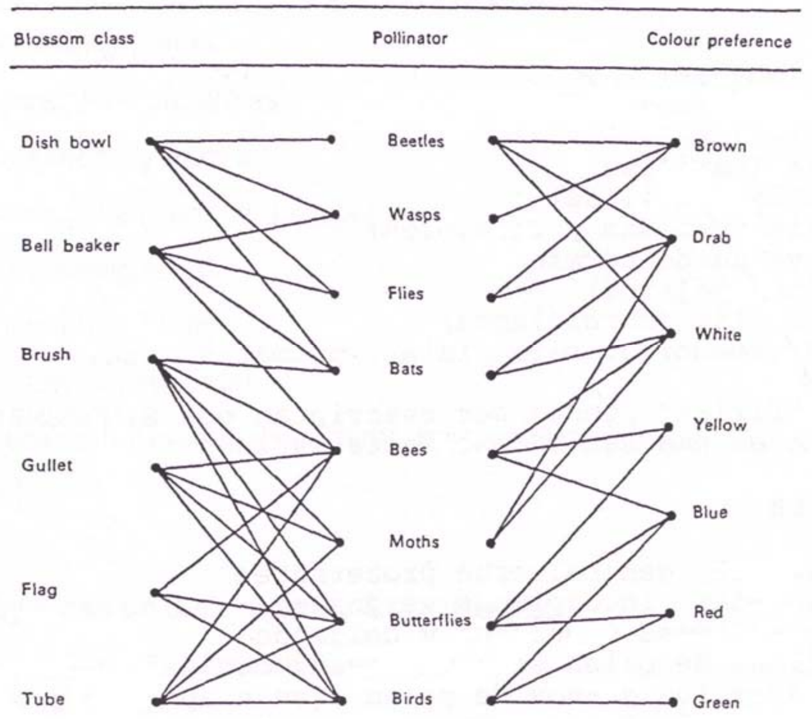
All the … phily’s can be described by SYNDROMES

A syndrome is a suite of characteristics:

I. Anemophily:
   a. Flower unisexual, often produced before leaves come out
   b. Flowers small, inconspicuous, greenish
   c. Anthers and stigmas exposed and hanging free
   d. Lots of small, dry pollen with smooth exine
   e. Sometimes pollen grains have special appendages for buoyancy in air
   f. Pollen: ovule ratio very high
   g. Plants grow in groups

II. Biotic pollination: the harmonic relations of blossoms and pollinators introduce the idea.

“Harmonic” relations between pollinators and blossoms

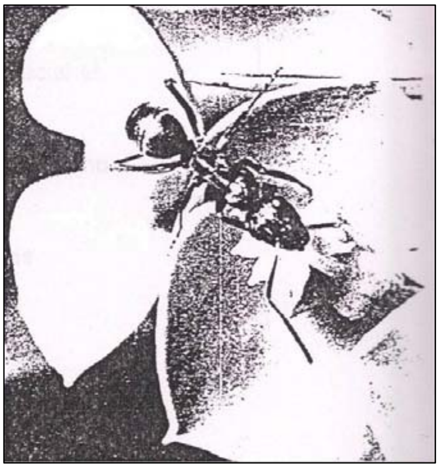


III. Syndrome of cantharophily
   a. Anthia (flowers or inflorescences) with few special attractants
   b. Not brightly coloured, no special or definitive shape, no stereomorphic effects, no nectar guides
   c. Generally large, flat, cylindrical or shallow bowls
   d. Easy access to beetles
   e. Odour strong, fruity to aminoid
   f. Rewards easily obtained, pollen, food bodies, nectar
   g. Sexual organs exposed
   h. (note: some beetles are specialist pollinators of highly evolved blossoms)

IV. Syndrome of myophily
   a. Anthia simple, regular, without stereomorphic effects
   b. Colours light, bright to dull
   c. Nectar guides often present
   d. Odour weak to imperceptible
   e. Nectar and pollen easily obtainable
   f. Sexual organs well exposed

V. Syndrome of sapromyophily
   a. Anthia usually radial, but with great depth
   b. Inflorescence has trapping guides (structure, colour, odour)
   c. Colours dull, dark, brownish-purplish-greenish
   d. Traps often with transparent windows
   e. Odour of decaying protein, musk
   f. Usually no reward
   g. Sexual organs hidden within the trap

VI. Syndrome of myrmecophily
   a. Blossoms small and produced close to the ground
   b. Colours light but not highly conspicuous
   c. Small amount of nectar produced
   d. Pollen sticky
   e. Number of ovules small
   f. Plants grow intermingled
   g. Mostly in hot, dry habitats
   e.g. some *Euphorbia* spp.

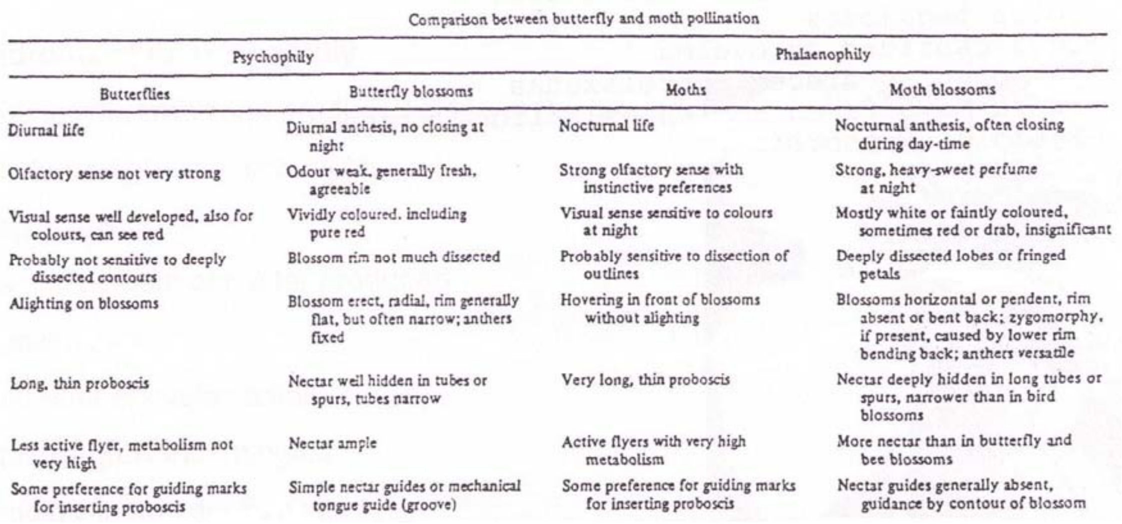


VII. Syndrome of mellitophily (most relevant to long and medium-long tongued bees)

   a. Blossoms zygomorphic with great stereomorphic effect
   b. Robust with landing places for bees
   c. Colours bright, yellow and blue
   d. Nectar guides mostly present
   e. Odours floral, not strong but pleasant
   f. Nectar and pollen well hidden, available in moderate quantities
   g. Sexual parts concealed
   h. Ovules few to many

   (Short-tongued bees are often associated with flowers that have some of the characteristics, but are smaller, or associated with brightly coloured flowers also pollinated by flies)

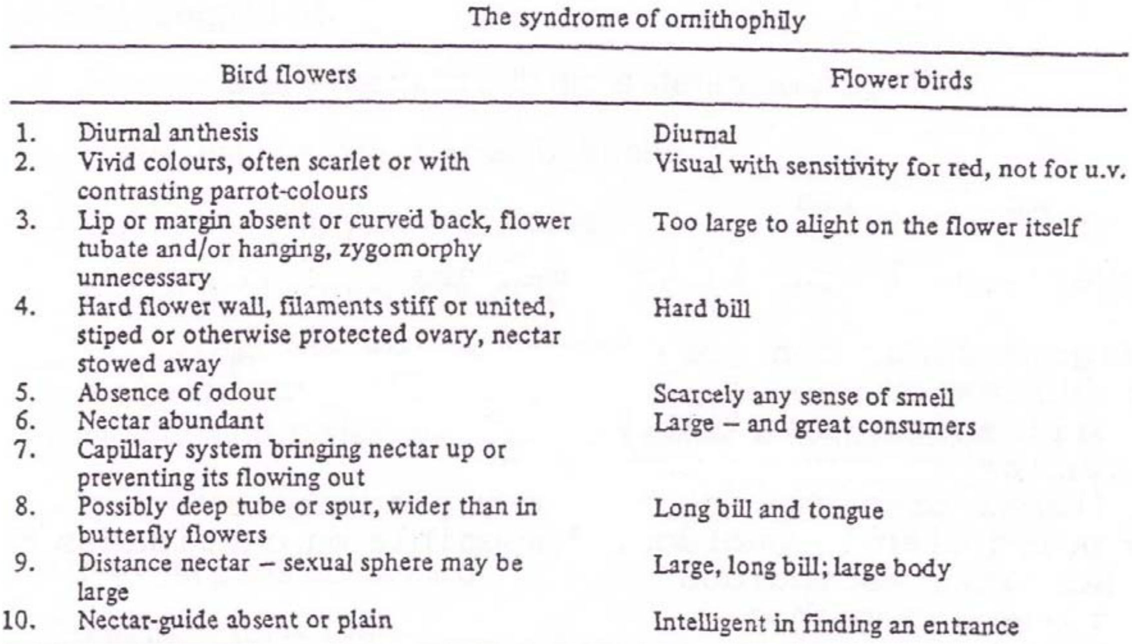
VIII. Syndromes of psychophily and phalaenophily: comparison in the following table:



Comparison between butterfly and moth pollination

Psychophily		Phalaenophily	
Butterflies	**Butterfly blossoms**	**Moths**	**Moth blossoms**
Diurnal life	Diurnal anthesis, no closing at night	Nocturnal life	Nocturnal anthesis, often closing during day-time
Olfactory sense not very strong	Odour weak, generally fresh, agreeable	Strong olfactory sense with instinctive preferences	Strong, heavy-sweet *perfume* at night
Visual sense well developed, also for colours, can see red	Vividly coloured, including pure red	Visual sense sensitive to colours at night	Mostly white or faintly coloured, sometimes red or drab, insignificant
Probably not sensitive to deeply dissected contours	Blossom rim not much dissected	Probably sensitive to dissection of outlines	Deeply dissected lobes or fringed petals
Alighting on blossoms	Blossom erect, radial, rim generally flat, but often narrow; anthers fixed	Hovering in front of blossoms without alighting	Blossoms horizontal or pendent, rim absent or bent back; zygomorphy, if present, caused by lower rim bending back; anthers versatile
Long, thin proboscis	Nectar well hidden in tubes or spurs, tubes narrow	Very long, thin proboscis	Nectar deeply hidden in long tubes or spurs, narrower than in bird blossoms
Less active flyer, metabolism not very high	Nectar ample	Active flyers with very high metabolism	More nectar than in butterfly and bee blossoms
Some preference for guiding marks for inserting proboscis	Simple nectar guides or mechanical tongue guide (groove)	Some preference for guiding marks for inserting proboscis	Nectar guides generally absent, guidance by contour of blossom

IX. Syndrome of ornithophily



The syndrome of ornithophily

	Bird flowers	Flower birds
1.	Diurnal anthesis	Diurnal
2.	Vivid colours, often scarlet or with contrasting parrot-colours	Visual with sensitivity for red, not for u.v.
3.	Lip or margin absent or curved back, flower tubate and/or hanging, zygomorphy unnecessary	Too large to alight on the flower itself
4.	Hard flower wall, filaments stiff or united, stiped or otherwise protected ovary, nectar stowed away	Hard bill
5.	Absence of odour	Scarcely any sense of smell
6.	Nectar abundant	Large – and great consumers
7.	Capillary system bringing nectar up or preventing its flowing out	
8.	Possibly deep tube or spur, wider than in butterfly flowers	Long bill and tongue
9.	Distance nectar – sexual sphere may be large	Large, long bill; large body
10.	Nectar-guide absent or plain	Intelligent in finding an entrance

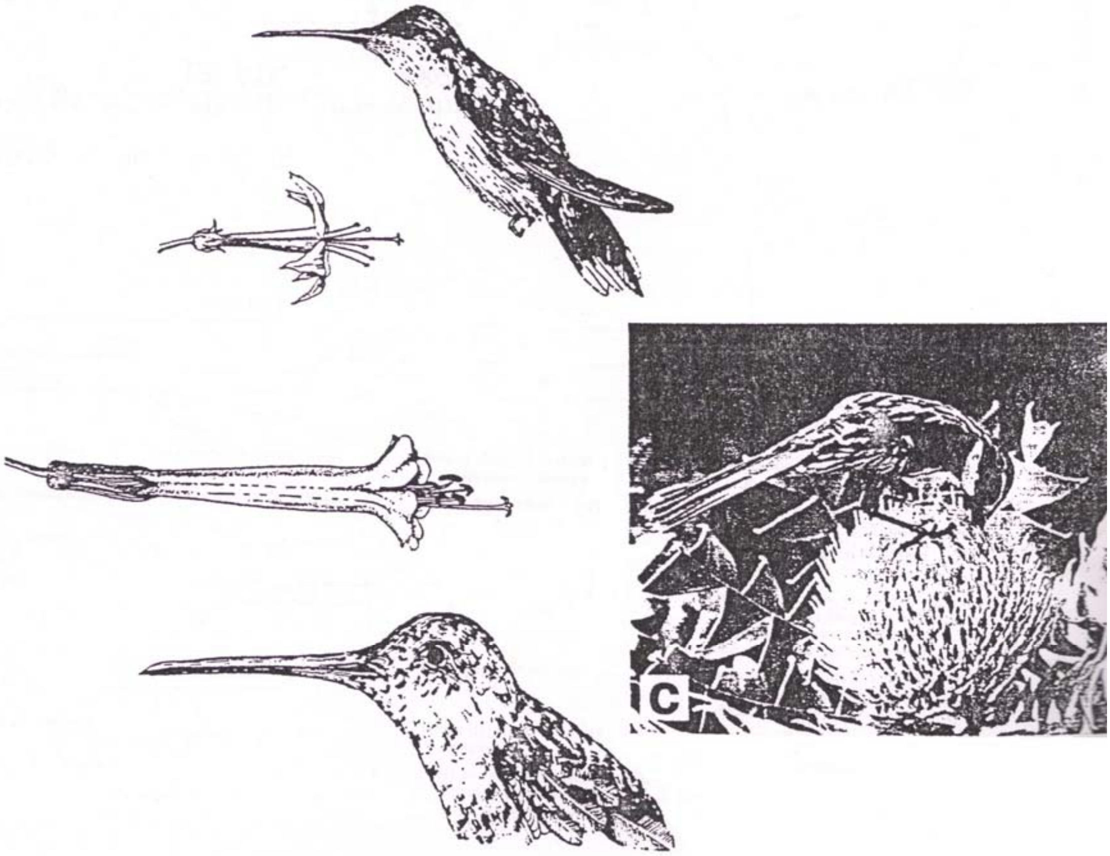
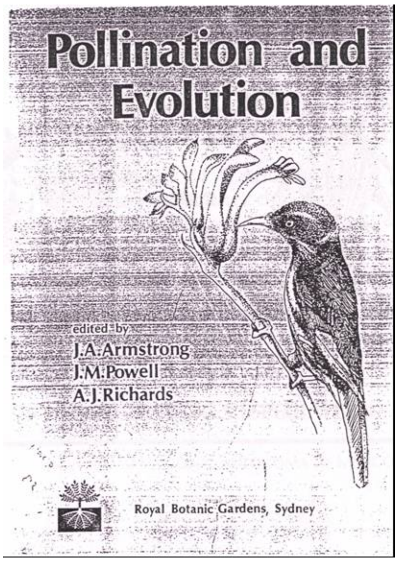
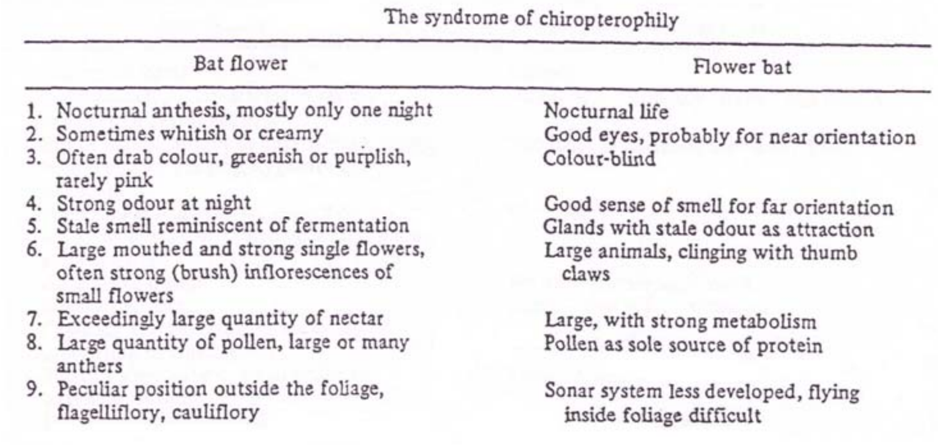


Fig. 40. Size relations between western American and Andean hummingbirds and hummingbird flowers. Above: Ipomopsis aggregata and Selasphorus rufus. Below: Cantua candelilla and Patagona gigas. All life size.

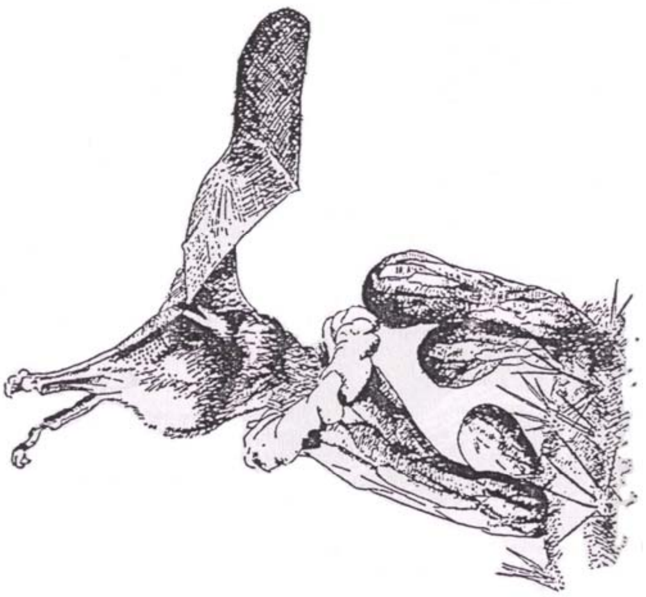


X. Syndrome of chiropterophily



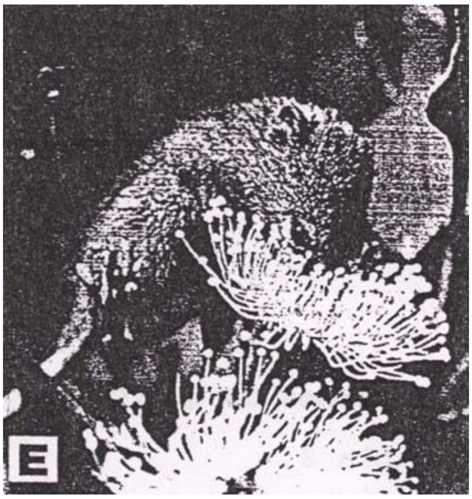
The syndrome of chiropterophily

Bat flower	Flower bat
1. Nocturnal anthesis, mostly only one night	Nocturnal life
2. Sometimes whitish or creamy	Good eyes, probably for near orientation
3. Often drab colour, greenish or purplish, rarely pink	Colour-blind
4. Strong odour at night	Good sense of smell for far orientation
5. Stale smell reminiscent of fermentation	Glands with stale odour as attraction
6. Large mouthed and strong single flowers, often strong (brush) inflorescences of small flowers	Large animals, clinging with thumb claws
7. Exceedingly large quantity of nectar	Large, with strong metabolism
8. Large quantity of pollen, large or many anthers	Pollen as sole source of protein
9. Peculiar position outside the foliage, flagelliflory, cauliflory	Sonar system less developed, flying inside foliage difficult

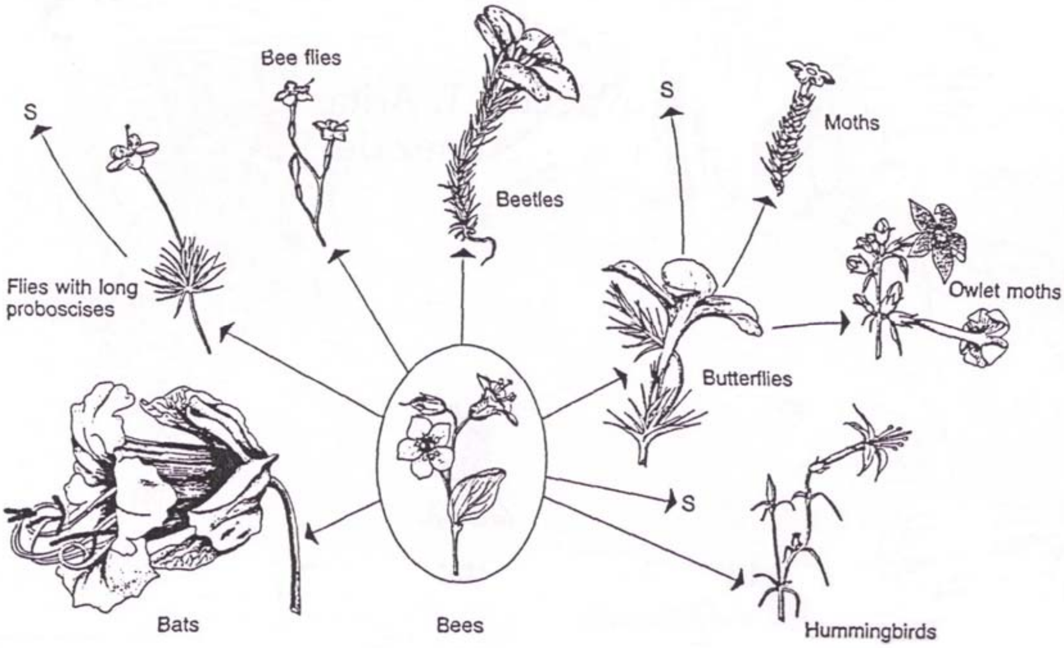


XI. Syndrome of pollination by scansorial (nom-flying) mammals

a. Flowers often in tight inflorescences, strongly attached to stems
b. Nocturnal anthesis and reward production
c. Copious amounts of reward (nectar)
d. Reward easily obtained
e. Sexual parts robust and well exposed
f. Colours dull to light
g. Odour musky



XII. One Family of plants well illustrates various syndromes: Phlox family (Polemoniaceae) studied by Grant & Grant


S
Bee flies
Beetles
S
Moths
Flies with long proboscises
Owlet moths
Butterflies
S
Bats
Bees
Hummingbirds

Zoological Diversity in Pollination Biology

Zoological Diversity in Pollination Biology

Pollinators ranges from the lowliest insects to the fantastic array of bees and butterflies, to various birds, and mammals as diverse as marsupials to rodents and primates.

Can some generalizations be made?

I. Springtails (Collembola):
   a. Minute soil inhabiting insects are known as flower visitors
   b. Consume pollen, and perhaps nectar
   c. Perhaps among the earliest insects associated with plant reproduction. 400 million years ago at the start of terrestrialization of life on earth.

II. Orthopteroids (grasshoppers, crickets, roaches, mantids, etc.)
   a. Known as flower visitors
   b. Tettigoniids (Conocephalus) normally predatory will feed on pollen
   c. Roaches and earwigs thought to be mostly destructive
   d. Flower mimicing leaf-insects obtain cryptic protection from predators in flowers
   e. Australian **Zaprochilidae** with slender, prognathous heads may be specially adapted to anthophily

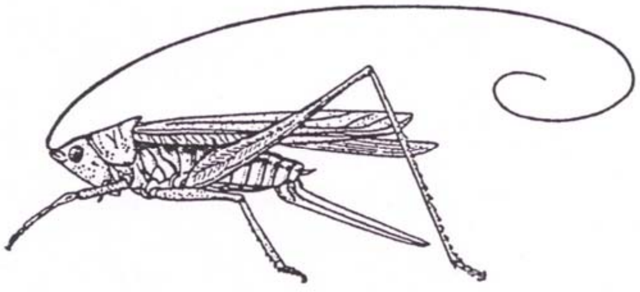
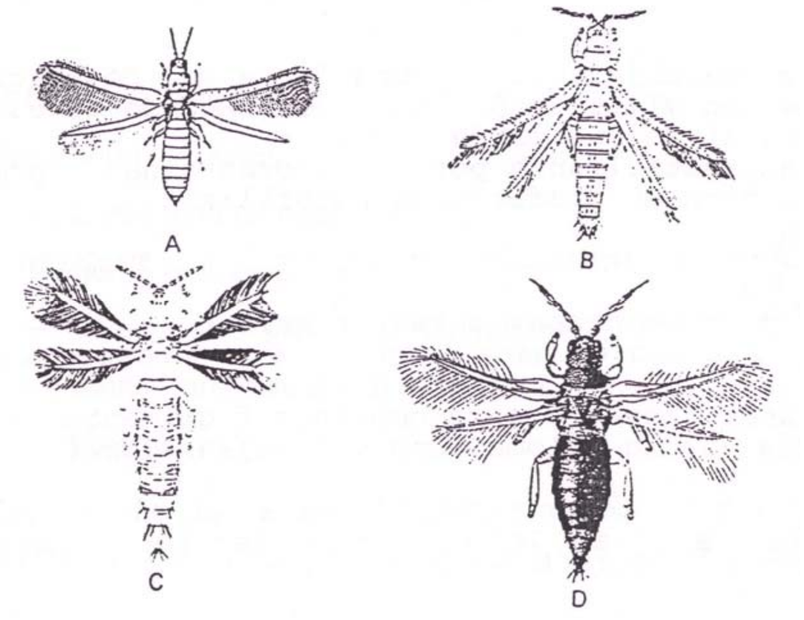


Figure 14–14. A meadow grasshopper, *Conocéphalus fasciàtus* (De Geer), female. (Courtesy of Institut de Biologie Générale, Université de Montréal.)

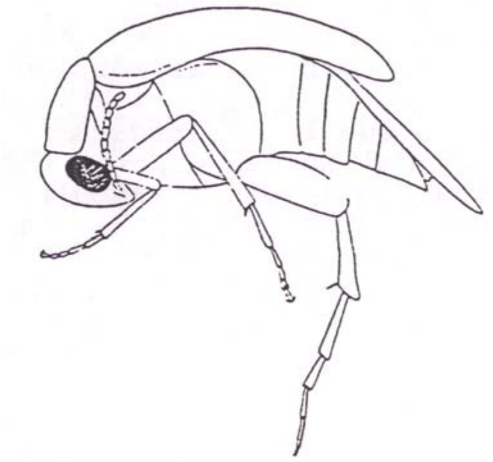
III. True bugs (Hemiptera and Homoptera)
   a. Are often found in flowers
   b. Some feed on nectar
   c. Some feed on pollen
   d. Some wait for prey (e.g. Phymatidae)
   e. Usually on flowers with easily accessible rewards

    f. Some Flatidae gregariously band together and seem to mimic flowers.
    g. Bug pollination may be more important than generally realized.
    h. The whole subject needs rewiew

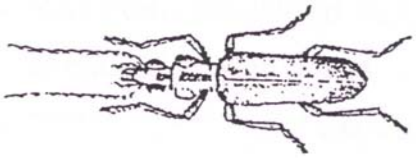
IV. Thysanoptera (thrips) notorious flower visitors
    a. Mostly thought of as destructive
    b. Spread disease on ornamental and crop plants
    c. Minute insects with feathery wings
    d. *Thrips imaginis* on roses: populations up to 1600/flower!
    e. Some with specialized, asymmetrical mouthparts adept at cracking pollen grains
    f. Thrips pollination of Ericaceae in Faroes of North Sea suggested
    g. Thrips important pollinators of Dipterocarpaceae, important trees of tropical forests of Asia.



V. Coleoptera
   a. Beetles considered to be the original flower visitors and pollinators, 130 million years of relationship with flowering plants.
   b. Generally the predactory suborder, Adephaga, not anthophiles.
   c. Among the Polyphaga, great diversity of Anthophiles.
   d. Some families and many genera exclusively anthophilous as adults, e.g. Tumbling Flower Beetles (Mordellidae).



   e. False Blister Beetles (Oedemeridae).



   f. Soft-winged Flower Beetles (Melyridae).

   g. A few with specialized mouthparts for flower visiting, e.g. Nemognatha (Meloidae) and Ipomoea.

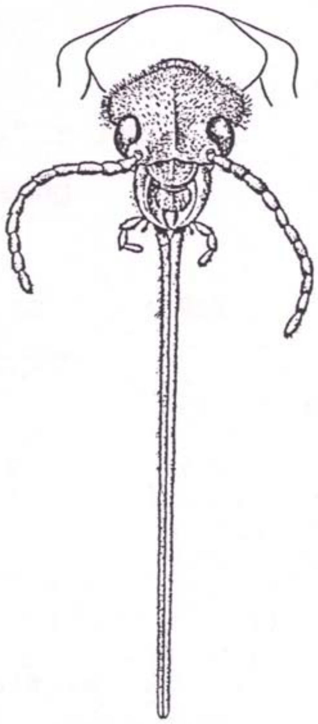
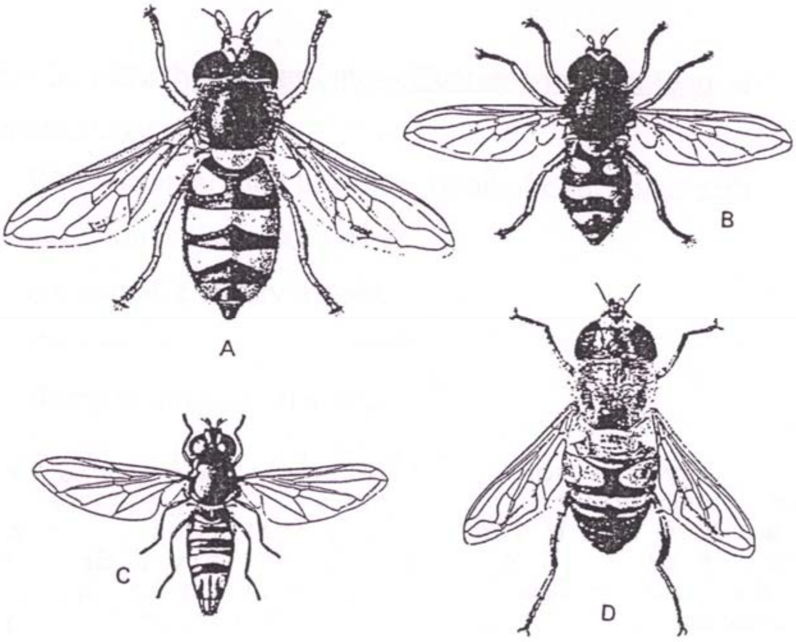


Fig. 31:
A rare case: a beetle with a long proboscis for sucking nectar out of deep flowers (*Nemognatha*).

VI. Diptera (flies) have also been considered as the original flower visitors. They have suctorial or lapping mouthparts well designed for ingesting nectar.
   a. The suborder Nematocera have filamentous antennae.
      i. The mouthparts are generally short, but variable in form.
      ii. Most nematocerous flies are small and some are important pollinators.
      iii. Mosquitoes pollinate some Orchids.
      iv. Ceratopogonids pollinate Cacao.
      v. Most Nematocera visit flowers with accessible nectar.
      vi. Some midges also puncture and suck pollen.
   b. The Diptera Brachycera are more diverse and most feed at flowers as adults.
      i. Well known are the bee-flies, Bombyliidae, some with very long proboscides. Many are parasitic on larval bees.
      ii. Closely related Nemestrinidae are also flower visitors, e.g. from South Africa.
      iii. Dance flies (Empididae) also visit many kinds of flowers.

c. In the Diptera Cyclorrhapha are the groups Aschiza, Acalypterae, and Calypterae. In all are flower visitors. Some highly specialized.
   i. The Flower or Hover Flies (Syrphidae) stand out in the Aschiza.
   ii. They feed extensively on pollen and nectar and have generally lapping mouthparts, but their proboscides may be long.
   iii. There are many which a close mimics of bees and wasps.



Syrphid flies. A: *Didea fasciata* Macquart; B: *Syrphus torvus* Osten Sacken; C: *Allograpta obliqua* (Say); D: *Eristalis tenax* (L.). (A and B, courtesy of Metcalf and the Maine Agricultural Experiment Station; C and D, courtesy of USDA.)

d. In the Acalypterae, the Conopidae are well-know flower visitors.
    i. Their larvae are parasites of bees and wasps.

e. The Calypterae are diverse with many families recorded as being flower feeders as adults. Most feed on nectar, but some also ingest pollen. Conspicuous flower visitors are the Bristle Flies (Tachinidae) but Blowflies, Houseflies and their relatives are often attracted to saprymorphilous flowers. Anthomyids visit open bowl-shaped flowers for nectar or pollen or both.

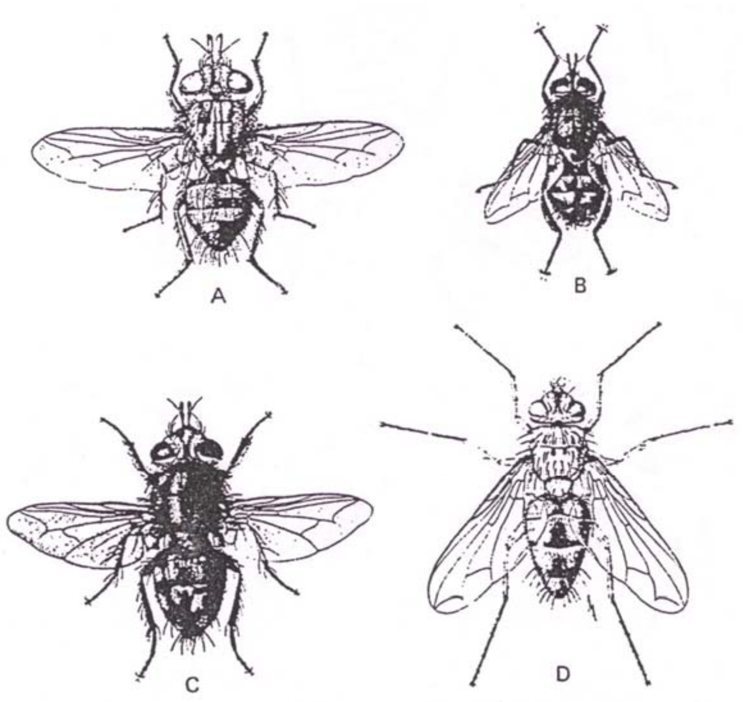
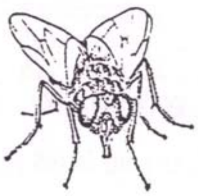
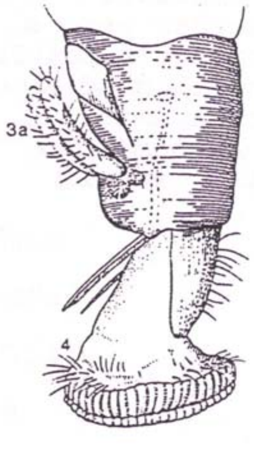


Figure 32–82. Tachinid flies. **A,** *Euphorócera claripénnis* (Macquart); **B,** *Winthèmia quadripustulàta* (Fabricius); **C,** *Árchytas marmoràtus* (Townsend); **D,** *Dexílla ventràlis* (Aldrich). (Courtesy of USDA.)

    i. They have lapping mouthparts:



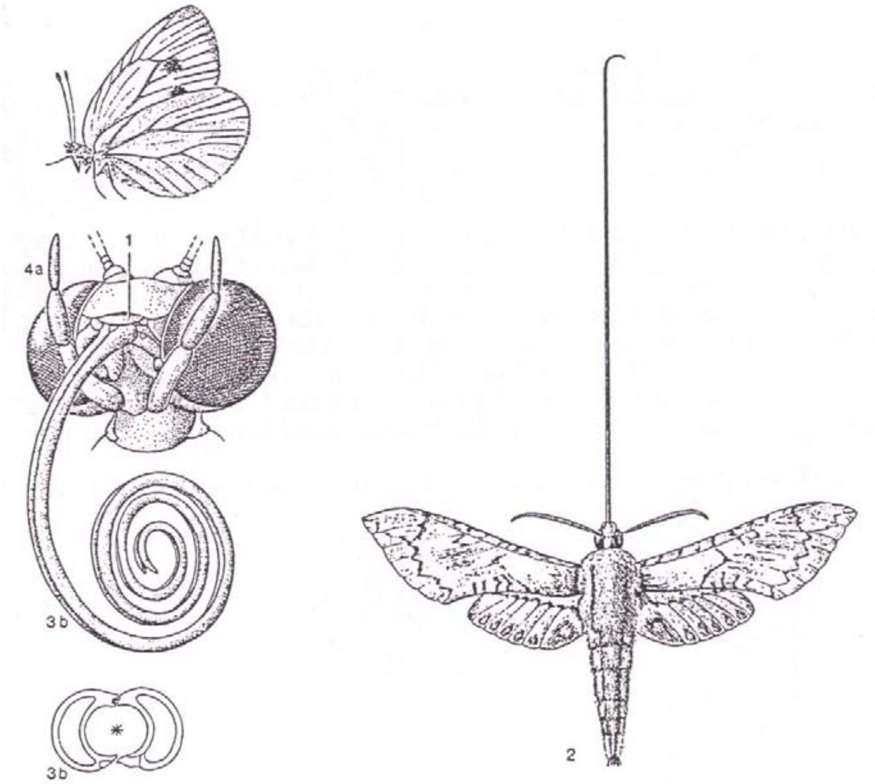


f. Lepidoptera (Butterflies and Moths) almost all feed at flowers as adults. Those which do not either do not feed at all and are short lived, or, as in some specialized moths in tropical Asia they feed on animal secretions or even blood. Most feed only on nectar. A few use pollen.

   i. Notable are the *Heliconius*, *Battus*, and *Parides* butterflies and their making a soup of nectar and pollen leachate on flowers and imbibing it.

   ii. Nectar may be converted to fat in migratory moths.

   iii. The proboscis of Lepidoptera is an amazing example of natural engineering.



g. The Hymenoptera is the most important order of anthophiles because it contains the bees.
   i. Even the phylogenetically primitive sawflies are often found feeding on floral nectar, pollen, or floral parts.
   ii. The Apocrita comprise the Parasitica and Aculeata.
   iii. The Parasitica range from minute parasitic wasps to large parasitic ichneumon wasps.
   iv. Nectar is a well known food for these insects and without it their longevity and fecundity is reduced.

v. They are associated with flowers with easily accessible nectar, often the flowers are white. They have short sucking mouthparts.

vi. Special relationships of wasps in this group include some Orchid pollination (hammer orchids of Australia), mimetic pheromones and pseudocopulation.

vii. Especially fascinating is the intimate relationship of figs and their pollination by Agaonid wasps.

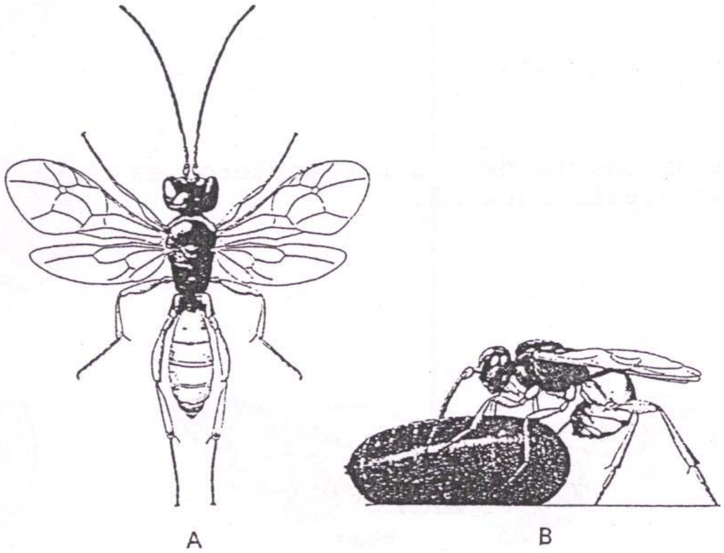


Figure 35–47. A hyperparasitic ichneumonid, *Phygadeùon subfúscus* Cresson (Phygadeuontìnae). A, adult male; B, female ovipositing in puparium of the host. The host of this ichneumonid is a tachinid fly, *Aplomyiópsis epiláchnae* (Aldrich), which is a parasite of the Mexican bean beetle, *Epiláchna varivéstis* Mulsant (see Figure 32–83). (Courtesy of USDA.)

h. The Aculeata include ants, wasps, and bees.

i. Ants use floral nectar from small, open-bowl shaped flowers.

ii. Social wasps may be frequently seen visiting flowers. They collect nectar from various flowers, but especially urn shaped (bell-shaped) flowers which are dull in colour.

iii. The bees (Apoidea) are the most important pollinators and the most highly evolved for anthophily. They gather nectar and pollen for provisioning their nests and the cells wherein the females lay eggs.

iv. Bees are diverse in form, some have short proboscides, others very long proboscides.

v. Highly complex relationships exist between bees and plants.

vi. Monoletic bees are restricted to one species of host plant are known e.g. squash bees, some cactus bees.

vii. Oligolectic bees visit a wide variety of plants (honeybees are polylectic).

viii. Among bumblebee species in a given habitat is separation of the flowers they visit according to the length of their proboscides.

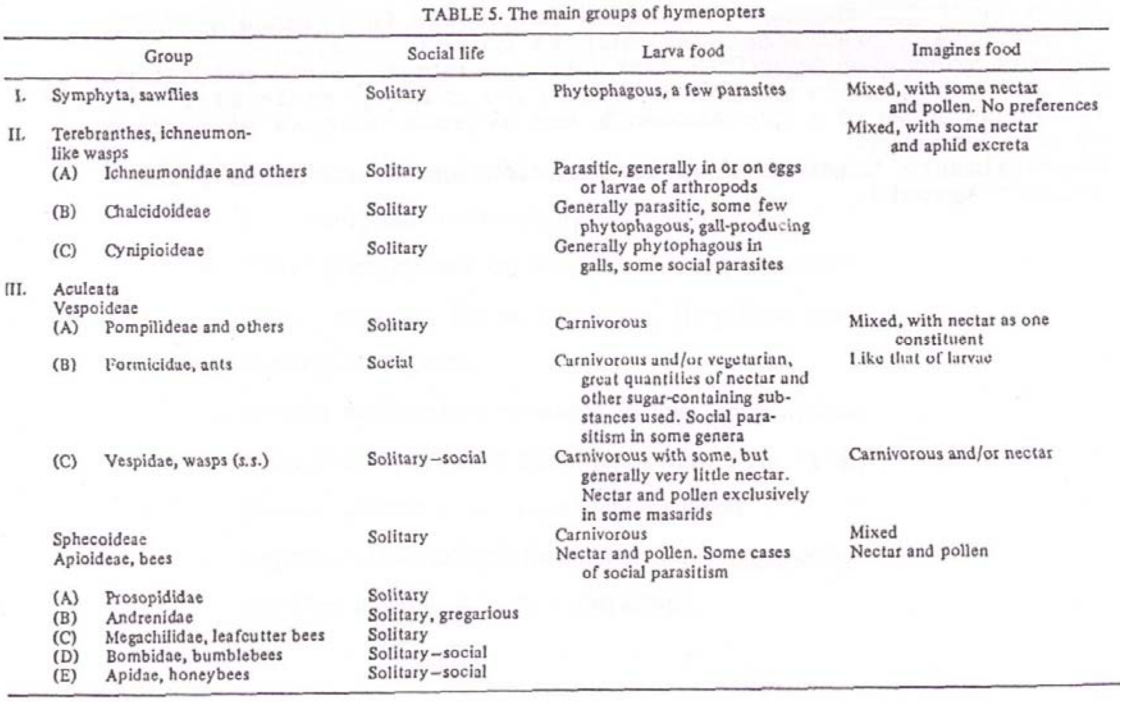
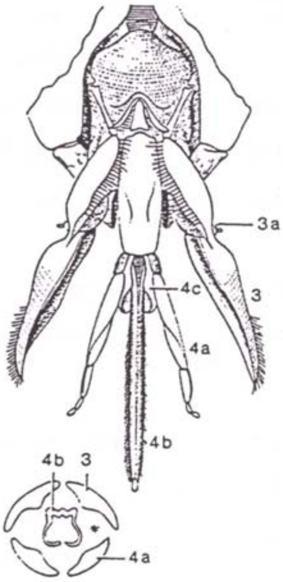


TABLE 5. The main groups of hymenopters

Group		Social life	Larva food	Imagines food
I.	Symphyta, sawflies	Solitary	Phytophagous, a few parasites	Mixed, with some nectar and pollen. No preferences
II.	Terebranthes, ichneumon-like wasps			Mixed, with some nectar and aphid excreta
	(A) Ichneumonidae and others	Solitary	Parasitic, generally in or on eggs or larvae of arthropods	
	(B) Chalcidoideae	Solitary	Generally parasitic, some few phytophagous, gall-producing	
	(C) Cynipioideae	Solitary	Generally phytophagous in galls, some social parasites	
III.	Aculeata Vespoideae			
	(A) Pompilideae and others	Solitary	Carnivorous	Mixed, with nectar as one constituent
	(B) Formicidae, ants	Social	Carnivorous and/or vegetarian, great quantities of nectar and other sugar-containing substances used. Social parasitism in some genera	Like that of larvae
	(C) Vespidae, wasps (s.s.)	Solitary–social	Carnivorous with some, but generally very little nectar. Nectar and pollen exclusively in some masarids	Carnivorous and/or nectar
	Sphecoideae	Solitary	Carnivorous	Mixed
	Apioideae, bees		Nectar and pollen. Some cases of social parasitism	Nectar and pollen
	(A) Prosopididae	Solitary		
	(B) Andrenidae	Solitary, gregarious		
	(C) Megachilidae, leafcutter bees	Solitary		
	(D) Bombidae, bumblebees	Solitary–social		
	(E) Apidae, honeybees	Solitary–social		



Floral Attractants

Floral Attractants

Advertising the flower and its products to pollinators.

Appeal to senses of pollinators
- Photosensory
- Chemosensory
- Mechanosensory
- Thermosensory
- Chronosensory

Photosensory vision
- Colour and colour patterns
- Size
- Shape
- Motion

Chemosensory olfaction & gestation
- Smells
- Taste

Mechanosensory tactile or touch
- Texture

Thermosensory temperature sense

Chronosensory time sense

1. Photosensory attractants (vision)
    a. Discrimination of wavelengths (colour)
    b. Sharpness of vision resolving power of the eye visual acuity (shape & size)
    c. Reaction spedd of optical nerve cells (motion).
    d. Eyes
        i. Camera eye of vertebrates
            1. Light enters the eye throught the cornea, aqueous humor, blocked by iris, enters pupil, through lens where most focusing occurs, through vitreous humor and image cast on retina; retinal cells photoreceptor nerve cells.

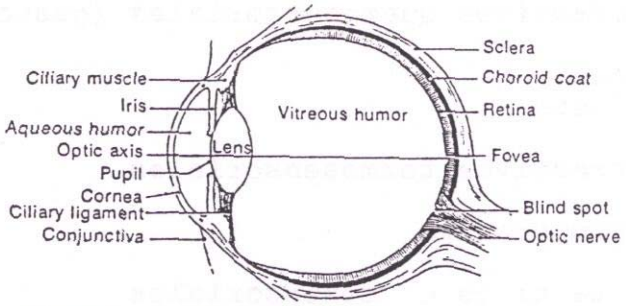
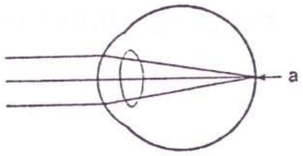


Figure 24–12 Diagrammatic section of the human eye. *The retina contains the light-sensitive rods and cones; the* lens and cornea focus light rays on the retina; and the iris regulates the amount of light entering the eye by changing the diameter of the pupil. The human eye changes focus for near and far vision by changing the shape of the lens; certain birds change the curvature of the cornea; fish change the position of the lens in the eye; and mollusks shorten the eye, bringing the retina nearer the lens for distant vision.



2. Receptor cells
    - a. Rods: 125 million not colour sensitive
    - b. Cones: 6,5 million colour sensitive, especially densely packed at fovea.
3. Cones of 3 types: blue, green, and red receptors (lots of overlap)
    - a. Rods and cones contain visual pigments
    - b. Retinal (=vitamin A aldehyde) + proteins (=opsins)
    - c. Rhodopsin = visual purple, non-colour vision
    - d. Iodopsin = visual pigment for colour vision
4. Mechanism:
    - a. Rhodopsin + light quantum → lumirhodopsin (unstable)
    - b. Lumirhodopsin breaks down, excites nerve cell, nerve impulse to brain
    - c. Break down products resynthesized to rhodopsin, but takes time in humans a light flash of 1 x 10-6 sec lasts 1/10 sec as image in eye
    - d. Image persistence allow fusion of flickering images movies, TV, fluorescent lights at about 30 images/sec
5. Colour vision less understood
    - a. Blue cones peak sensitive at 436nm

        b. Green cones = 546nm
        c. Red cones = 700nm
            i. Lots of overlap, e.g. green cones excited by light from 450 to 675nm
        d. Three primary colours = trichromatic colour vision
            i. (compare with TV colours, colour printing)
        e. In hummingbirds there are red pigments in optic humors
        f. Bats have Achromatic vision, no colour, black & write vision
        g. Vertebrates with colour vision:
            i. Some fish, some reptiles, most birds, many primates

ii. Compound eye of insects
    1. Insect vision through compound eye gives mosaic vision
    2. Compound eye up of facets (=ommatidia)

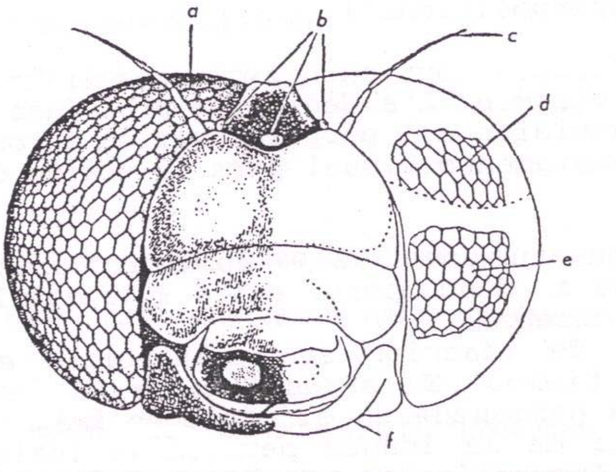


Fig. 1. Semischematic drawing of the head of the dragonfly *Libellula quadrimaculata* (frontal view). After Mazokhin-Porshnyakov (1959). *a:* faceted eye. *b:* three simple dorsal ocelli. *c:* antenna. *d:* larger facets in the eye's upper half. *e:* smaller facets in the eye's lower half. *f:* buccal apparatus.

    3. Light enters each facet through corneal lens (crystalline cone) focused onto retinula cells. Retinula cells visual pigments, as in vertebrates, stimulate nervous impulses to brain.

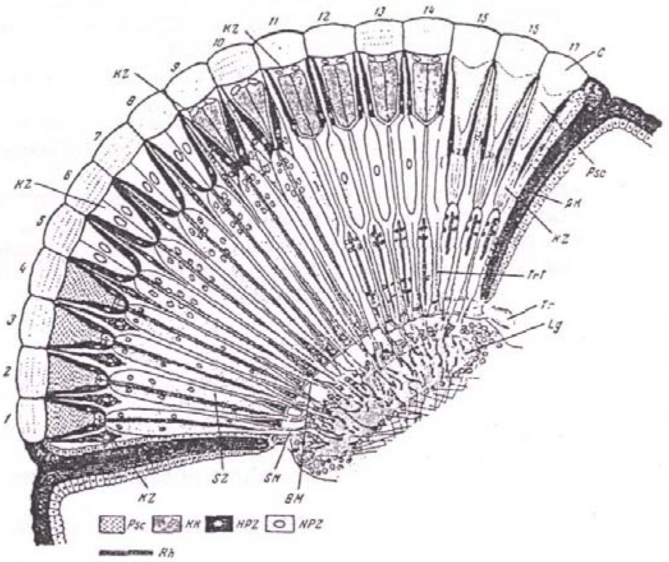
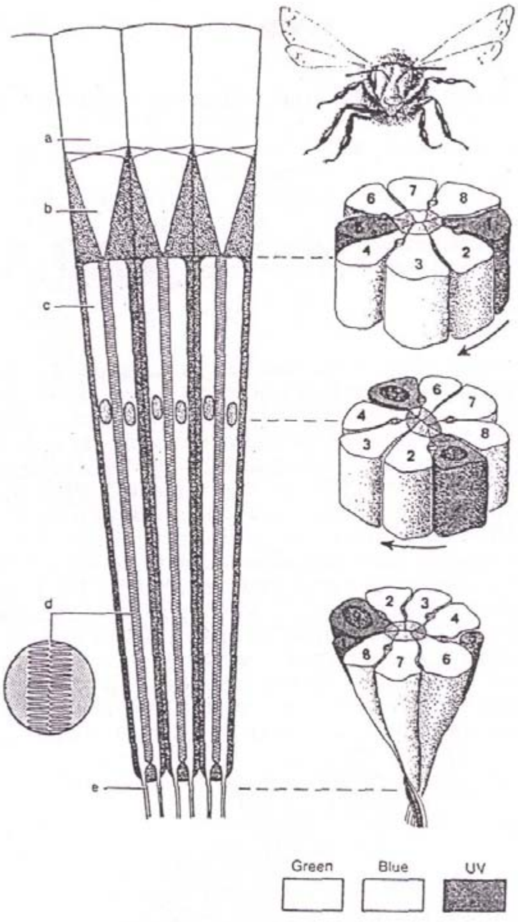


Fig. 2. Schematic structure of faceted eye. After Weber (1949). *1–10:* ommatidia of an apposition eye; *1–4:* pseudocone ommatidia with soft crystalline cone; *5–8:* acone ommatidia; *9–10:* eucone ommatidia with terminal cone; *11–17:* ommatidia of a superposition eye; *11:* ommatidium in state of light adaptation; *11–14:* eucone ommatidia with central cone; *15–17:* pseudocone ommatidia with cuticular cone. *AK:* eye capsule. *C:* cornea. *KK:* crystalline cone. *KŽ:* cells of Semper. *HPZ:* Primary (corneagenous) pigment cells. *NPZ:* secondary iris (accessory) pigment cells. *BM:* basament membrane. *Lg:* axons of the neurons of the lamina gangliouaris *Psc:* pseudocone. *SZ:* visual cells. *Tr:* trachea. *TrT:* tracheal tapetum. *Rh:* rhabdom. *SN:* axon of a visual cell (post-retinal fiber).

Fig. 37:
Individual ommatidia in the eye of the honeybee. (a) Lens; (b) crystalline cone; (c) visual cell; (d) the central rhabdom formed by fine membrane projections of the individual visual cells and containing the visual pigment; (e) fiber from the visual cell that conducts its signals to the next processing station. On the right are cross sections of one of the ommatidia at different levels. It is constructed of nine sense cells, which except for the short cell number 9 are twisted about the long axis. Each ommatidium contains all three types of visual cells: green-sensitive (3, 4, 7, 8), blue-sensitive (2, 6), and ultraviolet-sensitive (1, 5, 9).



4. Iris cells have light shielding pigments. Pigments can change position according to amount of light, bright light pigments shield ommatidia from each other, dim light light can penetrate from one ommatidium to next.
    a. Bright light apposition image
    b. Dim light superposition image

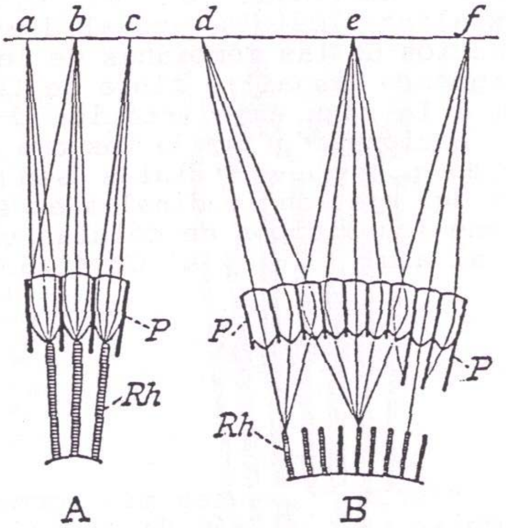


Fig. 23. Diagram showing image formation by the compound eye

A, eye forming apposition image. B, eye forming superposition image. *a–f*, luminous points with the course of the rays emitted by them; *P*, pigment; *Rh*, rhabdom. At the right side the migration of pigment into the light adapted position results in an apposition image; all rays except those entering the central facet are intercepted. (*From* Wigglesworth *after* Kuhn)

5. Each ommatitium bundle of cells spiral around rhabdom
6. Cells sensitive to three colours in many insects
7. Again Trichromatic Colour Vision: most work on honeybees (*Apis mellifera*)
8. But three primary colours are different:
    a. Ultraviolet (UV)
    b. Blue-green
    c. Yellow

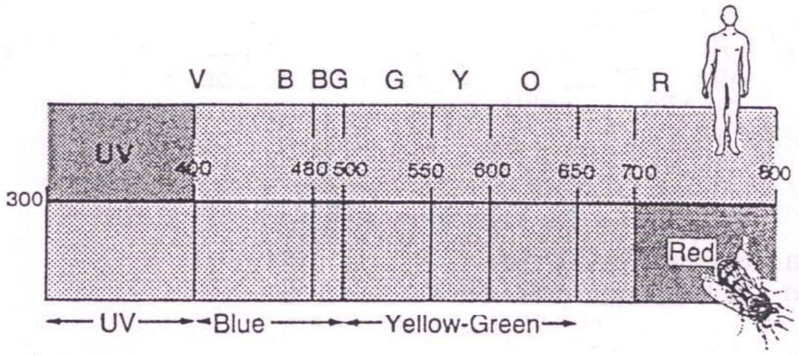


Fig. 33:
Color vision; a comparison of the wavelength spectra visible to humans and bees. Unlike the bee, the human cannot see ultraviolet (UV); unlike the human, the bee cannot see red (R).
V violet, B blue, BG blue-green, G green, Y yellow, O orange. The numbers give the wavelengths of the light in nanometers.

9. Insects (most so far examined) see UV but not red.

10. Humans (and other vertebrates) see red but not UV.

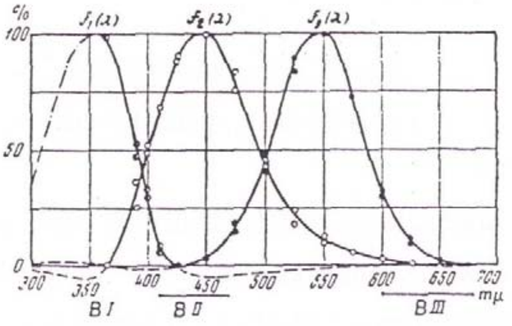
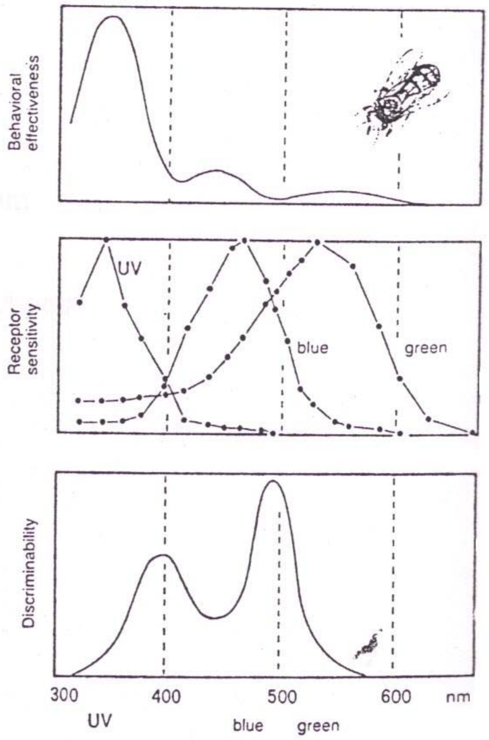


Fig. 90. Color composition curve for the eye of *Bombus distinguendus*.



11. But still trichromatic colour vision mixing lights of different wavebands create secondary colour.

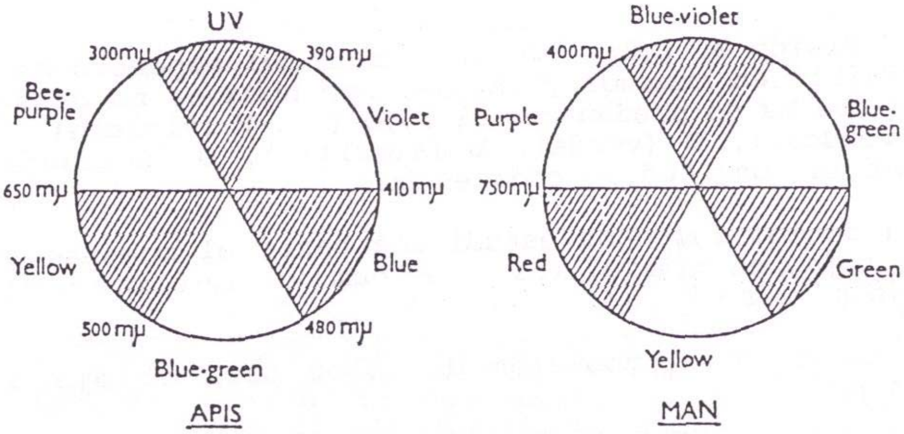


FIG. 88 Colour circle of man and honey bee (*Apis mellifera*) (*after* Burkhardt, 1964, and Daumer, 1956). Cross-hatched areas denote primary colours, white areas the secondary colours. Pairs of complementary colours lie at the opposite ends of diameters of the circle. A mixture of appropriate quantities of two complementary colours will appear indistinguishable from white light

Apidologie (1993) 24, 309-331 © Elsevier/INRA/DIB/AGIB

Review article

Color vision and color choice behavior of the honey bee

W Backhaus

Institüt für Neurobiologie, Freie Universität Berlin, Konigin-Luise-Str 28-30, 1 000 Berlin 33, Germany

(Received 29 October 1992; accepted 22 April 1993)

Summary - A general introduction to color vision in honeybees has been presented. Documenting the current state of research in this field, the theory of color vision and color choice behavior of the honeybee has been reviewed. Several tests of the predictions of the theory for behavioral and electrophysiological experiments have been presented. The properties of color memory have been derived. A complete neuronal interpretation of the color theory has been given. The decision-making process has been discussed with respect to the fluctuations in the neuronal network. In specifically designed experiments, the information provided by the color vision system has been combined with the information from other perceptual systems in color choice behavior. Respective extensions of the color theory for the bee have been discussed.

Apis mellifera / honey bees / color vision / choice behavior / perception / psychophysics / electrophysiology

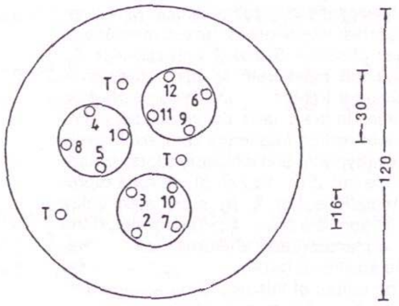
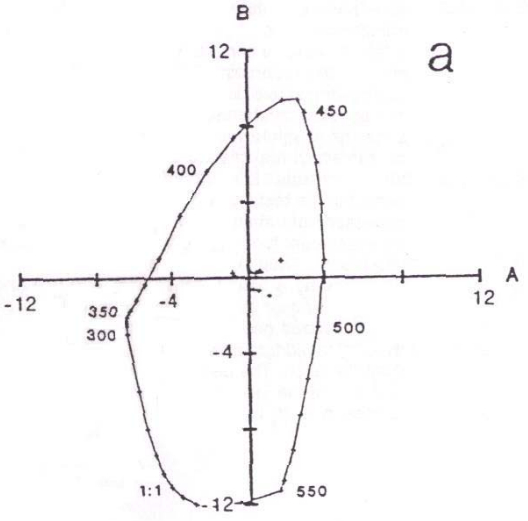


Fig 1. Sketch of the vertical arrangement for the multiple choice experiments performed for multidimensional scaling analysis for determining the subjective color space of the bee (from Backhaus *et al*, 1987). The experiments were performed outdoors with free-flying bees. The color stimuli presented in the tests (indicated by numbers) were cardboards and glass-filters covered with UV-transparent Plexiglass. The arrangement was illuminated by northern sky light (no direct sunlight). During training, the rewarded color signal T was presented at 3 different places outside the 3 groups of 4 color signals. During the tests, these stimuli were covered with a sheet of the same grey as the background.



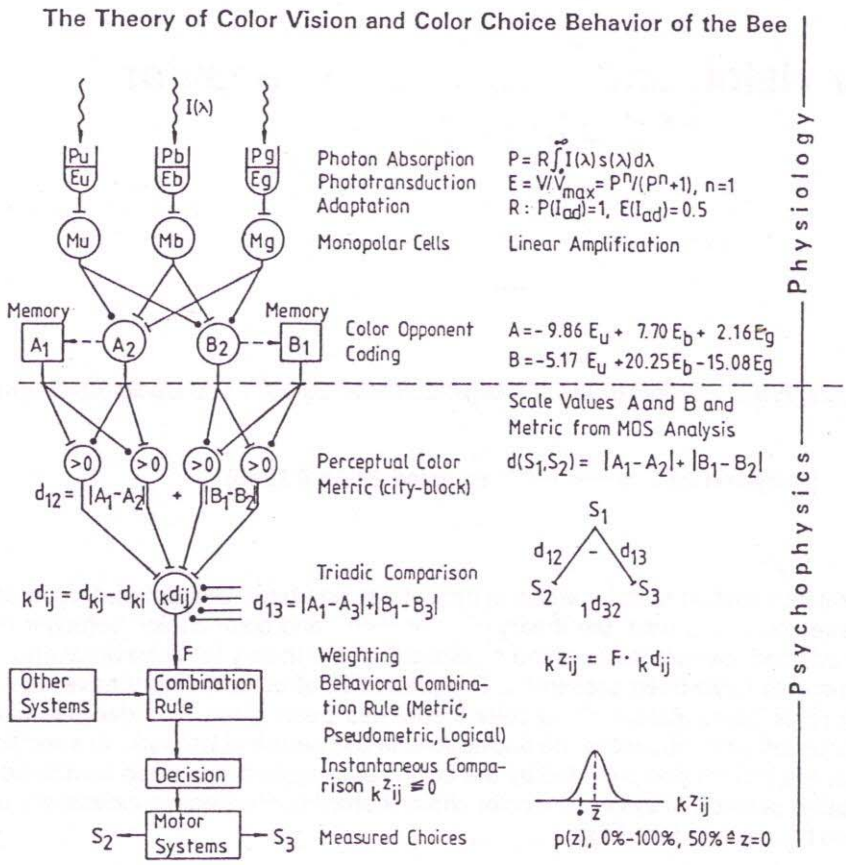


Fig 3. The theory of color vision and color choice behavior of the bee. The upper part (above dashed line) is related to the physiology of the color vision system. The lower part is related to psychophysics of color vision. The complete mathematical description (right side) and the neuronal interpretation of the theory (left side) is presented. $I(\lambda)$: light intensity; u,b,g: photoreceptor cell types; R: range sensitivities; $s(\lambda)$: spectral sensitivity; P: absorbed photon flux; E: cell excitation; V: cell potential; M: monopolar cell; A,B: excitations of color opponent coding neurons (circles: interneurons, boxes memories); d_{ki}: color difference of 2 stimuli S_k and S_i; ${}_kd_{ij}$: judgment values of stimuli S_i and S_j with stimulus S_k; F: experiment type dependent scaling factor; ${}_kd_{ij}$: weighted judgment values; $p(z)$: inverse z-transformation to choice percentages p. Also the psychophysical part of the theory (lower part, right side) allows for a complete neuronal interpretation. All the neurons in the small network possess simple (linear) properties: >0: 2 antagonistic coding neuron types with resting frequency zero, exclusively coding for positive differences in the synaptical inputs. Excitatory (hyphen) and inhibitory (dots) synapses appear interchanged in both neuron types. So the sum of the ouput of this pair of neurons represents the absolute value of the difference in the (memorized) excitations A or B. ${}_kd_{ij}$: a judgment value neuron which realizes the city-block metric by adding the results from the pairs of (>0)-neurons. If the training stimulus is not shown (but stored as A and B values in memory) and 2 alternatives are presented in the tests, this neuron gets an inhibitory input from the additional (>0)-neurons, providing the necessary information about the additional color difference. The output of this neuron is weighted by an experiment type-dependent factor F. In mixed contexts, in which the behavior is not exclusively related to color vision, other perceptual systems can contribute to the choice behavior as well which is described by a behavioral combination rule (metric, pseudometric or logical relation) (see text). The decision process is related to the actual sign of weighted judgments values. The decision process is well described according to Thurstone's (1927) law of comparative judgment Case V (see text), describing the judgment values ${}_kd_{ij}$ as fluctuating according to a Gaussian function with a constant standard deviation. The decision process is instantaneous, *ie* the decisions are made according to the actual sign of the judgment values ${}_kd_{ij}$ at the moment of decision. If ${}_kd_{ij}$ is >0, for example, stimulus S_3 is chosen; if ${}_kd_{ij}$ is <0, stimulus S_2 is chosen.

e. How to measure colour colorimetry
  i. Need to know amount of available in wavelength of each primary colour.
  ii. Methods:
    1. Reflectance spectrophotometry. Does not provide detailed information on colour patterns, but gives accurate measures of reflectance.
    2. Photography through a series broad-band monochromatic filters. Gives approximate measures of reflectance if done correctly with calibrated gray-scale (steps from write to black through shades of gray) but does give detailed information on fine colour patterns.
  iii. Why is a gray-scale needed?

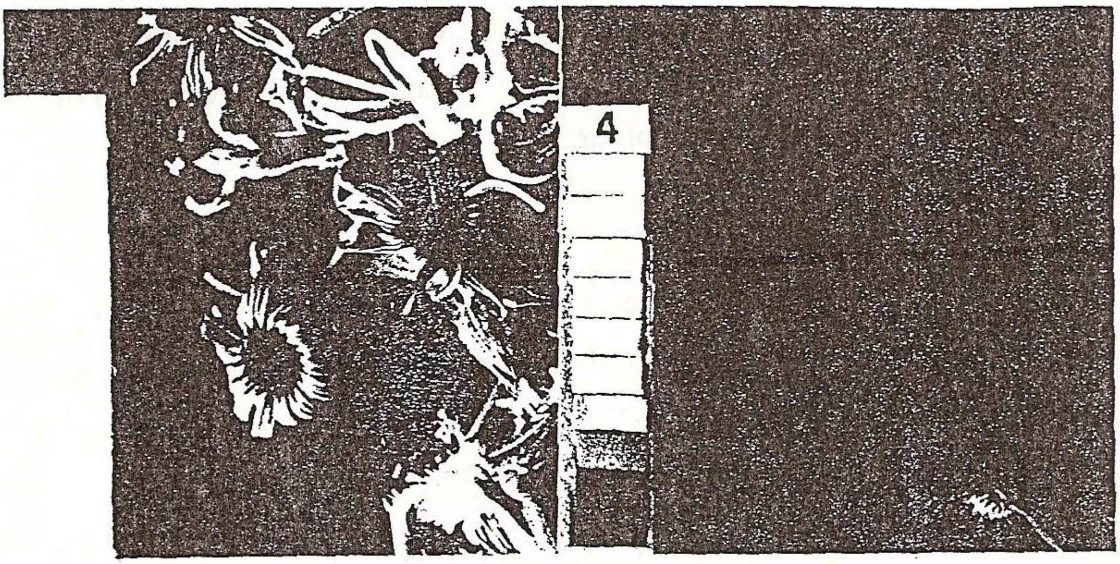


Fig. 2. Over-exposed photograph of *Haplopappus lyallii* in UV (left). Illusion of bright UV reflectance is given, but reflectance of ligulate florets corresponds to dark end of grey-scale (gradient lost by over-exposure compared with correctly exposed photograph on right) at about 5% only. Hirsute vegetation on right is also almost invisible in UV light. Both photographs were taken on the same occasion on the same roll of film. Printing was identical for both.

    1. To assure correct exposure
    2. To assess approximate reflectance
  iv. Result: spectral reflectance curve for all parts of the flower
  v. Next step: plotting colours on colorimetric co-ordinates on trichromaticity diagram (triangular) and using relative amounts of reflectance to generate each point or locus. Easy to understand if only one colour is reflected
    1. Blue, a blue flower
    2. Red, a red flower (but insects do not see red as a colour)
  vi. But what if 2 or 3 colours are reflected?
    1. Calculations needed
      a. From spectral reflectance curve obtain

i. Reflectance in each of the three primary colour wavelengths: Rs, Rm, Rl where s, m, l mean shortest, middle, and longest wavelength (for humans blue, green, red: for insects UV, blue-green, yellow).
ii. Sum the reflectance values: Rs+Rm+Rl
iii. Take each primary colour reflectance value and divide by the sum to obtain relative amounts of light reflected in each primary colour waveband. e.g. Rm/(Rs+Rm+Rl)=M
iv. Plot point for M, L on trichromaticity diagram.
v. e.g. for a pure blue flower Rs=30%, Rm=0%, Rl=0%, S=1, M=0, L=0
   locus is 0, 0 right down in blue corner of the diagram
vi. e.g. for a write flower Rs=30%, Rm=30%, Rl=30%, S=0.33, M=0.33, L=0.33
   locus is 0.33, 0.33 right in the centre of the diagram
vii. Can do exactly the same for the insect visual spectrum and plot in the same way using UV, blue-green, and yellow.

Examples:

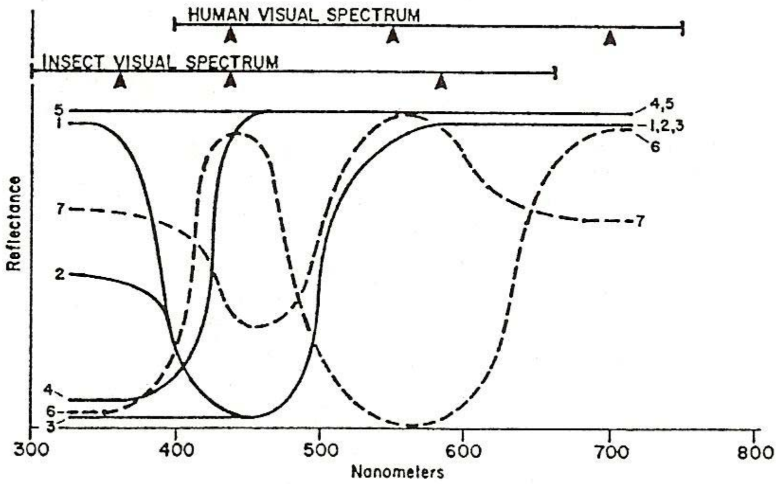


Figure 1-5. Spectral reflectance curves for some hypothetical colors. The human and insect visual spectra are given and the primary colors pointed out for each (arrowheads). Curve 1 is yellow, or insect-purple; curve 2 is yellow, or insect-reddish-purple; curve 3 is yellow, or insect-red; curve 4 is white, or insect-yellow; curve 5 is white, or insect-white; curve 6 is purple, or insect-green; curve 7 is greenish-yellow, or insect-mauve. (See also Figs. 1-6 and 1-7.)

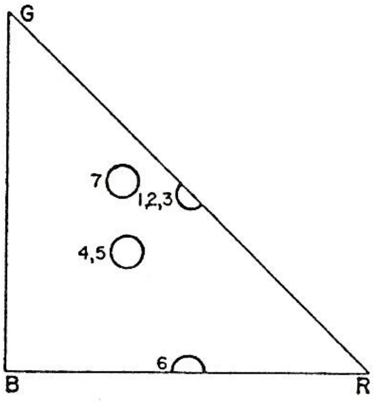


Figure 1-6. Trichromatic plots for the colors described in Fig. 1-5 on a color triangle for the human visual spectrum.

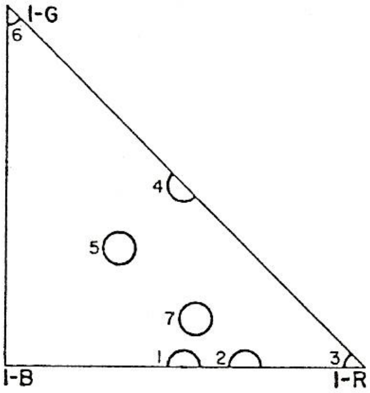
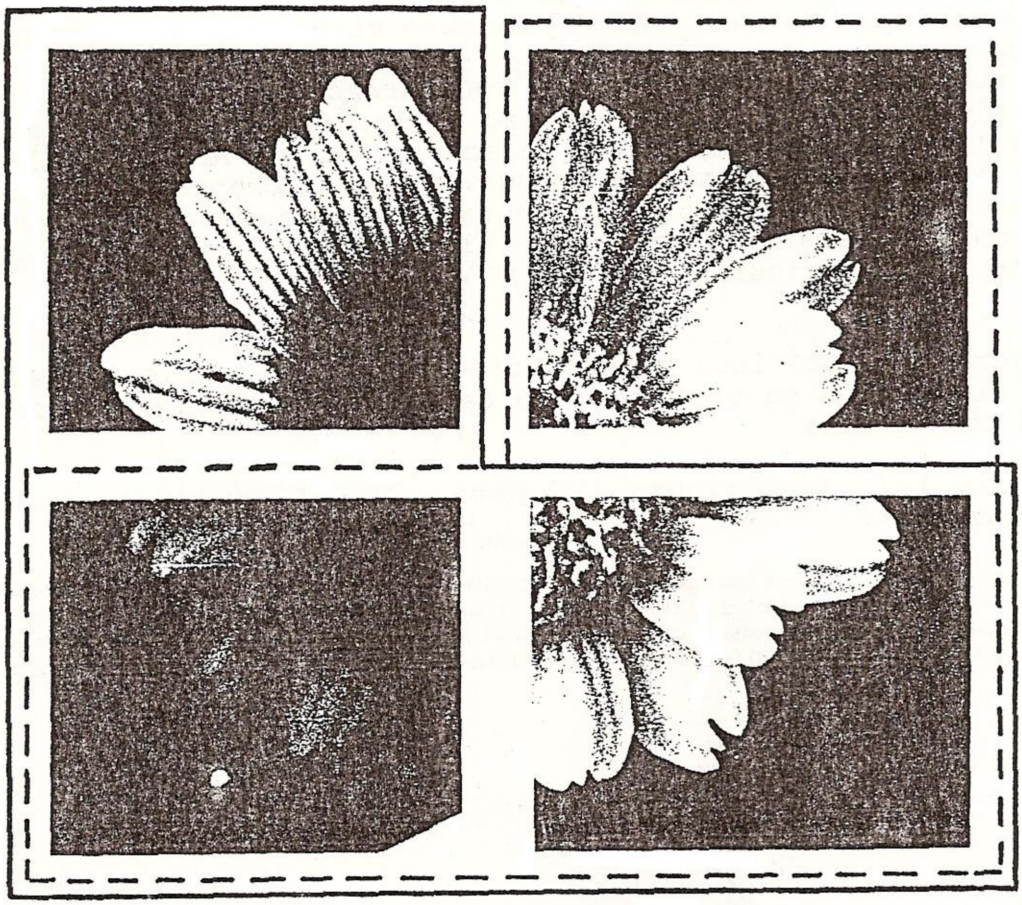
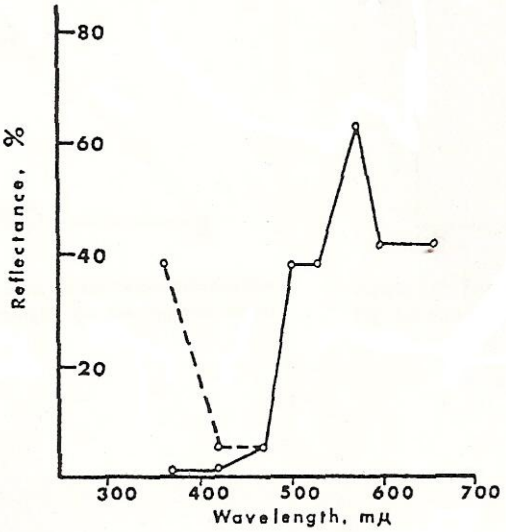
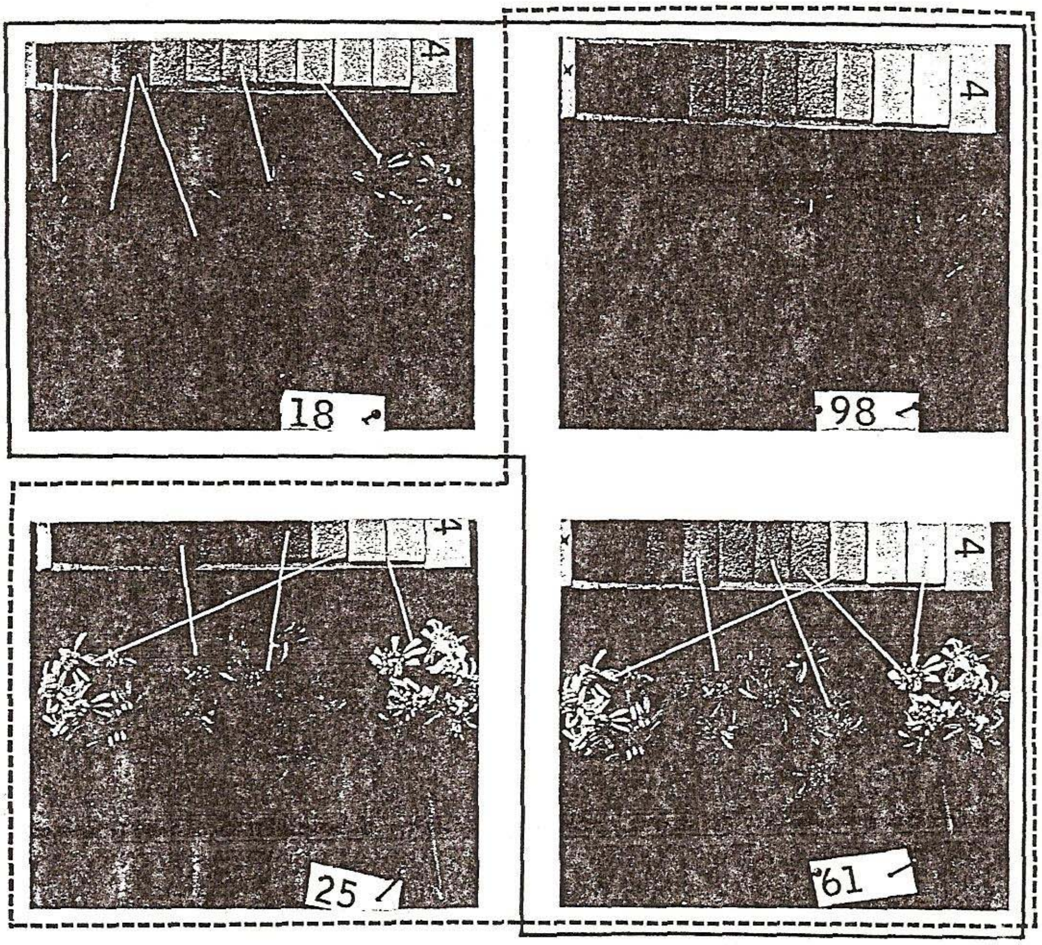
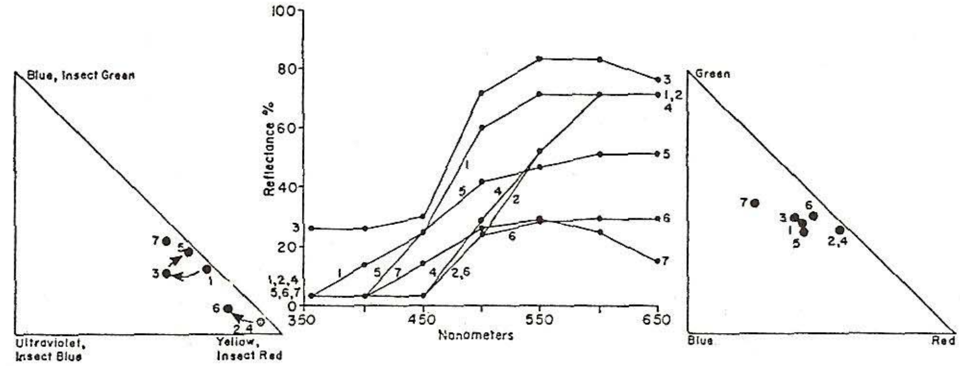


Figure 1-7. Trichromatic plots of the colors described in Fig. 1-5 on a color triangle for the insect visual spectrum.




Reflectance, %
80
60
40
20
300
400
500
600
700
Wavelength, mμ


4
18
4
98
4
25
4
61


Blue, Insect Green
Ultraviolet, Insect Blue
Yellow, Insect Red
7
5
3
1
6
2,4
Reflectance %
Nanometers
100
80
60
40
20
0
3
350
450
550
650
1,2,4
5,6,7
1
5
7
4
2,6
1
5
4
2
6
3
1,2
4
5
6
7
Green
Blue
Red
7
3
6
1
5
2,4

P. G. KEVAN

Something very interesting eventuates when **whole floras are represented** on such a diagram for the colours of their flowers

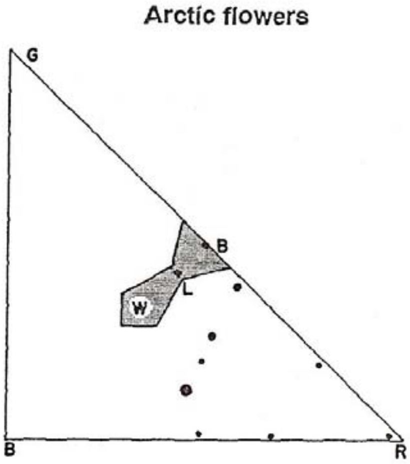


Figure 1-8. Trichromatic plots of the colors of flowers in the Canadian High Arctic on a color triangle for the human visual spectrum. *B* is Blue; *G* is Green; *R* is red; *W* is equiproportionate reflectance white. Diameters of spots outside shading are proportionate to number of species represented (1, 2, or 3). Width of the shaded area is proportionate to the number of species; 22 yellow, 6 pale yellow, and 20 white flowers or flower parts. (Data from Kevan, 1970, 1972.)

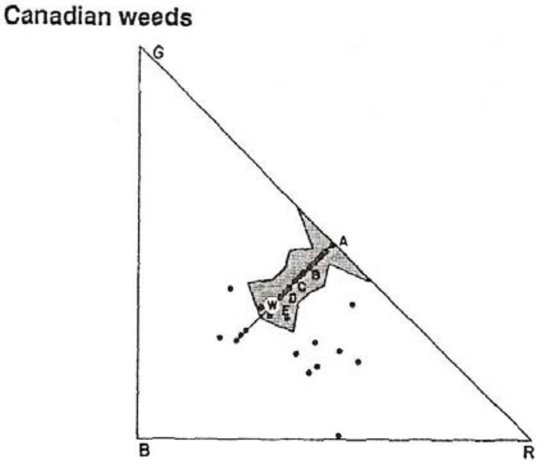


Figure 1-10. As Fig. 1-8, but for the weeds around Ottawa, Canada. The width of the shaded area at each letter represents for *A*, 37 observations; *B*, 21; *C*, 5; *D*, 6; *E*, about 22 (= *W*). Other spots represent single observations of flowers or floral parts. (Data from Mulligan and Kevan, 1973.)

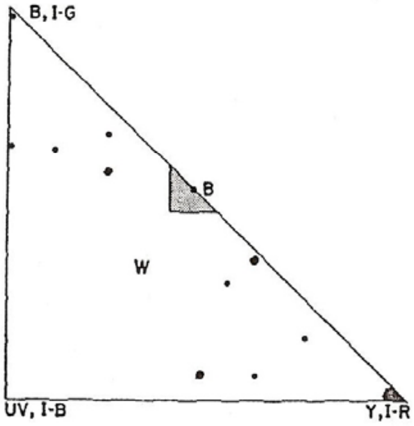


Figure 1-9. As Fig. 1-8, but on a color triangle for the insect visual spectrum. Insect-yellow (shaded area) shows 13 observations, and insect-red shows 14. *UV, I-B* is ultraviolet or insect-blue; *B, I-G* is blue or insect-green; and *Y, I-R* is yellow or insect-red; *W* is equiproportionate reflectance white.

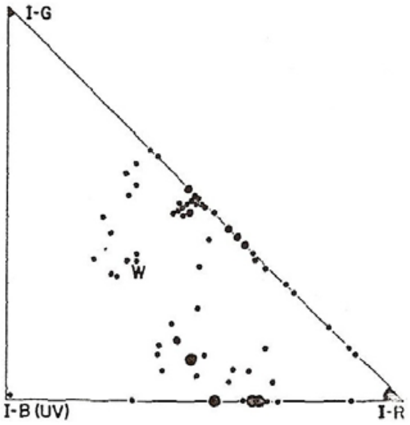


Figure 1-11. As Fig. 1-9, but for weeds around Ottawa, Canada. Points represent only 1, 2, or 3 observations of flowers or floral parts. At *I-R*, insect-red, there are 37 observations, many of floral parts in color combination with other loci.

Lessons:

1. There are more floral colours in the Insect Visual Spectrum than in the Human
2. The colours are more discrete
3. There are more colour combinations
4. More of the Trichromaticity space is taken up
5. Each primary colour is equally important (UV is not any more special than the other two primary colours)
6. Floral coloration and insect colour vision and the photic environment must be considered together.

Pergamon

0042-6989(93)E0089-P

Vision Res. Vol. 34, No. 11, pp. 1489-1508. 1994

0042-6989/9457.00 + 0.00

Ultraviolet as a Component of Flower Reflections, and the Colour Perception of Hymenoptera

LARS CHITTKA,* AVI SHMIDA,t NIKOLAUS TROJE,t RANDOLFMENZEL*

Received 5 April 1993; in revised form 12 August 1993

Based on the measurements of 1063 flower reflection spectra, we show that flower colours fall into distinct clusters in the colour space of a bee. It is demonstrated that this clustering is caused by a limited variability in the floral spectral reflectance curves. There are as few as 10 distinct types of such curves, five of which constitute 85% of all measurements. UV reflections are less frequent and always lower in intensity than reflections in other parts of the spectrum. A further cluster of colour loci is formed in the centre of the colour space. It contains the colour loci of green leaves, several other background materiais and only very few flowers. We propose a system to classify the reflection functions of flowers, and a set of colour names for bee colours.

Colour coding Colour vision Flower colours Hymenoptera Signals Spectral reflectance Ultraviolet

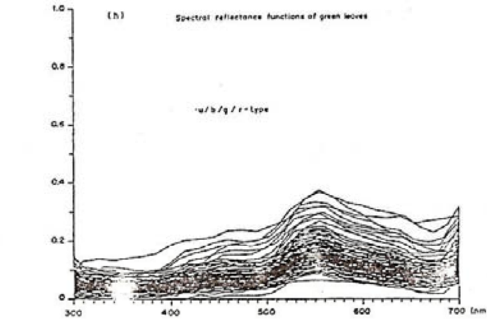
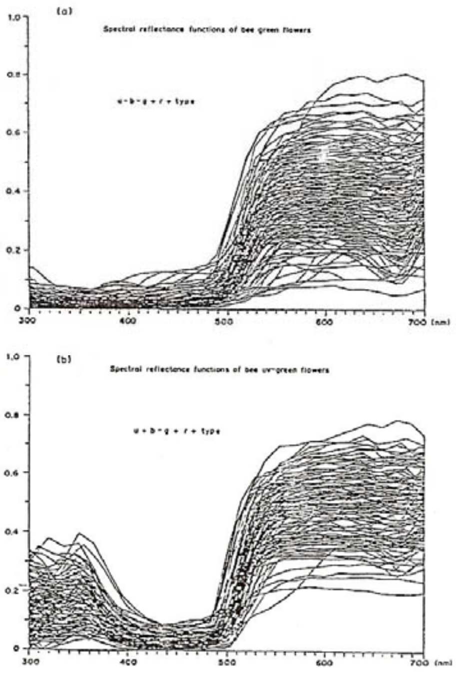


FIGURE 6 (a–h) The spectral reflectance functions of all flowers and leaves. Seven figures (a–g) contain the spectral reflections of flowers that yield loci within the seven bee colour categories UV, UV-blue, blue, blue-green, green, UV-green, and uncoloured. (h) The spectral reflection functions of green leaves. If a graph contains more than one basic curve type, then insets show the curve types included.



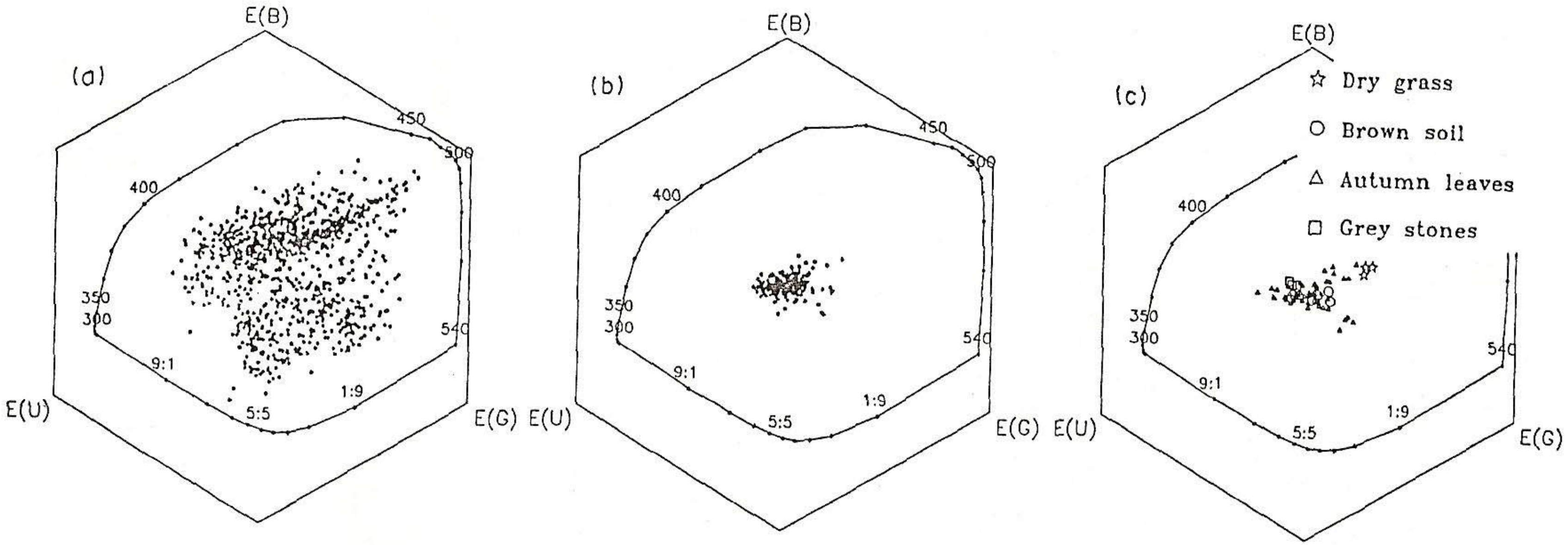


FIGURE 2. The loci of all 1063 measured flower colours are plotted in the colour hexagon (a), as well as the loci of 243 leaves (b) and the loci of several other materials that serve as backgrounds for some flowers (c). The spectrum locus (solid line) connects the loci of monochromatic lights. Together with the UV-green line, it marks the border of the colour space outside which no colour loci can be obtained. Since the locus of a colour changes if the intensity is altered (Backhaus, 1992; Chittka, 1992), the intensity for each monochromatic light is adjusted so that a maximal distance from the centre of the diagram is achieved.

Nectar guides very common:

- Some visible to humans
- Some invisible to humans, but visible to insects (guides in UV)

Butterfly flowers:

- 83% with guides, 63% in UV, 66% in human visible

Zygomorphic flowers

- 76% with guides, 42% in UV, 68% in human visible

Capitulate flowers/inflorescences

- 67% with guides, 56% in UV, 30% in human visible

Open bowl flowers

- 50% with guides

Function of nectar guides has been shown experimentally

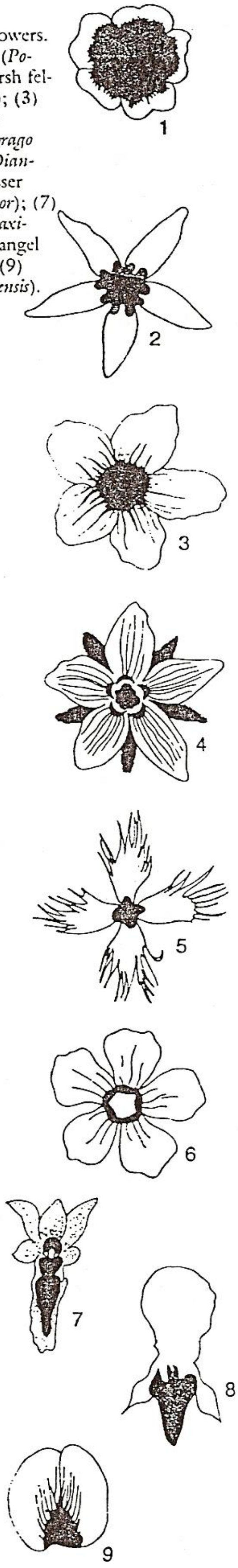


Fig. 39:
Ultraviolet marks of flowers. (1) Golden cinquefoil (*Potentilla aurea*); (2) marsh felwort (*Swertia perennis*); (3) white bryony (*Bryonia dioica*); (4) borage (*Borago officinalis*); (5) pink (*Dianthus arenarius*); (6) lesser periwinkle (*Vinca minor*); (7) Jersey orchid (*Orchis laxiflora*); (8) yellow archangel (*Galeobdolon luteum*); (9) broom (*Cytisus canariensis*).

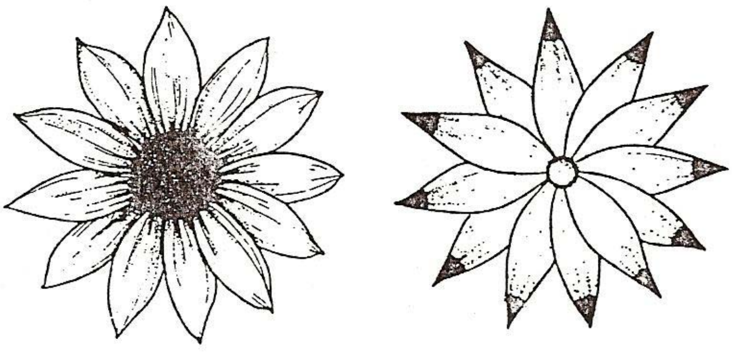


Fig. 42:
In an experiment on the head-proboscis reaction the ray florets are plucked out and put back together in the reverse orientation, so that the UV-absorbing marks (black) point outward.

Positive effects of guides on pollinator landings on artificial flowers:

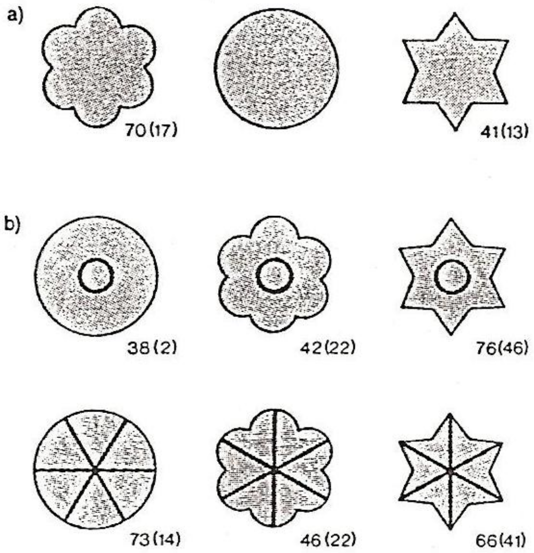


Fig.41: On which flower models does the honeybee land M(ilegível) often? (a) First the bees were trained to the round model in the middle (diameter 3cm). Then in the test they were confronted with the round model and one of the two others; they clearly preferred each of the two alternatives to the round model. The number of landings is shown below the models, with the value for the round model in parentheses). (b) In the second series of experiments the bees had to choose between a pure vellow model with no marks and a model of the same shape with blue marks. It preferred the model with the nectar guide. The number of the landings is given under each model, with the value for the model without a nectar guide in parentheses.

Positive effect of guide on probing accuracy by months.
Affects orientation of pollinators on flowers.

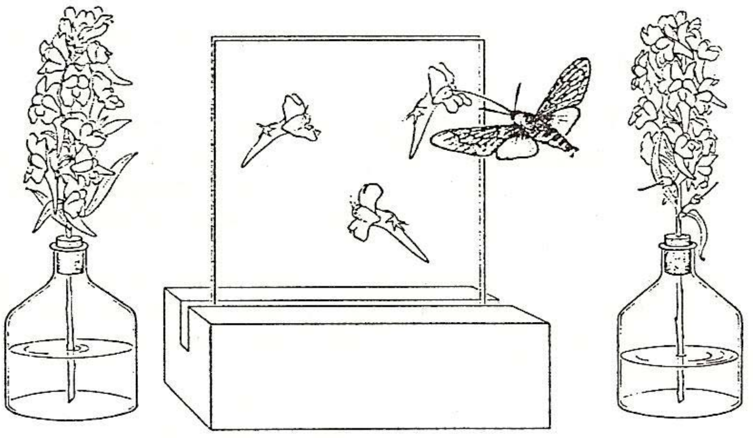


Fig. 40:
The hummingbird hawkmoth (*Macroglossum stellatarum*) in an experiment to demonstrate the effectiveness of the nectar guides of the common toadflax (*Linaria vulgaris*). The moth's proboscis leaves traces exactly over the nectar guides of the flowers mounted between the panes of glass.

N.B. there are other kinds of guides besides visual ones, scent and texture.

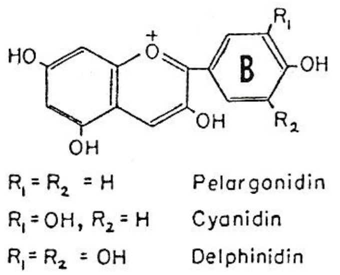
Chermical of colour floral pigments

Three types of pigments:

- Flavonoids
- Carotinoids
- Betalains

Flavonoids are water soluble and in cell vacuoles

- Two kinds:
- Anthocyanin pigments
    - Most widely distributed colours in reds, blues, purples, pinks, and orange
    - pH indicators
    - Red if acidic, blue if basic
    - Change in pH of cell protoplast as flowers age, change in colour, commonly from pink to blue in Boraginaceae, Leguminosaceae, Labiatae.



Substitutions of R make for different colour:

Pelargonidin (orange)
R1=R2=H

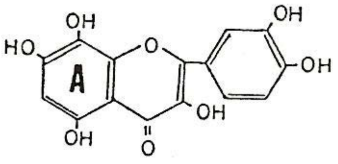
Delphinidin (blue)
R1=R2=OH

Cyanidin (magenta)
R1=OH, R2= H

- Anthochlor pigments (yellow to orange)
    - pH causes changes in colour, basic then change from yellow to orange.
    - Two kinds, chalcones and aurones.

- Flavonoids pigments (yellow to orange)
    - Substitutions in ring change colours

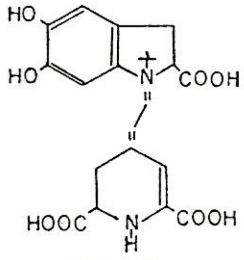
(b)



Gossypetin

- Carotinoid pigments
    - Are lipid soluble and held in chromoplasts
    - Xanthophylls (pale yellow)
    - Carotenes (intense yellow)
- Betalain pigments
    - Are water soluble and in plant vacuoles
    - Restricted to Centrospermae (Caryophyllales)
    - Two types Betaxanthins (yellows), Betacyanins (red to purplish)
    - Representative betalain

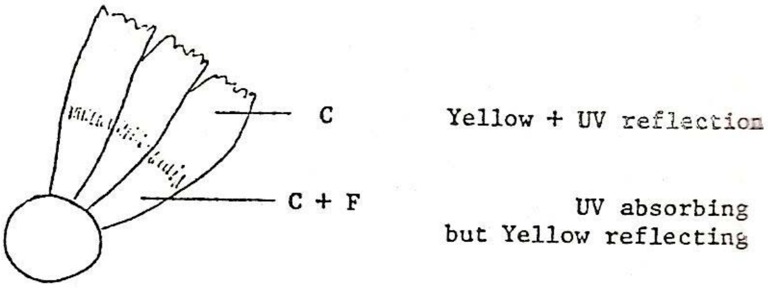
(c)



Betanidin

UV reflectance and pigments understood in yellow Compositae

- Whole ray has carotenoids (reflect yellow)
- Proximal part of rays with flavonoids (absorb UV)
- Distal parto f rays without flavonoids (reflect UV)
- Two-colour bull's eye pattern: centre is yellow = insect red, periphery is yellow + UV = insect purple



What about the vegetational background behind flowers in bloom? Most vegetation is fairly evently reflecting in the insect visual spectrum, generally dull. Green appearance to humans mostly caused by intense absorbtion of red light. Thus, to insects coloured flowers bloom against a dull yellowish-grey background.

Floral size

- Not much investigated.
- Positive correlations between numbers of pollinators visiting

inflorescences of various plants (milkweeds to roses) and size of inflorescence.

- Inflorescence is the attractive unit.
- For individual flowers, little information, one study on bumblebees showing larger flowers attract over greater distances than do smaller ones.
- No quantified and rigorous studies as for colour.

Questions to be addressed:

1. Resolving power of insect eye: for humans it is about 1 second solid angle

   For honeybees about 1.4 degrees
   For housefly about 4 degres

   Has to do with mosaic vision which is not very sharp.

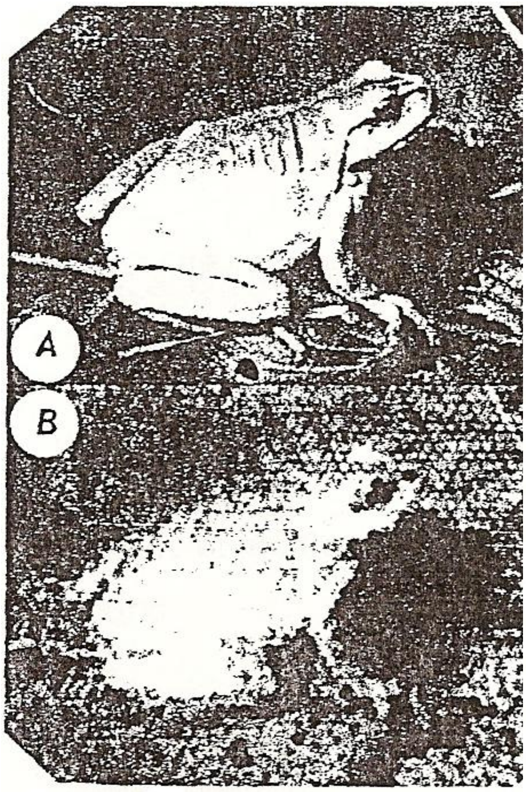


Fig. 54: The frog *Hila* (A) and its mosaic image (B) as perceived by the fly *Eristalis* at a distance of 8.5 cm.

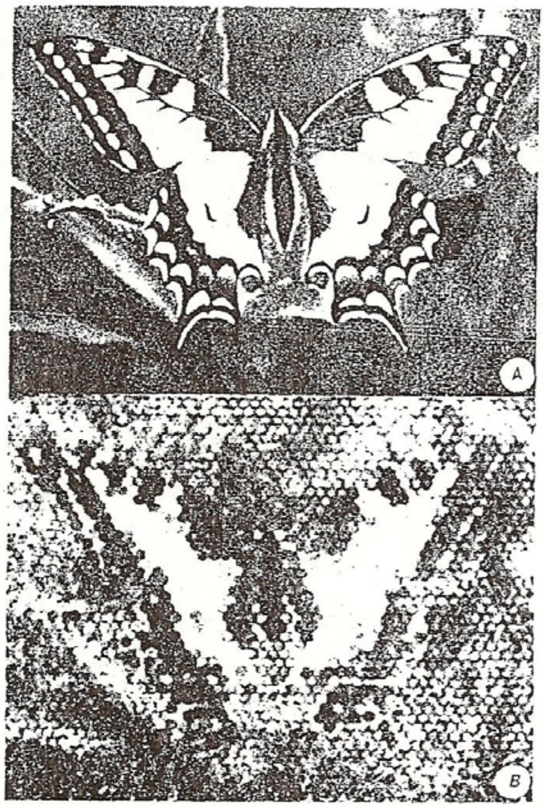


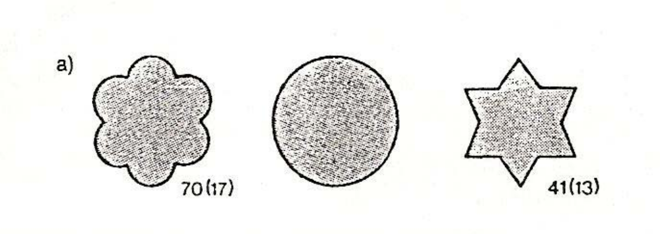
Fig. 55. *Papilio machaon* (*A*) and its mosaic image (*B*) as perceived by the dragonfly *Aeschna* at a distance of 10 cm. After Mazokhin-Porshnyakov (1958)

2. Contrast against background: 10% difference in reflectance is probably enough (data range 1% to 23%) for insects.

Use these concepts to determine how far away from a patch of flowers/an inflorescence/or floral part a pollinator must be to see it.

Floral shape

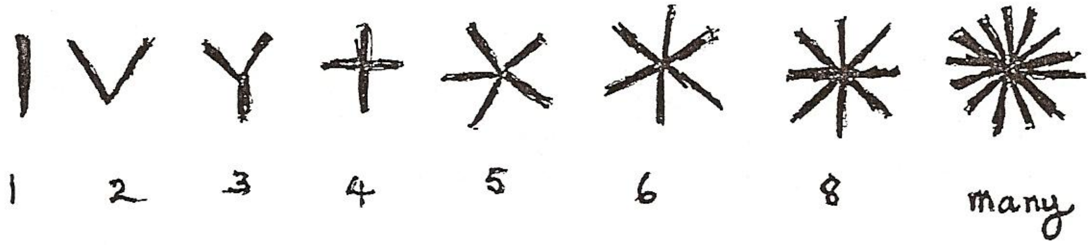
- Better understood, but has to be considered along with form and pattern.
- Honeybees and butterflies are attracted to divided shapes more than to uniform ones.



Honeybee shape discrimination:

Fig. 44:
Whereas honeybees easily learn to distinguish each of the upper figures from any of the lower ones, they cannot discriminate within the upper or the lower group.

Formalize to “Figure Numerals” described by Leppik:



And further to Pattern recognition described by Gould in 1985.

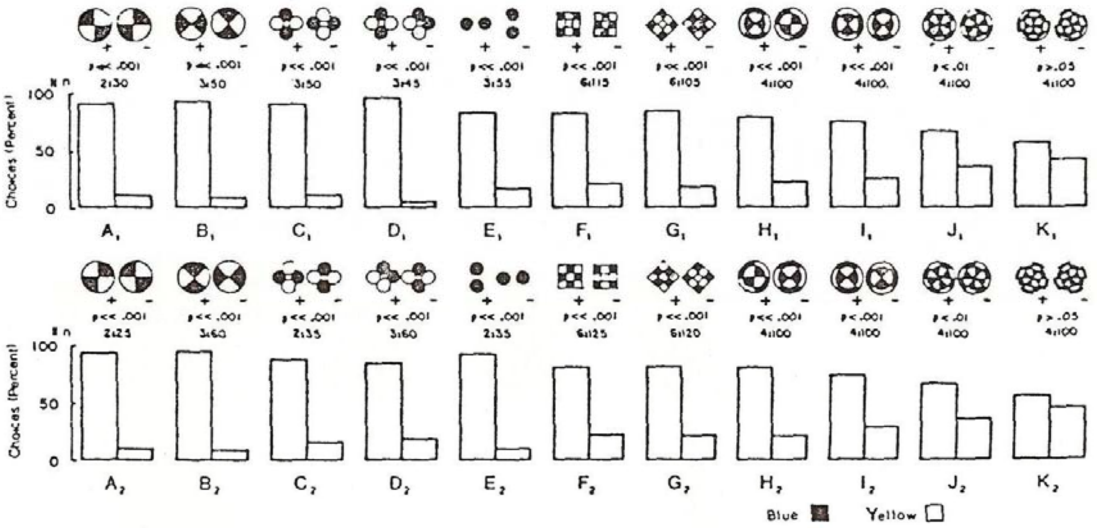


Fig. 1 - Bees were trained to find food at the center of the pattern marked "+". Number of bees tested (N) and number of landings (n) are indicated as N:n under the P values. The center squares in the patterns of experiments F and G were green, the same color as the background. The percentage of choices of the correct (+) and incorrect (-) patterns are indicated by the bar graphs under the alternative patterns.

Figure Numerals are reminiscent of radiating petals, which honeybees apparently count! Patterns used by Gould are not especially reminiscent of flowers forms.

Floral motion

- Very little studied.
- Some flowers with mobile appendages which seem to attract pollinators.
- Whole flowers move (sway to flicking back and forth in the wind) and may be more visually attractive than stationary flowers.
- Experiments are needed.

Chemosensory attractants (smell and taste)

- Smell on Antennae
- Insect has exoskeleton, box of chitin all over outside
- Chemosensory information must penetrate to nerve cells inside
- On exoskeleton are specialized microscopic area for sensory transduction

Sensilla (sensillium)

- Honeybee worker has 40,000 sensilla/antenna
- Various types
- Hairs (trichodea)
- Hairs with pores
- Pegs with and without pores
- Plates with and without pores
- 6,000 pore plate sensilla on a worker honeybee antenna
- Each plate 12 microns across
- Each plate with 18 or so cells beneath
- Each plate with 3,500 pores
- Each pore 15 x 10-6 mm across

Electrophysiological recordings to determine what chemicals the sensilla react to

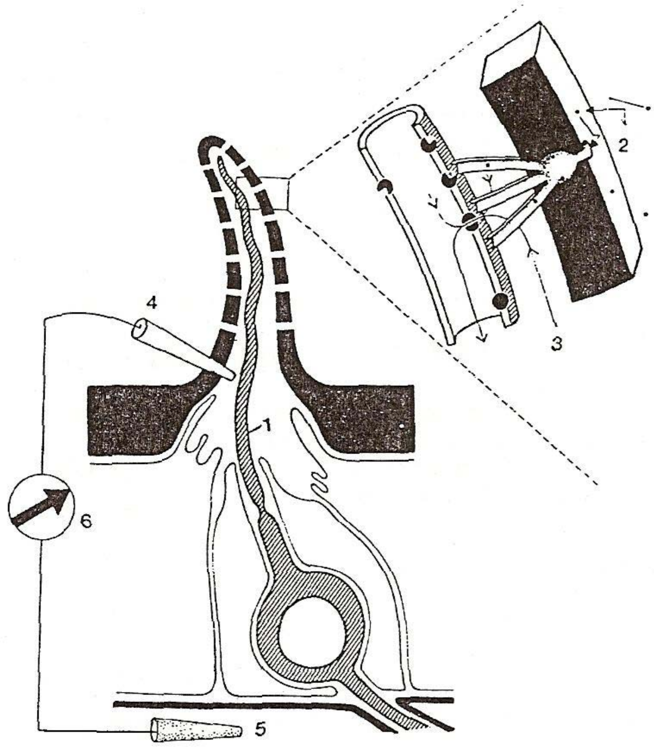
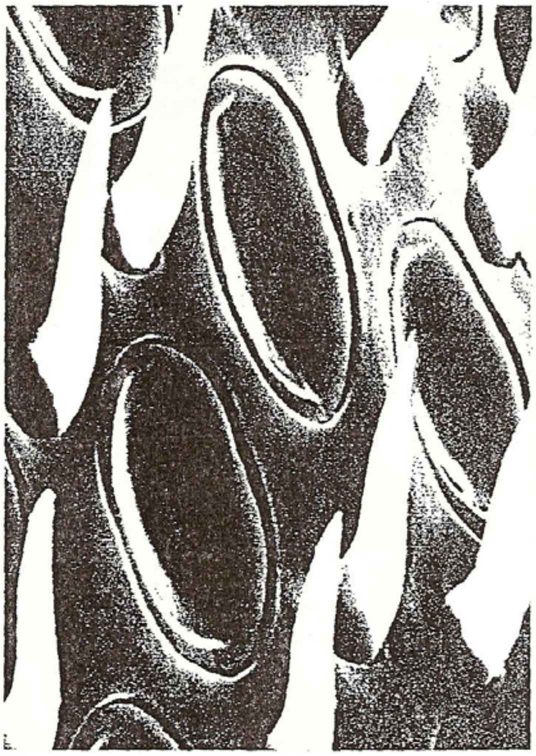


Fig. 57:
The lepidopteran olfactory hair. (1) The stimulus-receiving process of the sense cell; (2) one of the many pores in the hair wall, enlarged; (3) flow of current through the membrane after a scent molecule has struck it; (4) probe to measure the electrical response of the sense cell to the stimulus; (5) reference electrode in the blood within the branch; (6) measurement and display instrument (oscilloscope).

Scent diffuses in and excites nerve ending below the plate



Pore plates on antenna of honeybee.

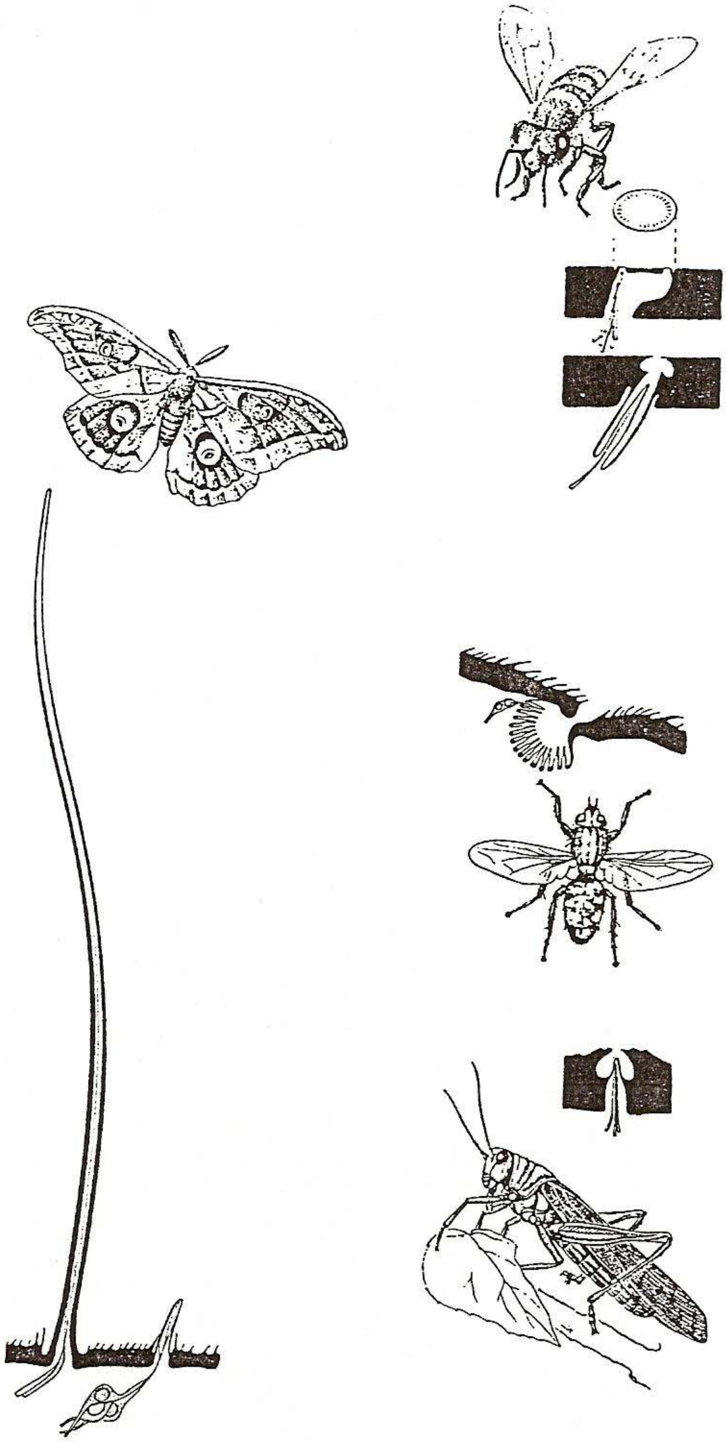


Fig. 52:
Typical olfactory sense organs on the antennae of lepidopterans (long and short hairs), bees (pore plates above, sunken pegs below), flies (composite pit organ), and grasshopper (simple pit organ).

Behavioural experiments also determine the sensitivity of insects to various scents.
Orientation in odour fields (olfactometry)

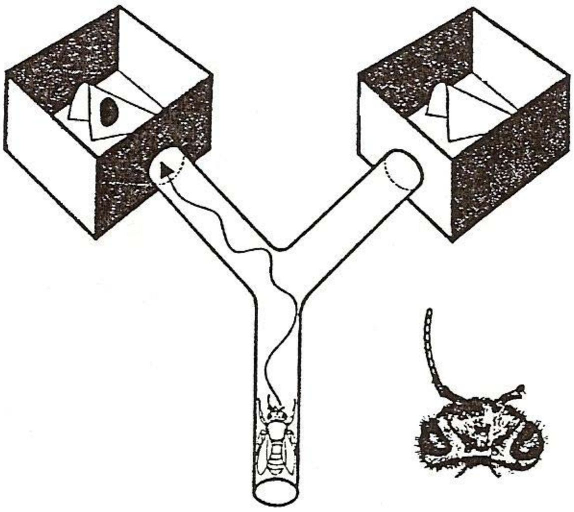


Fig. 49:
A bee without a right antenna and with left antenna fixed, in a choice experiment. It follows a typical oscillating path to the scented paper.

Honeybees abilities to perceive scents is a little better than our own human ability to discriminate between scents seems remarkable.
Of 1,816 odour pairs presented to honeybees, they could discriminate between the two 1,729 times!
Insects can learn scents and the order of scents.

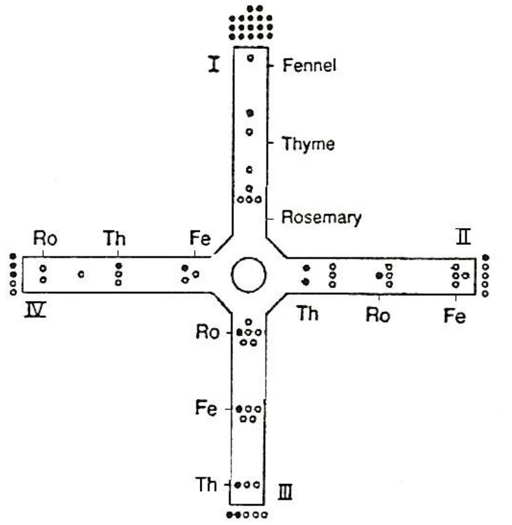


Fig. 51:
An odor arena; the bees enter through the opening in the middle. Then most of them (68.5 percent of runs) proceed through Passage I, with the combination "rosemary-thyme-fennel" to which they were trained. They have learned to break down a sequence of neighboring odors into its components, in the right order. The symbols in the passages indicate reversal points, where the run was interrupted. ○ one event, ● five events.

Insects discriminate scents
e.g. honeybees on alfalfa
bumble bees on *Polemonium viscosum*

- *Polemonium viscosum* flowers of two types in terms of smell
- Sweet smelling
- Skunky smelling
- Bumblebees given a choice of evenly spaced, alternating array of

the two types of flowers preferred sweet smelling flowers over skunky ones between 80% and 60% of the time and had to avoid skunky flowers when going between sweet smelling ones.

Within flowers scent patterns exist

- Probably 90% of flowers have scent patterns on the flower
- Scent patterns also parallel visual nectar guides
- Flowers with no visual nectar guides have olfactory nectar guides
- Most common guide is scent gradient intensifying towards the “centre” of the flower
- Some flowers have different scents on different parts

Much more research is needed, since 1954 almost nothing has been done.

What are floral scents?

- It is difficult to generalize in terms of chemistry
- Most floral scents have no counterpart outside flowers,
- Those that do are mimetic
- Floral scents are volatile, oxygenated, derivatives of alcohols/esters/aldehydes/ketones
- Some are terpenoid, some non-aminoid

Perhaps it is more useful to think of the scents in terms of the pollinators

Some commonly known floral scents

- Phenylacetaldehyde (of hyacynth and lilac)
- Geraniol (of roses)
- Citral (of orange and lemon blossoms)

Nocturnal flowers have heavy, often terpenoid and aminoid scents

- Attract moths and bats from afar
- Close-in attractant is pale colour

Diurnal flowers are less scented

- Visual attractants from afar
- Close-in attractant is scent and scent guides

Mimetic or deceit scents

- Dung and carrion mimicing flowers
- Aminoids, indole and scatole attractant flies (*Stapelia*, *Rafflesia*, *Araceae*)
- Pheromone mimicing scents
- Terpenoids, cadinene etc. attractant male bees and wasps to pseudocopulation

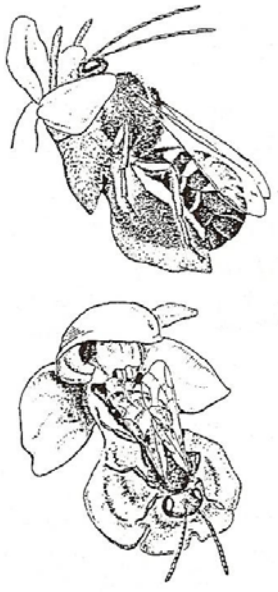


Fig. 68:
Pseudocopulation on *Ophrys* flowers. *Above*, the wasp *Gorytes mystaceus* on *Ophrys insectifera*; *below*, the bee *Andrena maculipes* on *Ophrys lutea*.

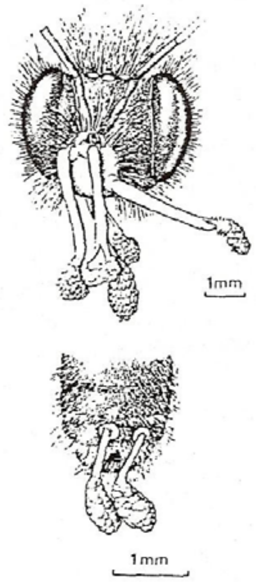


Fig. 69:
Above, the head of a long-horned bee (*Eucera nigrilabrus*) with pollinia of various *Ophrys* species; *below*, the abdomen of a bee (*Andrena maculipes*) with the pollinia of *Ophrys lutea*.

Insect perfume industry

- Orchid scents (oily mono-terpenoids in droplets) collected by bees, specially some Euglossines, and used as attractant for female bees
- Lots of interesting complexities to the story

Thought: if textural details are distinctive enough to be used by taxonomist, then what is the functional significance of the details

- Can pollinators tell flowers apart by micro-texture?
- Answer: Yes!!!!

Honeybees in a Y maze and given choice of texture (sunflower ray floret distal end first) to which they were trained to associate a reward (nectar from a capillary tube at the distal end of the floret) and another texture with reward tube in analogous place, but blocked off or open. Other textures were sunflower ray upside down, sunflower ray proximal end first, ray of *Xylorhiza*.

Results:

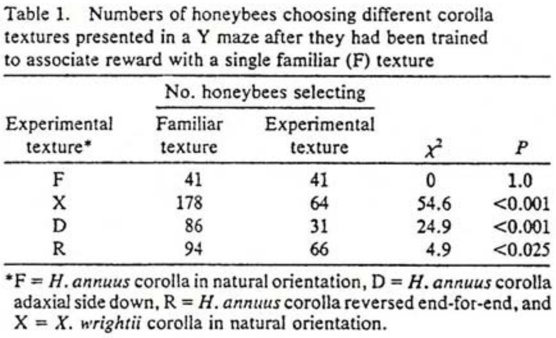


Table 1. Numbers of honeybees choosing different corolla textures presented in a Y maze after they had been trained to associate reward with a single familiar (F) texture

	No. honeybees selecting			
Experimental texture*	Familiar texture	Experimental texture	χ^2	P
F	41	41	0	1.0
X	178	64	54.6	<0.001
D	86	31	24.9	<0.001
R	94	66	4.9	<0.025

*F = *H. annuus* corolla in natural orientation, D = *H. annuus* corolla adaxial side down, R = *H. annuus* corolla reversed end-for-end, and X = *X. wrightii* corolla in natural orientation.

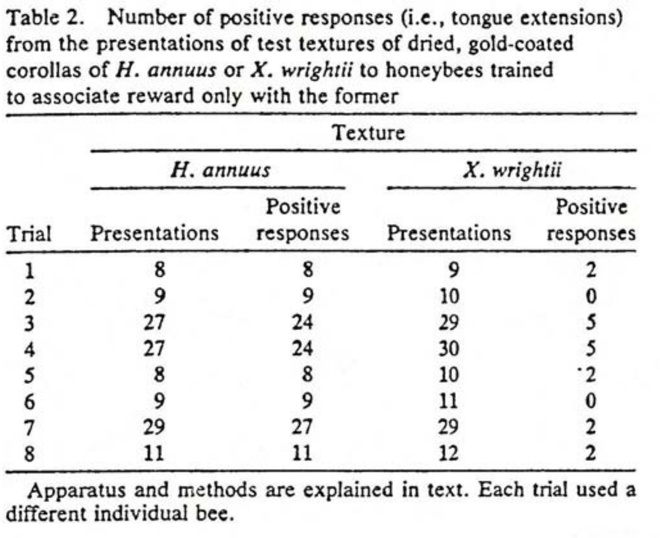


Table 2. Number of positive responses (i.e., tongue extensions) from the presentations of test textures of dried, gold-coated corollas of *H. annuus* or *X. wrightii* to honeybees trained to associate reward only with the former

	Texture			
	H. annuus		*X. wrightii*	
Trial	Presentations	Positive responses	Presentations	Positive responses
1	8	8	9	2
2	9	9	10	0
3	27	24	29	5
4	27	24	30	5
5	8	8	10	2
6	9	9	11	0
7	29	27	29	2
8	11	11	12	2

Apparatus and methods are explained in text. Each trial used a different individual bee.

Honeybees tethered in a drinking straw, only their poking out, then presented with distal end of sunflower ray floret and droplet of syrup.

Those that learned to present their tongues got fed. Next step, to give another texture and watch for tongue presentation.

No other insects have been investigated, although texture discrimination is known for a number at a much coarser-grained level.

Honeybee, and other pollinator discrimination is probably at the level of 1 micron or less! Physiological mechanisms through deflection of hairs (trichoid sensilla) and stimulation of nerve cells beneath.

Thermosensory attractants (heat or temperature)

- Not known to be an attractant to flowers per se.
- Some flowers produce heat, e.g. Araceae which may volatilize scent.
- Heat may serve to retain and protect trapped pollinators.
- Some flowers capture heat, which may be used by pollinating insects.

Taste on antennae, feet, mouthparts

- Sensilla are hairs and plates with pores and same mechanism as for smell except that contact with non-vaporized chemical distinguishes taste from smell.

Scent and taste can almost be thought of as being the same very little essential difference between the two.

Mechanosensory attractants (touch)

- Texture discrimination
- Floral surfaces have textures
- Fine textural details of petal epidermal cells used by taxonomists to distinguish species, especially in Compositae.

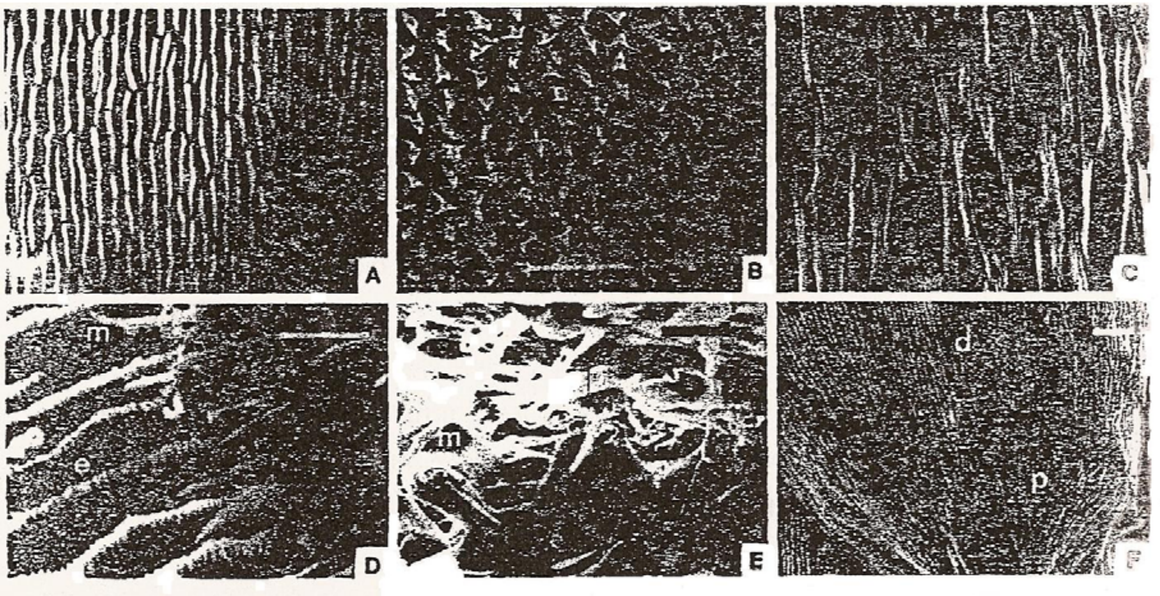


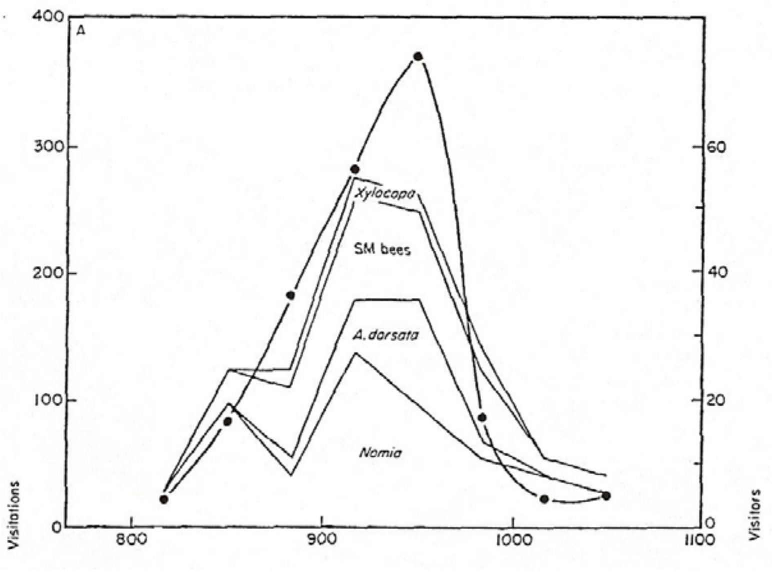
FIG. 1. (*A–C*) Scanning electron micrographs of the adaxial surfaces of Compositae ray corollas. (*A*) *Heterotheca inuloides*. Note the ridges and grooves of the major textural pattern and the orthogonal minor pattern. (*B*) *H. annuus*. Note the thin-walled papillate cells. (*C*) *X. wrightii*. Note the long-rectangular cells and difference in overall pattern from *Heterotheca* and *Helianthus*. (×525; bar = 50 μm.) (*D* and *E*) Antennae in contact with corollas. (*D*) *Apis mellifera* antenna in contact with *H. inuloides* corolla. (*E*) Megachilidae antenna in contact with *H. annuus* corolla. Note the correspondence of size and spacing of the mechanoreceptive sensilla (m) with the components of the corolla epidermal texture (e). (×2000; bar = 10 μm.) (*F*) *Bradburia hirtella* corolla, showing the longitudinal direction of the major pattern from the distal (d) to the proximal (p) portion of the corolla, where pollinator reward is located. (×100; bar = 100 μm.)

These uses of heat by pollinators and plants are better described under Floral Rewards.

Chronosensory attractants (timing)

- This area of pollination biology is not well studied
- It is well known that some flowers produce rewards at specific times of day
- And pollinators abound on the flowers at that time.

Bees learn that time of day when rewards are presented and forage accordingly, e.g. *Apis dorsata* on *Decaspermum parviflorum* in Indonesia, flowers every second day, pollen the only reward and offered only in the morning.



Floral Rewards for Pollinators

Floral Rewards for Pollinators

What are they?

- Pollen
- Nectar
- Floral tissue
- Oils
- Perfume
- Resins and gums
- Comfort
- Sex
- Prey

Pollination by animals (Zoophily) is thought to have arisen with the Angiosperms about 100 million years ago.

- First floral rewards thought to have been pollen and floral tissue for betle pollination in such flowers as Magnolia

or

- Thought have been nectar and perhaps pollen offered by fly pollinated primitive plants as in Winteraceae

Nectar is now the prime reward sought after by almost pollinators.

What is nectar?

- Nectar is mostly sugars dissolved in water (mostly from Baker & Baker)
- Minor constituents include amino acids, proteins, lipids, anti-oxidants, alkaloids, organic acids, dextrins, minerals, vitamins, alcohols, and others.
- Sugars are the carbohydrate fuel for pollinator flight
- Heat of combustion for pure sucrose 16.53 joules/gm
- Three most important sugars include Melezitose, Maltose, Galactose, Lactose, Raffinose some of which may even be toxic to some pollinators (e.g. Galactose and Lactose to honeybees).
- Most nectars are mostly mixtures of Glucose, Sucrose, and Fructose.

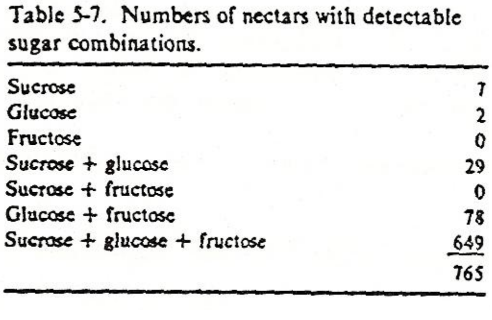


Table 5-7. Numbers of nectars with detectable sugar combinations.

Sucrose	7
Glucose	2
Fructose	0
Sucrose + glucose	29
Sucrose + fructose	0
Glucose + fructose	78
Sucrose + glucose + fructose	649
	765

Within species, sugars present in nectar are generally constant e.g. *Gelsemium sempervirens*.

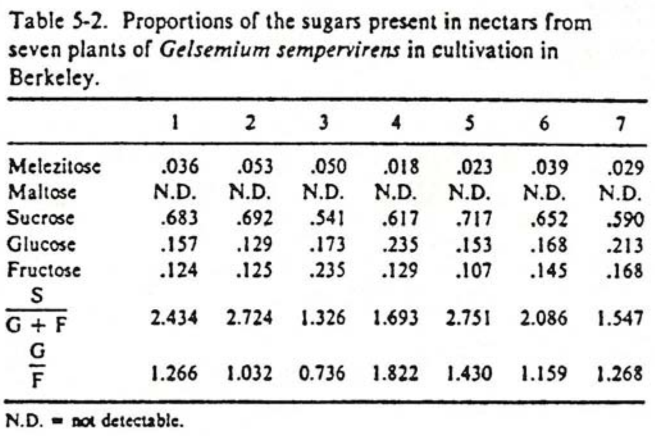


Table 5-2. Proportions of the sugars present in nectars from seven plants of *Gelsemium sempervirens* in cultivation in Berkeley.

	1	2	3	4	5	6	7
Melezitose	.036	.053	.050	.018	.023	.039	.029
Maltose	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
Sucrose	.683	.692	.541	.617	.717	.652	.590
Glucose	.157	.129	.173	.235	.153	.168	.213
Fructose	.124	.125	.235	.129	.107	.145	.168
$\frac{S}{G+F}$	2.434	2.724	1.326	1.693	2.751	2.086	1.547
$\frac{G}{F}$	1.266	1.032	0.736	1.822	1.430	1.159	1.268

N.D. = not detectable.

The ratio of the amounts of the major sugars in nectar is a remarkable predictor of plant taxonomy and pollinator type.

The ratio: Sucrose/(Glucose + Frutose)

1. hexose dominant (almost no or no sucrose), ratio <0.1
2. hexose rich, 0.1 to 0.49
3. sucrose rich, 0.5 to 0.99
4. sucrose dominant, >0.999

General occurrence of ratios from 765 species of plants

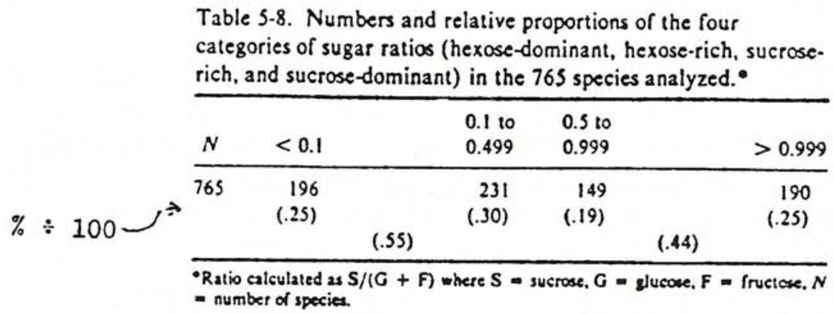


Table 5-8. Numbers and relative proportions of the four categories of sugar ratios (hexose-dominant, hexose-rich, sucrose-rich, and sucrose-dominant) in the 765 species analyzed.*

N	< 0.1		0.1 to 0.499	0.5 to 0.999		> 0.999
765	196 (.25)		231 (.30)	149 (.19)		190 (.25)
		(.55)			(.44)	

% ÷ 100

*Ratio calculated as S/(G + F) where S = sucrose, G = glucose, F = fructose, *N* = number of species.

Occurrence of ratios in some larger and more common plant families reflect taxonomic status and consistency.

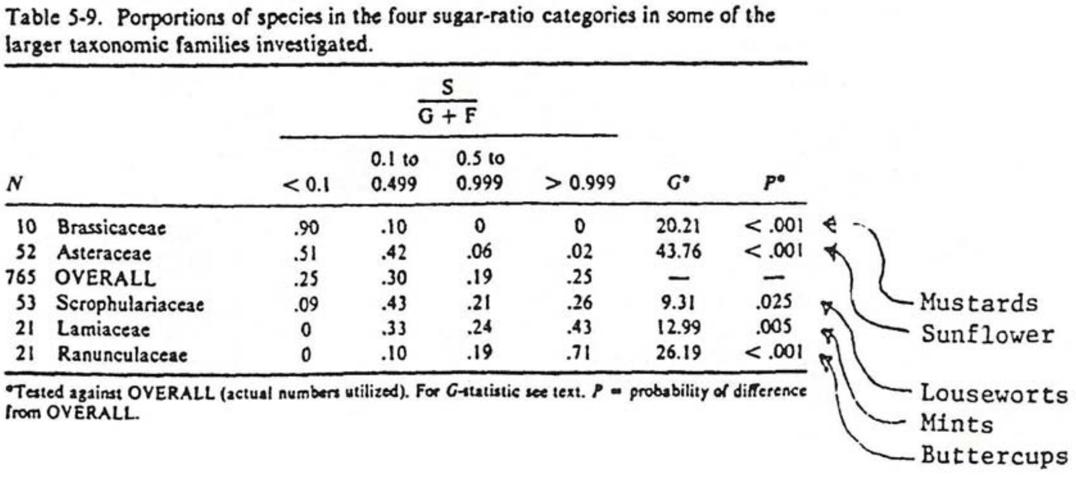


Table 5-9. Porportions of species in the four sugar-ratio categories in some of the larger taxonomic families investigated.

N		$\frac{S}{G+F}$ < 0.1	0.1 to 0.499	0.5 to 0.999	> 0.999	*G**	*P**
10	Brassicaceae	.90	.10	0	0	20.21	< .001
52	Asteraceae	.51	.42	.06	.02	43.76	< .001
765	OVERALL	.25	.30	.19	.25	—	—
53	Scrophulariaceae	.09	.43	.21	.26	9.31	.025
21	Lamiaceae	0	.33	.24	.43	12.99	.005
21	Ranunculaceae	0	.10	.19	.71	26.19	< .001

*Tested against OVERALL (actual numbers utilized). For *G*-statistic see text. *P* = probability of difference from OVERALL.

Mustards

Sunflower

- Hexoses

Louseworts

Mints

Buttercups

- Sucroses

- Particularly fascinating is the consistency of sugar ratios with pollinator type
- Hummingbirds at sucrose end
- Other birds at hexose end
- Moths and butterflies at sucrose end
- Flies at hexose end
- Long-tongued bees at sucrose end
- Short-tongued bees at hexose end

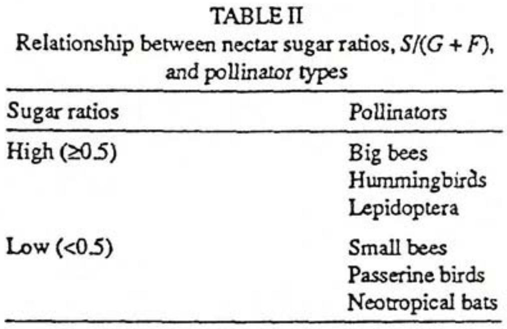


TABLE II

Relationship between nectar sugar ratios, $S/(G+F)$, and pollinator types

Sugar ratios	Pollinators
High (≥0.5)	Big bees Hummingbirds Lepidoptera
Low (<0.5)	Small bees Passerine birds Neotropical bats

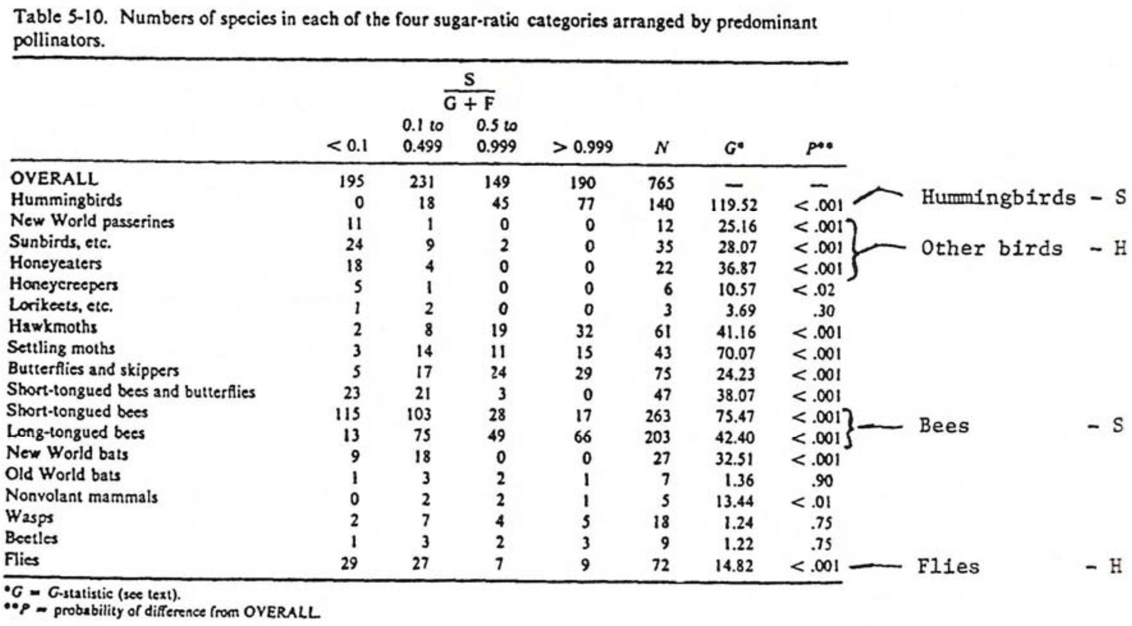


Table 5-10. Numbers of species in each of the four sugar-ratio categories arranged by predominant pollinators.

	$\frac{S}{G+F}$							
	< 0.1	0.1 to 0.499	0.5 to 0.999	> 0.999	*N*	*G**	*P***	
OVERALL	195	231	149	190	765	—	—	
Hummingbirds	0	18	45	77	140	119.52	< .001	Hummingbirds - S
New World passerines	11	1	0	0	12	25.16	< .001	Other birds - H
Sunbirds, etc.	24	9	2	0	35	28.07	< .001	
Honeyeaters	18	4	0	0	22	36.87	< .001	
Honeycreepers	5	1	0	0	6	10.57	< .02	
Lorikeets, etc.	1	2	0	0	3	3.69	.30	
Hawkmoths	2	8	19	32	61	41.16	< .001	
Settling moths	3	14	11	15	43	70.07	< .001	
Butterflies and skippers	5	17	24	29	75	24.23	< .001	
Short-tongued bees and butterflies	23	21	3	0	47	38.07	< .001	
Short-tongued bees	115	103	28	17	263	75.47	< .001	Bees - S
Long-tongued bees	13	75	49	66	203	42.40	< .001	
New World bats	9	18	0	0	27	32.51	< .001	
Old World bats	1	3	2	1	7	1.36	.90	
Nonvolant mammals	0	2	2	1	5	13.44	< .01	
Wasps	2	7	4	5	18	1.24	.75	
Beetles	1	3	2	3	9	1.22	.75	
Flies	29	27	7	9	72	14.82	< .001	Flies - H

**G* = *G*-statistic (see text).

***P* = probability of difference from OVERALL.

The situation for bees is given in greater detail as follows

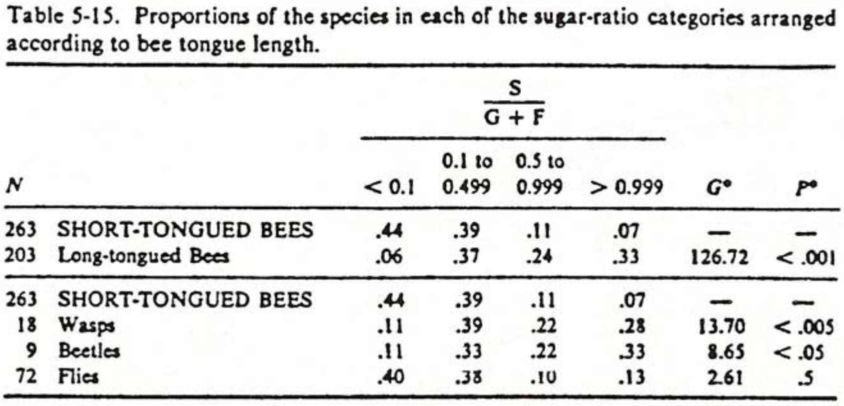


Table 5-15. Proportions of the species in each of the sugar-ratio categories arranged according to bee tongue length.

		$\frac{S}{G+F}$					
N		< 0.1	0.1 to 0.499	0.5 to 0.999	> 0.999	*G**	*P**
263	SHORT-TONGUED BEES	.44	.39	.11	.07	—	—
203	Long-tongued Bees	.06	.37	.24	.33	126.72	< .001
263	SHORT-TONGUED BEES	.44	.39	.11	.07	—	—
18	Wasps	.11	.39	.22	.28	13.70	< .005
9	Beetles	.11	.33	.22	.33	8.65	< .05
72	Flies	.40	.38	.10	.13	2.61	.5

But in lousewort (Scophulariaceae) family the taxonomic constraint is relaxed a great deal and sugar ratios correspond to the variety of pollinators involved for each species.

Table 5-17. Sugar ratios shown by species of *Penstemon, Keckiella,* and *Chionophila* (Scrophulariaceae).

HUMMINGBIRDS		INSECTS (MOSTLY BEES)	
P. barbatus	0.901	*P. heterodoxus*	0.452
P. centranthifolius	1.626	*P. oreocharis*	0.359
P. kunthii	1.068	*P. procerus*	0.226
P. bridgesii	1.130	*P. rydbergii*	0.297
P. newberryi	1.012	*P. virens*	0.143
K. cordifolia	0.502	*P. whippleanus*	0.210
K. ternata	1.275	*P. deustus*	0.577
$\bar{x} = 1.075$		*P. eriantherus*	0.853
Range 0.502–1.626		*P. alpinus*	0.261
?BEES OR HUMMERS		*P. speciosus*	0.329
P. campanulatus	0.413	*P. secundiflorus*	0.206
P. hartwegii	0.677	*P. spectabilis*	0.205
K. antirrhinoides	0.603	*P. azureus*	0.404
K. breviflora	0.727	*P. heterophyllus*	0.143
$\bar{x} = 0.605$		*P. laetus*	0.242
Range 0.413–0.727		*P. davidsonii*	0.087
		C. jamesii	0.045
		$\bar{x} = 0.296$	
		Range 0.045–0.853	

And other genera

TABLE III

Mean nectar sugar ratios, $S/(G+F)$, of species of the genus *Erythrina*[a] arranged according to pollinators

		Passerine (perching) bird-pollinated			
Hummingbird-pollinated		Old World species		New World species	
E. amazonica	1.05	*E. fusca*	0.05		
E. americana	0.75	*E. abyssinica*	0.05	*E. breviflora*	0.05
E. atitlanensis	1.36	*E. acanthocarpa*	0.07	*E. dominguezii*	0.04
E. berenices	1.67	*E. burana*	0.02	*E. falcata*	0.04
E. berteroana	0.89	*E. caffra*	0.04	*E. megistophylla*	0.02
E. chiapasana	2.18	*E. humeana*	0.04	*E. poeppigiana*	0.03
E. chiriquensis	0.67	*E. latissima*	0.08	*E. verna*	0.04
E. cobanensis	2.87	*E. lysistemon*	0.05		
E. corallodendrum	0.78	*E. perrieri*	0.08	$\bar{x} = 0.04$; S.D. = 0.01	
E. coralloides	0.86	*E. resupinata*	0.03		
E. costaricensis	1.03	*E. sacleuxii*	0.01		
E. eggersii	1.38	*E. sandwicensis*	0.05	*E. crista-galli*	0.03
E. flabelliformis	1.47	*E. senegalensis*	0.02		
E. folkersii	2.29	*E. sigmoidea*	0.04		
E. globocalyx	1.00	*E. subumbrans*	0.02		
E. guatemalensis	0.99	*E. tahitensis*	0.04		
E. herbacea	1.15	*E. variegata*	0.02		
E. lanceolata	0.73	*E. vespertilio*	0.04		
E. macrophylla	1.35				
E. mexicana	2.22	$\bar{x} = 0.04$; S.D. = 0.02			
E. pallida	1.72				
E. rubrinervia	1.16				
E. salviiflora	1.47				
E. smithiana	0.95				
E. speciosa	1.33				
E. standleyana	1.04				
E. tajumulcensis	0.76				
$\bar{x} = 1.30$; S.D. = 0.55					

---

[a] The names of the authors of *Erythrina* species are given in Barneby and Krukoff (1982), Krukoff (1979), and Krukoff and Barneby (1974).

See text for significance levels.

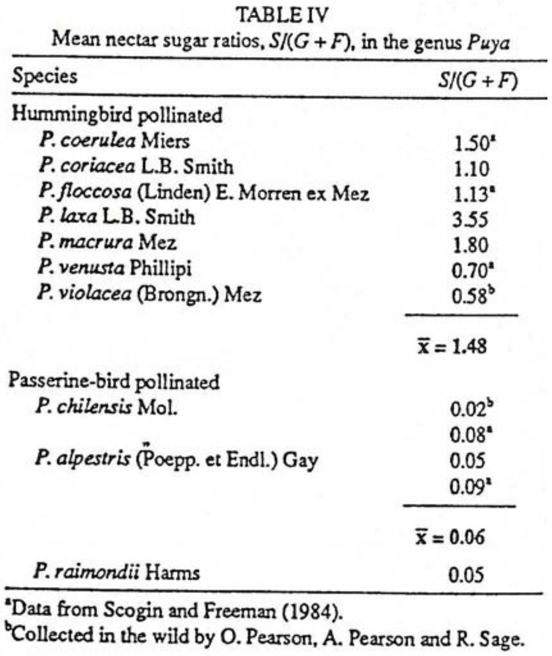


TABLE IV
Mean nectar sugar ratios, $S/(G+F)$, in the genus *Puya*

Species	$S/(G+F)$
Hummingbird pollinated	
P. coerulea Miers	1.50[a]
P. coriacea L.B. Smith	1.10
P. floccosa (Linden) E. Morren ex Mez	1.13[a]
P. laxa L.B. Smith	3.55
P. macrura Mez	1.80
P. venusta Phillipi	0.70[a]
P. violacea (Brongn.) Mez	0.58[b]
	$\bar{x} = 1.48$
Passerine-bird pollinated	
P. chilensis Mol.	0.02[b]
	0.08[a]
P. alpestris (Poepp. et Endl.) Gay	0.05
	0.09[a]
	$\bar{x} = 0.06$
P. raimondii Harms	0.05

[a] Data from Scogin and Freeman (1984).
[b] Collected in the wild by O. Pearson, A. Pearson and R. Sage.

Sugar concentration and volume secreted

- Again, mirrors the kinds of pollinators involved.

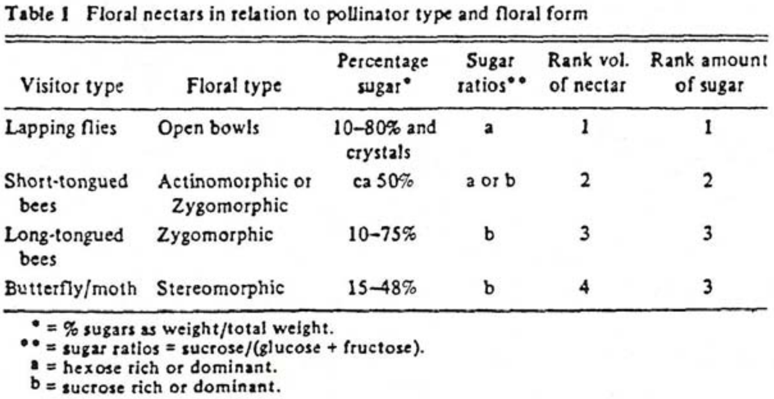


Table 1 Floral nectars in relation to pollinator type and floral form

Visitor type	Floral type	Percentage sugar*	Sugar ratios**	Rank vol. of nectar	Rank amount of sugar
Lapping flies	Open bowls	10–80% and crystals	a	1	1
Short-tongued bees	Actinomorphic or Zygomorphic	ca 50%	a or b	2	2
Long-tongued bees	Zygomorphic	10–75%	b	3	3
Butterfly/moth	Stereomorphic	15–48%	b	4	3

* = % sugars as weight/total weight.
** = sugar ratios = sucrose/(glucose + fructose).
a = hexose rich or dominant.
b = sucrose rich or dominant.

Nectar evaporates

Nectar protected

Even though those flowers which secrete greater volumes of nectar with lower concentrations of sugar, the flowers which secrete the most amount of nectar also secrete the most amount of sugars.

Sugar concentrations affect the viscosity of nectar. The higher the sugar concentration, the thicker the nectar, and the more energy it takes a pollinator to imbibe (suck up) the nectar. This is specially true for pollinators with long, tubular mouthparts (hummingbirds, moths, butterflies, long-tongued bees).

Viscosity is also affected by the kinds of sugars present, mixtures of sugars have lower viscosity than pure sugars, however, this aspect of nutrition and energetics not yet studied.

Nectar also contain Amino Acids

- Amino acid profiles in nectar taxonomic relations
- Complementarity in hybrid species
- Presence of amino acids in nectars mirrors that in nature generally.

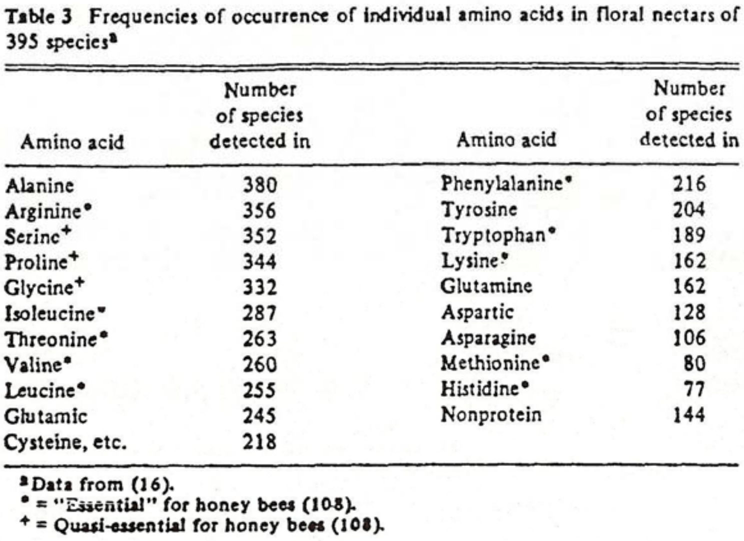
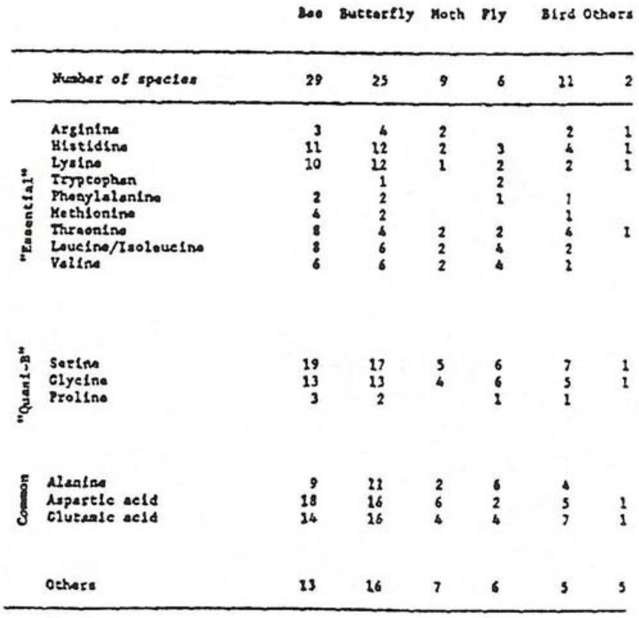


Table 3 Frequencies of occurrence of individual amino acids in floral nectars of 395 species[a]

Amino acid	Number of species detected in	Amino acid	Number of species detected in
Alanine	380	Phenylalanine•	216
Arginine•	356	Tyrosine	204
Serine+	352	Tryptophan•	189
Proline+	344	Lysine•	162
Glycine+	332	Glutamine	162
Isoleucine•	287	Aspartic	128
Threonine•	263	Asparagine	106
Valine•	260	Methionine•	80
Leucine•	255	Histidine•	77
Glutamic	245	Nonprotein	144
Cysteine, etc.	218		

[a] Data from (16).
• = "Essential" for honey bees (108).
+ = Quasi-essential for honey bees (108).

The amino acid profiles for nectar reflect pollinator type



		Bee	Butterfly	Moth	Fly	Bird	Others
	Number of species	29	25	9	6	11	2
"Essential"	Arginine	3	4	2		2	1
	Histidine	11	12	2	3	4	1
	Lysine	10	12	1	2	2	1
	Tryptophan		1		2		
	Phenylalanine	2	2		1	1	
	Methionine	4	2			1	
	Threonine	8	4	2	2	6	1
	Leucine/Isoleucine	8	6	2	4	2	
	Valine	6	6	2	4	1	
"Quasi-E"	Serine	19	17	5	6	7	1
	Glycine	13	13	4	6	5	1
	Proline	3	2		1	1	
Common	Alanine	9	11	2	6	4	
	Aspartic acid	18	16	6	2	5	1
	Glutamic acid	14	16	4	4	7	1
	Others	13	16	7	6	5	5

Summary table of amino acids identified in samples of nectar from plants growing in Berkeley. For each listed amino acid the number of occurrences is given for each pollinator type category and abould be considered in proportion to the number of species samples for each of these categories.

The total amounts of amino acids in nectar also reflect the pollinator type and the availability of amino acids in their diets.

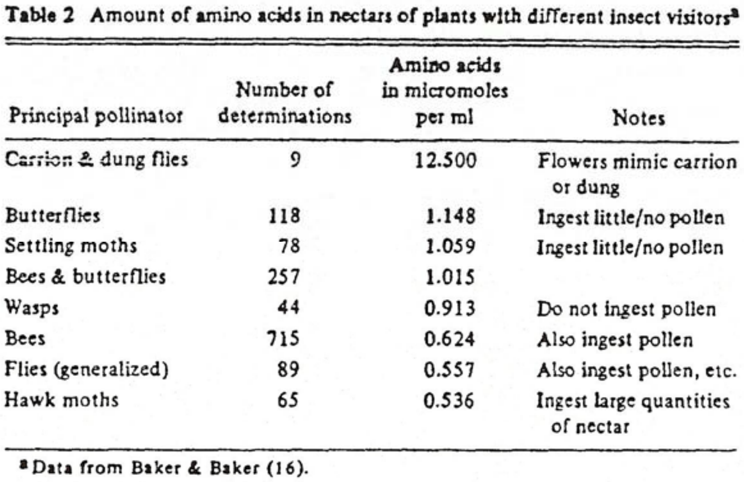


Table 2 Amount of amino acids in nectars of plants with different insect visitors[a]

Principal pollinator	Number of determinations	Amino acids in micromoles per ml	Notes
Carrion & dung flies	9	12.500	Flowers mimic carrion or dung
Butterflies	118	1.148	Ingest little/no pollen
Settling moths	78	1.059	Ingest little/no pollen
Bees & butterflies	257	1.015	
Wasps	44	0.913	Do not ingest pollen
Bees	715	0.624	Also ingest pollen
Flies (generalized)	89	0.557	Also ingest pollen, etc.
Hawk moths	65	0.536	Ingest large quantities of nectar

[a] Data from Baker & Baker (16).

- too much a.a. may be toxic

Although all these correlations have been noted, experimental evidence to test the hypotheses which are suggested is still not available.

- Do amino acids in nectar enhance longevity?
- Do amino acids in nectar enhance fecundity?
- Is too much amino acid in nectar toxic to hummingbirds?
- Is too much amino acid in nectar to hawkmoths?

Other nectar constituents

- Proteins: probably enzymatic (very small amounts)
- Lipids and oils: most often in nectars consumed by Hymenoptera and Diptera
- Role in nutrition is unknown
- Some oils coat nectar and prevent evaporation
- Anti-oxidants: ascorbic acid, perhaps prevent oxidation of nectar lipids
- Alkaloids and glycoside: narcotic to poisonous and can get into honey (e.g. *Rhododendron*, *Kalmia*, *Zigaedenus*)
- Phenolics (including tanins) higher amounts in arctic and alpine nectars
- Minerals: salts common in nectar, reflect soil minerals to some extent. Onion nectar rich in Potassium (1500 ppm) which is deterrent to honeybees.

Pollen

From pollinator viewpoint, what is pollen?

1. a food
2. a dust which has to be cleaned off
3. both of the above

For pure nectarivorous pollinators, 1. is the answer and pollen is, at worst, a nuisance.

If pollen is a food, then some interesting points to make:

- Pollen is highly nutritious

- Protein 9% to 45%, average 25%
- Free amino acids 10%
- Carbohydrates 25%
- Lipids variable from 1% to 20%, average 5%
- Enzymes, Co-enzymes, Pigments, Minerals, Stereols

Pollen is multicellular microgametophyte

- Must grow through stigma, down style, to ovary and then fertilize egg nucleus and endosperm nucleus
- Constituents of pollen grains related to these functions
- Energy source in large grains is starch
- Energy source in small grains is lipids
- Large grains usually associated with long styles
- Small grains associated with short styles

Pollinators use pollen as source of protein nutrition, especially bees use pollen as major food source for larvae various flies ingest pollen and use nutrients for ovarian maturation.

- Pollenivory in insects often related, even if distantly, to carnivory
- Some carnivorous bugs require pollen as well as prey
- Pollen nutrition in insects other than honeybees is not well studied
- Heat of combustion ca. 20-25 joules/gm, but only 50% digestible

Floral tissues are eaten by numerous herbivorous insects

- Some flowers have special food-bodies for pollinators, often false anthers (e.g. *Cassia* with sterile pollen-like material or *Commelia coelestis* with milky juice)
- Some insects eat petals, gynoecial or androecial tissue
- Special relationships not well investigated
- Personal observations of early stage grasshoppers feeding in flowers of *Opuntia* in Colorado. The grasshoppers are cryptically coloured to more or less match flower colours.
- The most famous examples of floral tissue as a pollinator's reward are of *Tegiticula* and *Yucca*
- Agaonid wasp pollinator in *Ficus*
- Hadena moths in Silene
- And the Oil Palm Weevils, *Elaeidobius* ssp. And oil palm.

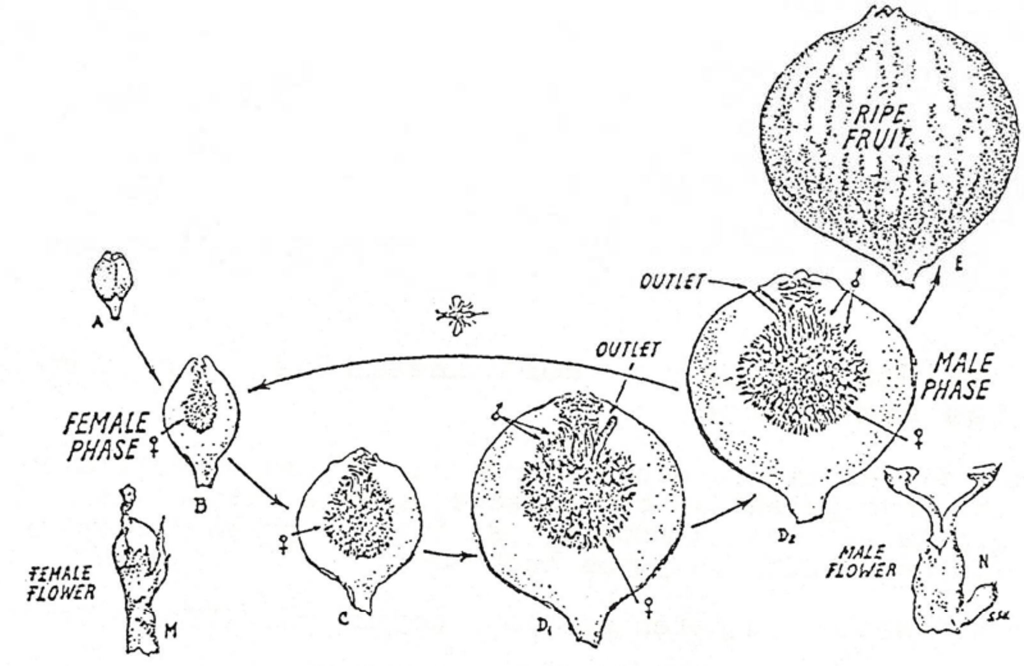


Fig. 6. Developmental cycle of the syconium.

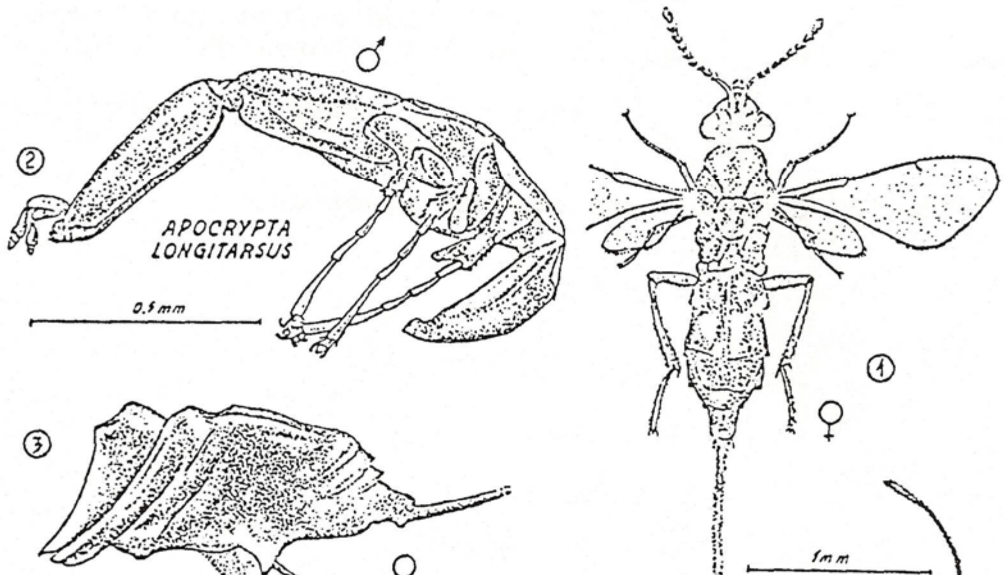
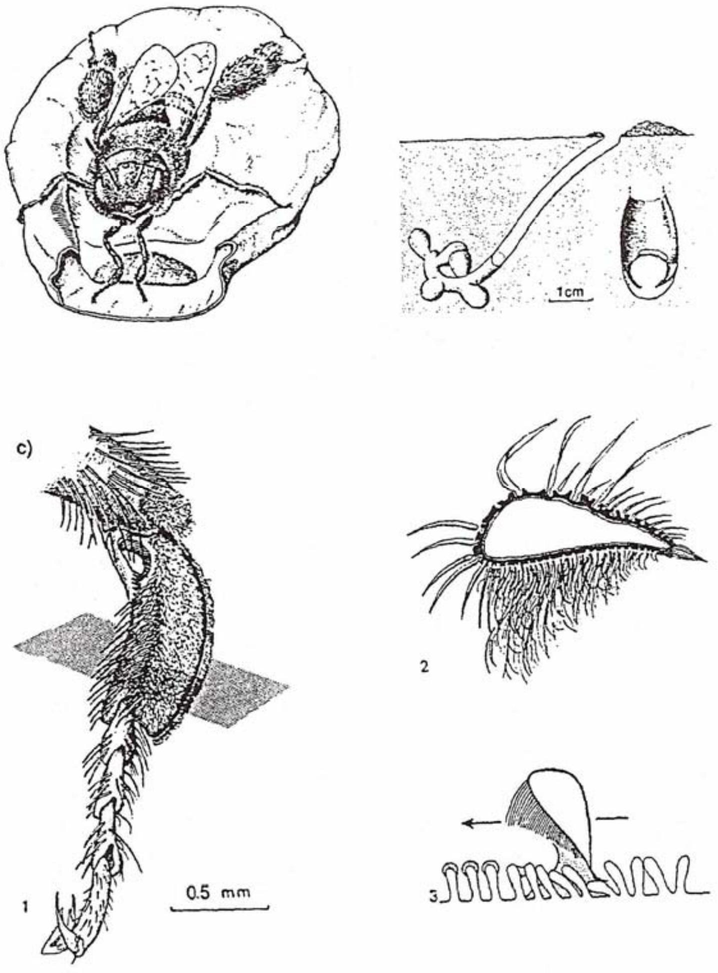


Fig. 5. Apocrypta sp. 1—female; 2—male; 3—abdomen of female.

Oil

- Oil is offered as reward for pollinators in some specialized relationships
- *Centris* bees with specialized tarsal brushes to collect oil from
- Specialized flowers (e.g. *Krameria*)

An anthophorid bee (*Tapinotaspis coerulea*) collecting the oil from an oil flower with the mops on its forelegs; note also the long-haired hindlegs, into which the collected oil is packed. *Right*: The bee carries the oil to its nest in the ground and supplies the larvae with a mixture of pollen and oil; the inset on the right shows a brood cell with the food mixture and an egg on top of it. (c) The oil-collecting apparatus of another anthophorid bee (*Paratetrapedia melampoda*). (1) The collecting mop on the foreleg with the scraping edge outward on the right.(2) Cross-section through the mop-bearing part of the leg; the mop is downward and the scraper on the right. (3) The 'scraper slides over the field of hairs in the oil gland and the mop absorbs the oil.



- Numerous examples now known since first documentations in late 1960's, but not well studied
- Oils are saturated free fatty acids or diglycerides
- Highly energetic, heat of combustion ca. 40 joules/gm and totally digestible

Perfume

- Perfume is gathered from orchids (various species) by male Euglossine bees.
- Relationships are complex and worked out for various species is South and Central America
- Some bees collect perfume by accident

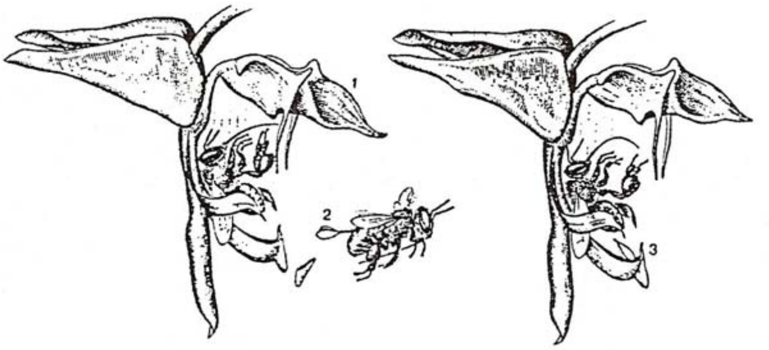


Fig. 64:
An orchid bee collecting odor substance on the slippery underside of the labellum (1) of *Gongora maculata* falls into the chute below, loads itself involuntarily with the pollen packet (2), and pollinates the stigma of the next flower with it when it again slides down the chute (3).

- Others more purposefully

Fig. 65:
The orchid *Coryanthes speciosa* forces the visiting bee to pollinate it, for when collecting odor substance at position (1) the bee slips and falls into a liquid-filled trap (2) from which the only exit is a narrow opening (3). In passing through it, the bee must crawl under the stigma and the pollinia.

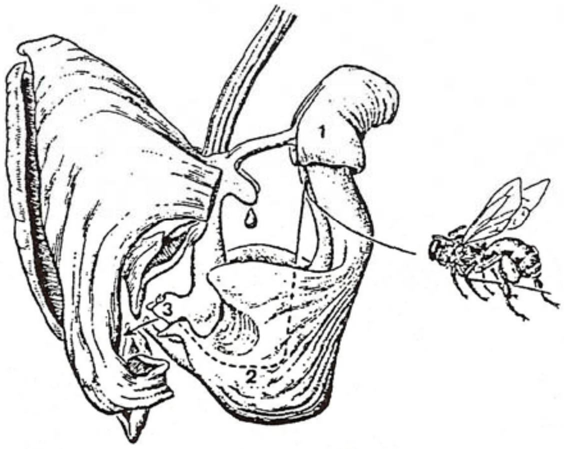
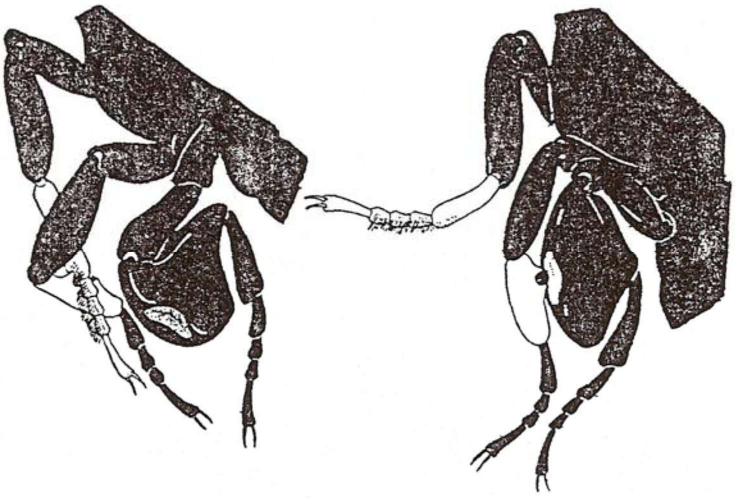


Fig. 63:
The orchid bee packing odor substance into the tibial container.



- Perfume collecting apparatus is complex

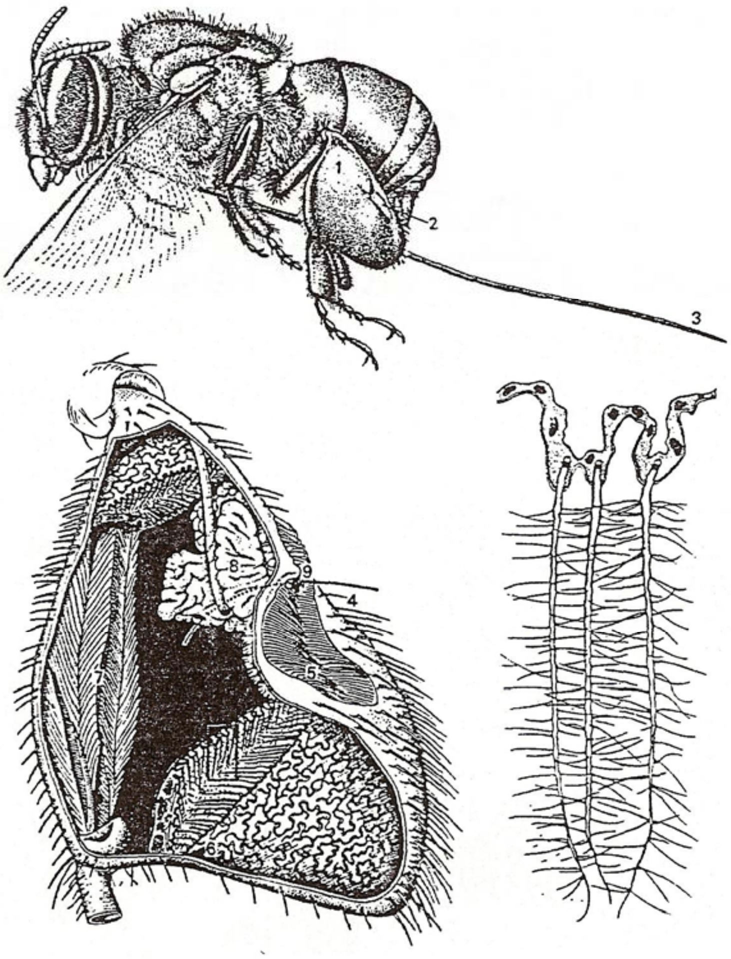


Fig. 62:
Orchid bees collect the odor substances of orchid blossoms. *Above*: A bee in flight: (1) the swollen tibia of the hindleg with the opening (2) to the scent container; (3) the typical long proboscis. *Below*: The interior of the scent container exposed. The opening to the outside (bristle (4) inserted for clarification) lies in the pan (5); part of the acrual scent container (6), with its dense hairs, has been removed here. (7) Leg musculature, (8) glandular tissue, (9) scaly cup around the entrance. On the right, part of the sponge (6) is enlarged.

- Components are eugenot and cineole (=eucalyptol)
- Highly attractive to male bees, also the reward
- Scents not attractive to female bees
- Male bees seem to transform the scent into a pheromone which is attractive to female bees
- Male bees use scent to attract mates
- Other insects use plants derived chemicals as pecursors to or as pheromones, e.g. butterflies feeding on alkaloid producing plants

Other flowers which have scents for rewards are *Gloxinia*, some Gesneriaceae, and some Araceae.

Resins and Gums

- Are produced by few flowers (e.g. *Dalechampia* and *Clusia*)
- Various bees, **euglossine**, **meliponine**, and **anthidiine** use floral gums for waterproof lining of nests
- Recent work in Canada suggests that oil pollen-kitt of pollen of Curcubitaceae may be used by squash bees to waterproof cells in their subterranean nests.

Comfort (Sleep and Warmth)

- Various insects are known to sleep in flowers
- Most insects sleeping in flowers are male bees
- No examples are well studied but in Canada my graduate student, Susan Willis, is examining the pollination of *Curcubita pepo* by the squash bee *Peponapis pruinosa*.
- The male bees enter the flowers just before they close for their one day of glory. The bees fall into a soporific stupor till, when they push their way out of their sleeping accommodations and resume feeing and searching for mates in the flowers. The females sleep in their subterranean nests.

Warmth can be found in flowers or inflorescences

- Inflorescences of Araceae become greatly warmed by metabolic heat
- This presumably drives off the mimetic scents (carrion, musk, dung) and attracts various flies
- The importance of the heat to the trapped flies has not been well studied
- Some flowers and inflorescences capture solar warmth
- Hairy heat traps
- Diaheliotropic solar furnaces
- Most studies from arctic or alpine regions
- e.g. Arctic *Dryas integrifolia* and *Papaver radicatum*
- Flowers are bowl shaped and focus sun’s rays
- And follow the sun for all or part of the day

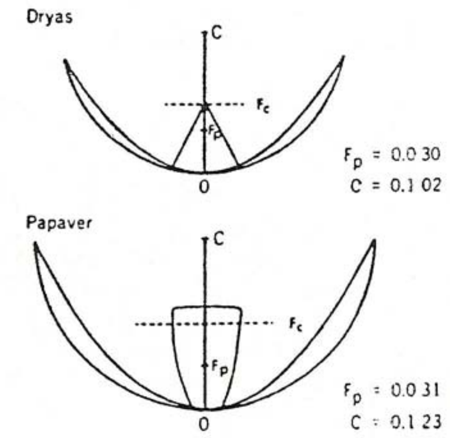


Fig. 2. Geometric rendition of flowers of *Dryas* and *Papaver* showing parabola (inside cup) with principal focus F_p and circle (outside cup) with center C and plane of foci F_c. Central masses represent gynoecia; the dotted line in *Dryas* represents the position of the androecium with its many stamens.

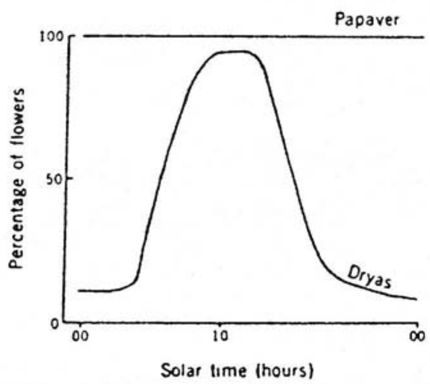


Fig. 1. Heliotropic periods for *Papaver* and *Dryas*. Data were obtained by counting the percentage of flowers facing the sun on several days [simplified from Kevan (*1*)].

- And become much warmer within than the surrounding air
- As do insects which bask in the flowers

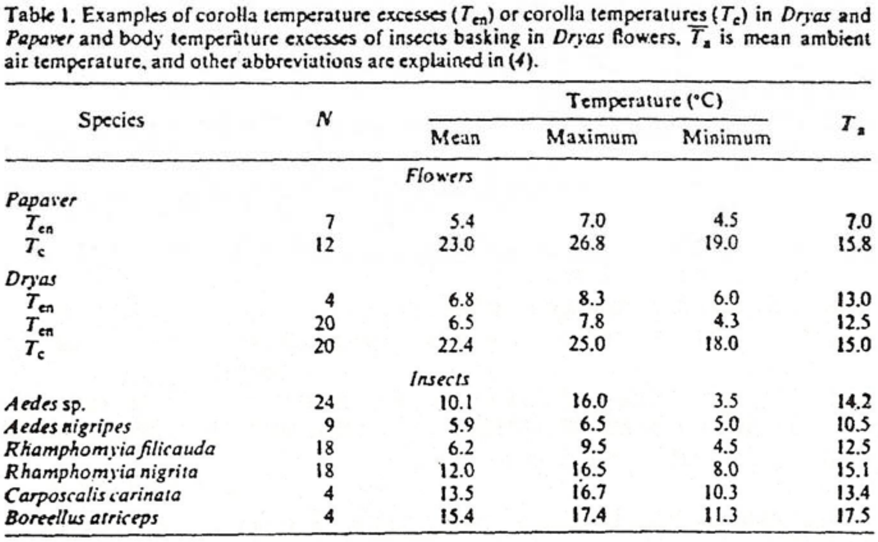


Table 1. Examples of corolla temperature excesses (T_{en}) or corolla temperatures (T_c) in *Dryas* and *Papaver* and body temperature excesses of insects basking in *Dryas* flowers. $\overline{T}_a$ is mean ambient air temperature, and other abbreviations are explained in (*4*).

Species	*N*	Temperature (°C)			T_a
		Mean	Maximum	Minimum	
		Flowers			
Papaver					
T_{en}	7	5.4	7.0	4.5	7.0
T_c	12	23.0	26.8	19.0	15.8
Dryas					
T_{en}	4	6.8	8.3	6.0	13.0
T_{en}	20	6.5	7.8	4.3	12.5
T_c	20	22.4	25.0	18.0	15.0
		Insects			
Aedes sp.	24	10.1	16.0	3.5	14.2
Aedes nigripes	9	5.9	6.5	5.0	10.5
Rhamphomyia filicauda	18	6.2	9.5	4.5	12.5
Rhamphomyia nigrita	18	12.0	16.5	8.0	15.1
Carposcalis carinata	4	13.5	16.7	10.3	13.4
Boreellus atriceps	4	15.4	17.4	11.3	17.5

- Net effect is probably as much as 8% to 25% additional heat units for growth during the cool arctic summer when heat is an important limiting factor to plant sexual reproduction.

Prey

- The role of predator prey relations in flowers has been hardly studied
- In tropical Asia there are flower mimicing mantids
- In many parts of the world there are cryptically coloured crab spiders (Thomisidae) which hide in flowers to catch their prey
- The ambush bug, *Phymata Americana*, is a well known pollinator predator
- It also assesses the richness of the floral resources and will remain where flowers are rich in nectar and pollinators abundant
- Various predatory flies and wasps take their prey from flowers
- Various birds capture insects at flowers

On the agricultural front:

- Now rats eat the male inflorescences of oil palms in Malaysia to get the larvae of the oil palm pollinating weevil, *Elaeidobius kamerunicus*, which was introduced into Malaysia recently for pollination.

Pollinator Foraging

Pollinators forage for floral rewards

- The rewards are used in enhancing the evolutionary fitness of the forager.
- How that works for a bumblebee colony is depicted as follows:

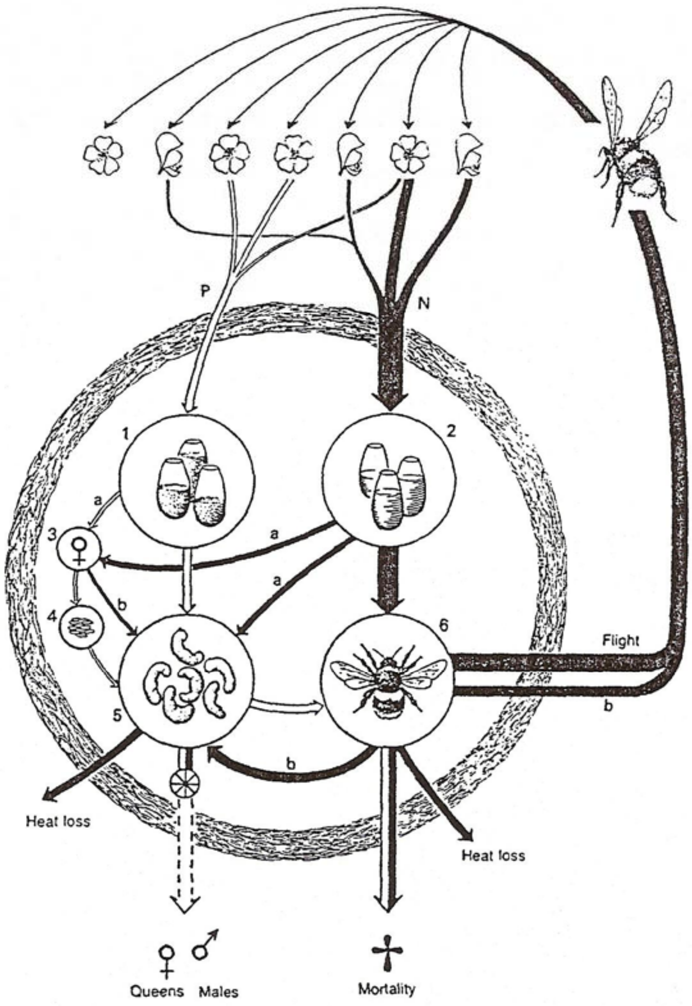


Fig. 88:
The flow of energy and materials through a bumblebee colony. P pollen and N nectar are the inputs to the system. They are stored in pollen pots (1) and honey pots (2). (a) Use as food for the queen (3), which lays the eggs (4), and for the larvae (5). (b) Use in thermoregulation; queen and workers (6) warm the brood and heat the nest. The outputs of the system: energy expenditure for flight and thermoregulation by the collectors, heat loss, losses by the departure of queens and males from the colony, and losses by the death of the animals in autumn.

- But keep in mind that fitness for a eusocial animal (e.g. honeybees, bumblebees, ants, termits) is mostly best considered at the level of the whole colony, not the individual.
- Foraging theory does not require special information about the nature of the rewards.
- Foraging for nectar, or pollen, or oil, or even prey from flowers should be done according to the same basic rules.

Rules conform to obtaining

- The most amount of reward
- With the minimum amount of effort
- And with the maximum amount of reliability and safety

1. We can measure the amount of reward collected
2. We can measure the amount of time taken to obtain that reward
3. We can measure, or estimate, the amount of energy expended in foraging per unit time
4. We can measure the amount of reliability in obtaining reward
5. Measuring the level of safety is difficult and has not been attempted often

Example: The volume of nectar of given sugar concentration can be converted to weight of sugar collected, and that converted to energy collected.

The amount of time taken to obtain that amount of energy can be combined with the amount of energy consumed in the foraging activity per unit time.

- Then the net return in energy can be calculated.
- The issue of reliability involves stochastic events, e.g. what is the chance that the flower a hummingbird visits actually has nectar in it, or has a super-abundance of nectar for flowers in the general area?
- The issue of safety also involves stochastic events, e.g. what is the chance of being killed during foraging? Flowers may harbour or attract predators/parasites of pollinators, flowers themselves may entrap and kill anthophiles, etc. Flower forages may appear to forage in energy expensive ways by showing innate predator-avoidance behaviour.

All the above are part of OPTIMAL FORAGING

- Does the theory of optimal foraging apply in nature to pollinators?
- Most of the research has been done on Bumblebees (*Bombus*).
- Most of the results indicate that Optimal Foraging strategies do apply.
- What sorts of examples support that conclusion?
- Bumblebee foraging paths in an open area of mixed herbaceous plants.

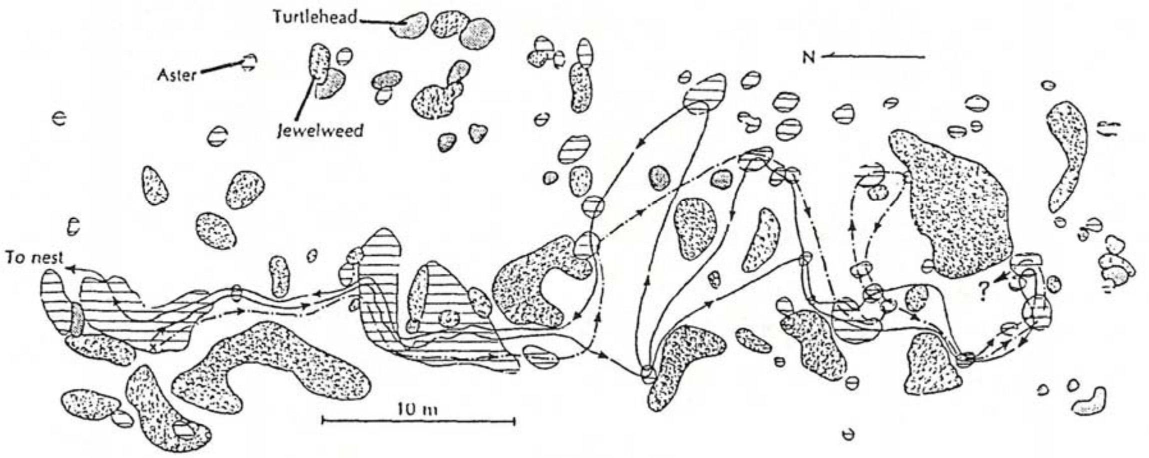


Fig. 8.5 Foraging path of a *Bombus fervidus* worker on two separate days, August 19 (———) and August 25 (—·—·—). Note that the bee's foraging area is about 50 meters in length and that the bee visited primarily aster. Many other *B. fervidus* were also specializing in aster, but most specialized in jewelweed. Each trip lasted about half an hour. The path shown here does not indicate movements within each of the flower clumps.

What do the two paths by the same marked bee on two different days tell us?

1. Bee tended to move in one direction, first South and return North, foraging in both directions.
    a. Pattern suggests efficiency.
2. Bee tended to follow the same general path, stopping at the same patches of flowers.
    a. Pattern suggests familiarity with environment (learning) and concomitant efficiency.
    b. "Trap-lining" is known to cover distances of 10's km by some specialized tropical bees going between widely separated patches of their host plants.
3. Bee did vary its path from day to day.
    a. Pattern suggests exploratory behaviour in looking for other sources of reward while foraging.
4. Bee visited inflorescences of Aster but not Impatiens.
    a. Pattern suggests that the bee specialized, flora constancy.

The elements of efficiency are well established in foraging over a large area.

What about within a patch of flowers?

- Example from alpine Bumblebee on *Castilleja* in alpine Colorado.

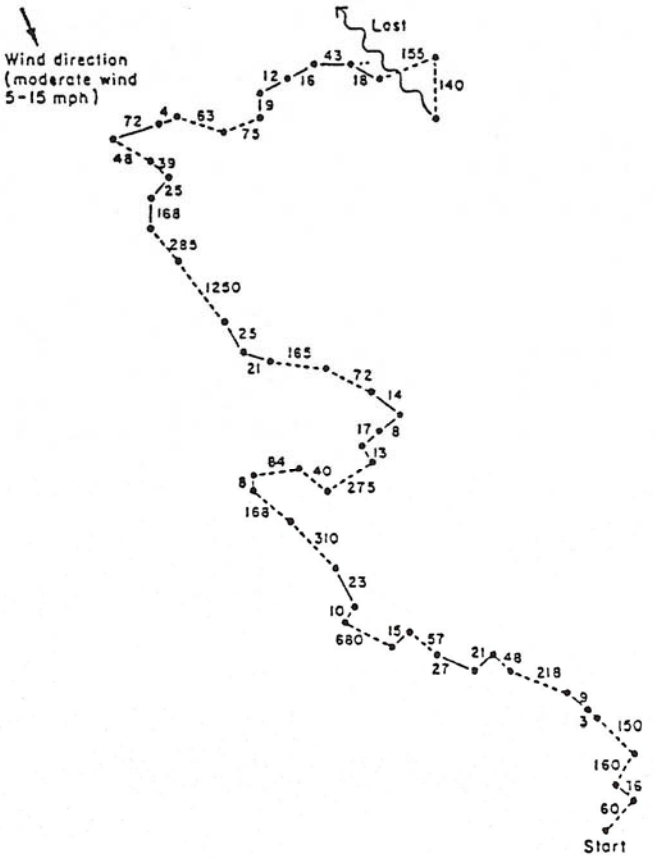


Fig. 10. Foraging map of *B. balteatus* worker on *C. occidentalis* at site 8. July 31, 1981. Distances in cm. Not drawn to scale.

What patterns are shown?

1. The bee flew more or less in one direction (Forwarding)
    a. Pattern suggests efficiency, especially in that it would be unlikely to cross its own path and encounter a flower it had already visited.
2. The bee flew more or less into the wind
    a. Pattern suggests that the bee used the wind to aerodynamic advantage in taken-offs and controlled landings.
3. The bee mostly alternated left and right turns unless it flew straight ahead.
    a. Pattern enforces the forward motion of the bee within the patch yet allows for visiting may flowers over a wide band of the patch.

Now, consider a patch flowers which is rich in reward versus on which is poor in reward.

- How should a forager behave?
- It would be efficient for the forager to remain in a rich patch, but to abandon a poor one.
- Bees have built in behaviour patterns which enforce that.

- If the patch is poor, foragers move mostly straight ahead and fly longer distances between flower visits.
- If the patch is rich, foragers make many more sharp turns to left or right and fly shorter distances between flower visits.

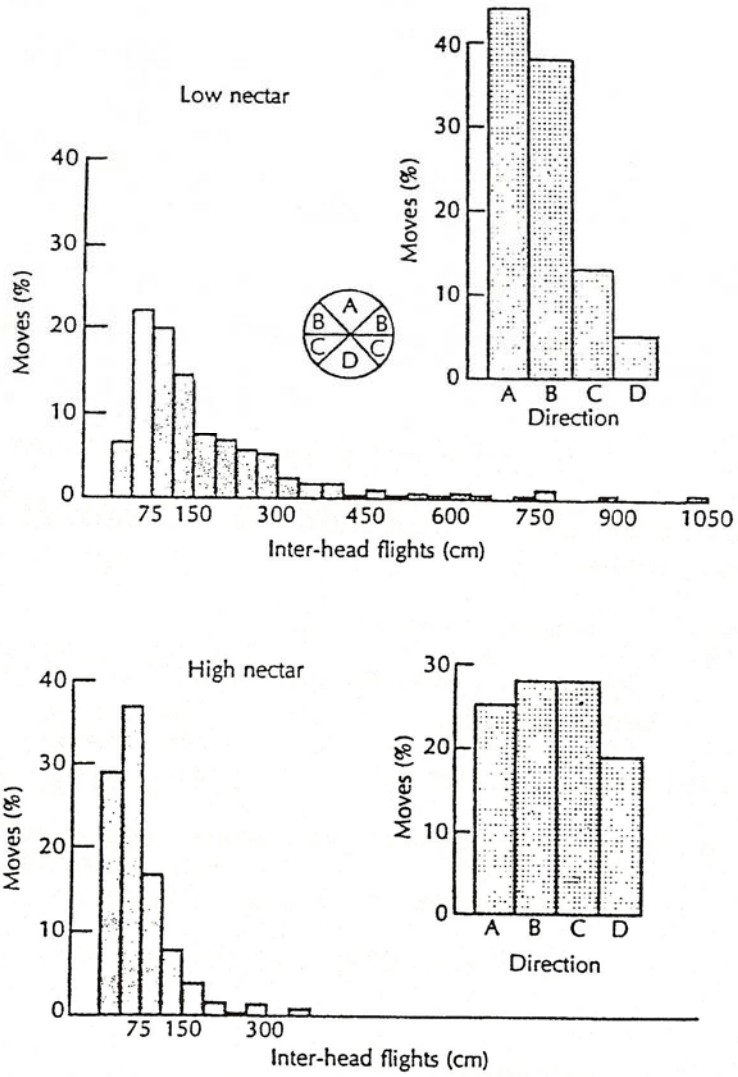


Fig. 8.7 Changes in foraging behavior of *B. terricola* workers in two patches of white clover, one that was utilized by many bumblebees and had only 0.003 mg sugar per flower (top), and one that had been screened with bridal veil to allow nectar to accumulate to a level of 0.01 mg sugar per flower (bottom). The left-hand graphs show that the bees skipped over many flower heads when nectar rewards were low. The right-hand graphs show that they no longer persisted in moving in the same direction after successively visiting flowers that contained high food rewards (the directions of movement are as shown in the clocklike figure—*A* is forward, *D* backward).

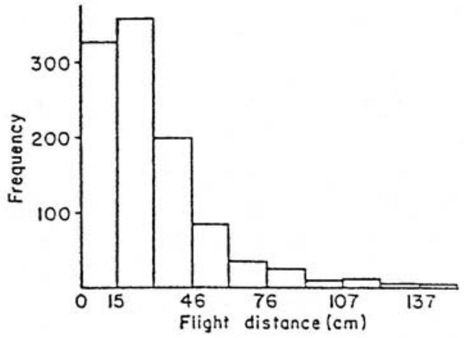


Fig. 4. Flight distances of bumble bees (*Bombus americanorum*) between successively visited inflorescenses of *Delphinium virescens* ($N = 1061$). After Waddington (1981).

The effect of the amount of nectar present in flowers and the distances foragers fly to the next inflorescences is clearly shown here.

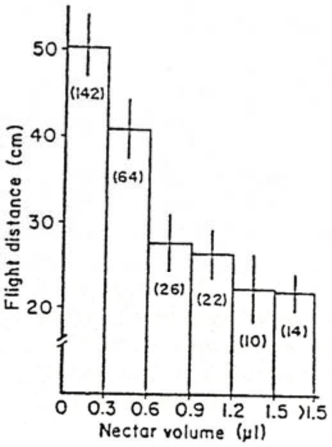


Fig. 5. Mean distances (± SE indicated by vertical bars) flown by bumble bees (*Bombus americanorum*) after visiting inflorescences of *Delphinium virescens* with the indicated mean volume of nectar in the two lowest flowers ($N = 228$). The two flowers are good predictors of rewards in other flowers on the same inflorescence. After Waddington (1981).

The net effect is despicted as follow:

- Efficiency in foraging is clear

Consider a step further in detail, **foraging on an inflorescence**.

- Most work has been done with vertical inflorescences.
- E.g. on Fireweed, *Epilobium* (*Chamaenerion*) *angustifolium*, *Delphinium* ssp., *Aconitum* ssp., *Pedicularis* ssp. etc.
- Pattern of foraging follows
- Upward movements by crawling and flying on the inflorescence
- And downward flights between inflorescences.

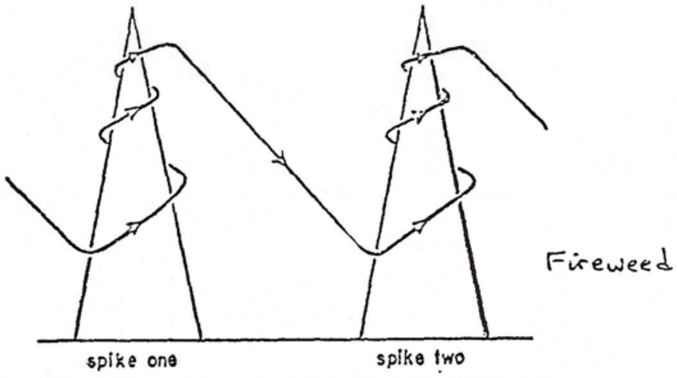


Fig. 3. The flight-path of bees visiting flower spikes of *C. angustifolium*.

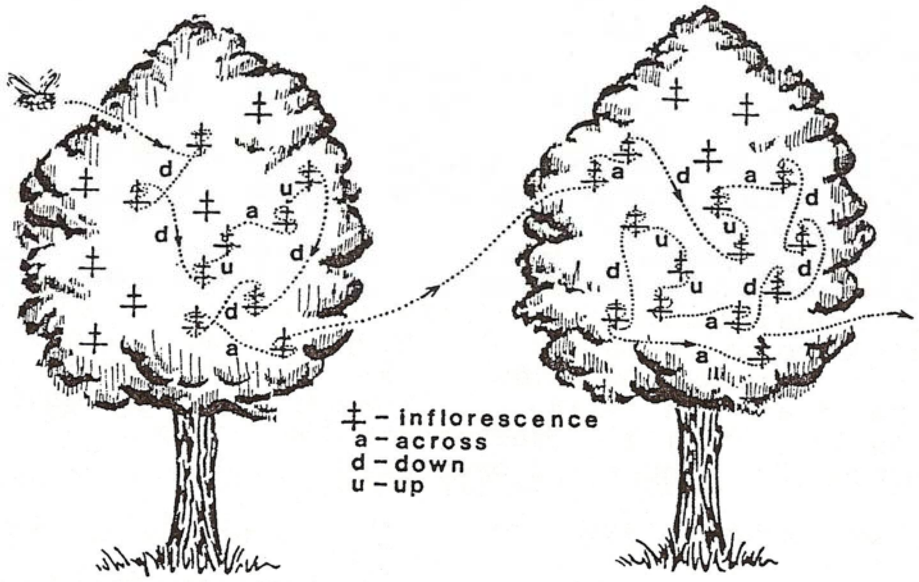
Explanations:

1. nectar in basal flowers is weaker in higher flowers so behaviour offsets gustatory saturation (wine or cheese tasting, start with mildest and progress to strongest).
2. the behaviour maximizes energy extracted per inflorescence (but this is doubtful and the argument not convincing).
3. the behaviour minimizes energy expenditure for short, upward movements (by crawling or short upward flights with landings finely controlled with the help of gravity) and in longer, energy conserving downward flights between inflorescences.

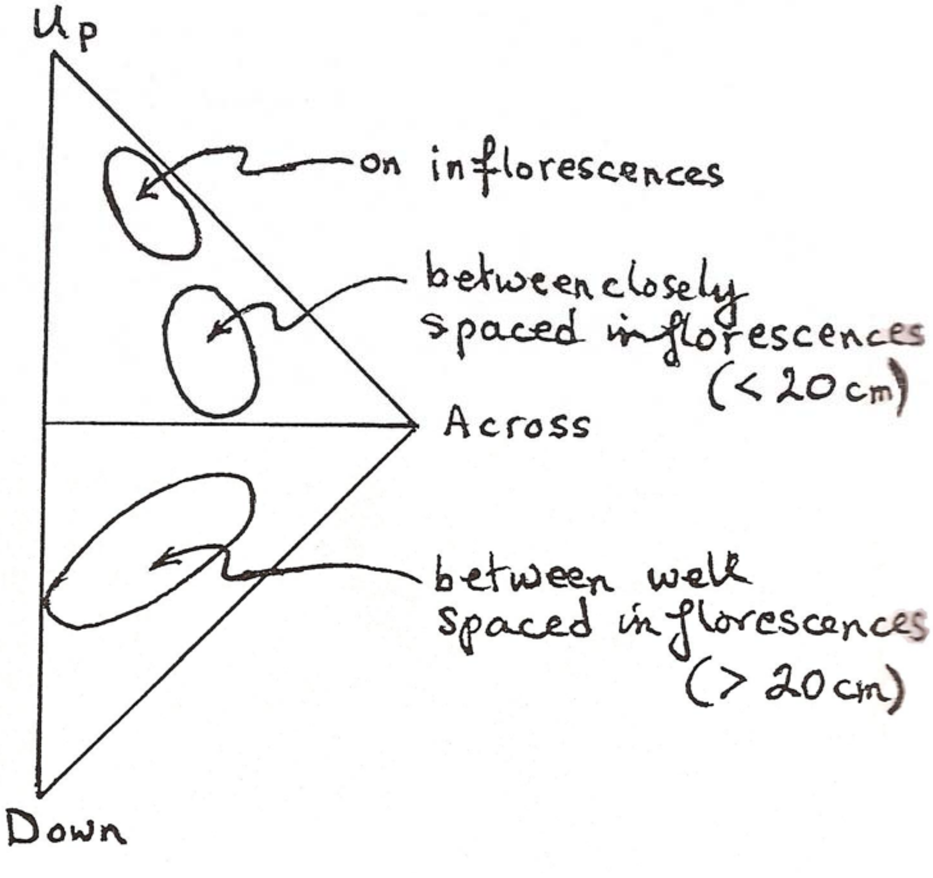
Experiments to test these ideas have not been made.

Most of the examples of optimal foraging come from horizontal environments with little depth (i.e. a patch of herbaceous flowering plants).

- What happens in vertical environments with little horizontal depth (i.e. on the surface of a flowering tree)?
- Observations on *Xylocopa* from Indonesia, Malaysia, and Maldive Islands and on Bumblebees from Canada, Norway, and Sweden all.
- Show the same thing on 8 species of trees:



- The bees forage on inflorescences as they would be expected to.
- The bees move between inflorescences as they would be expected to.
- But the bees tend to move downwards on the tree so that they leave the tree at a level below that at which they entered it.



Explanations:

- The bees behaviour can be explained as above (for inflorescence),
- But what about the downward trending flights on the tree?
- Behaviour can be explained in terms of loading.
- Non-loaded bee enters high in tree, and gains load as it descends. Once loaded, returns to nest. If partially loaded then slow climbing flight (energy efficient versus steep flight) to high in next tree.

Returning to the first map, one can ask why specialized on Aster?

- Specialization of foragers at flowers is well-known.
- Floral constancy or Floral fidelity.
- The phenomenon was well-known to Darwin who suggested that learning, memory and manipulative skills were important.
- Learning skills are well demonstrated in flower handling by bumblebees.

Fig. 74:
Learning curves for the discrimination of various shapes by the honeybee. Upper curve: discrimination between large and small round disks. Middle and lower curves: discrimination between four- and twenty-four-pointed stars; the training pattern was either the twenty-four-pointed star (middle curve) or the four-pointed star (lower curve).

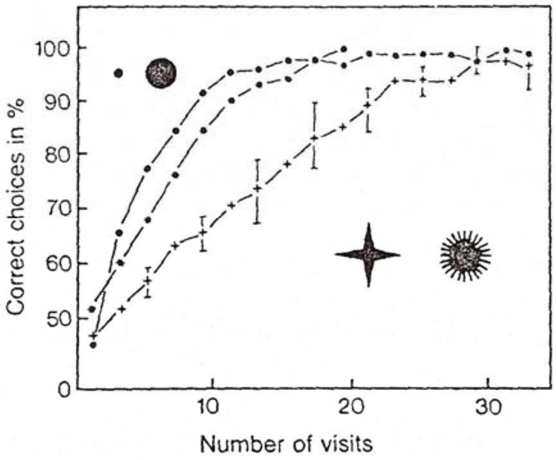
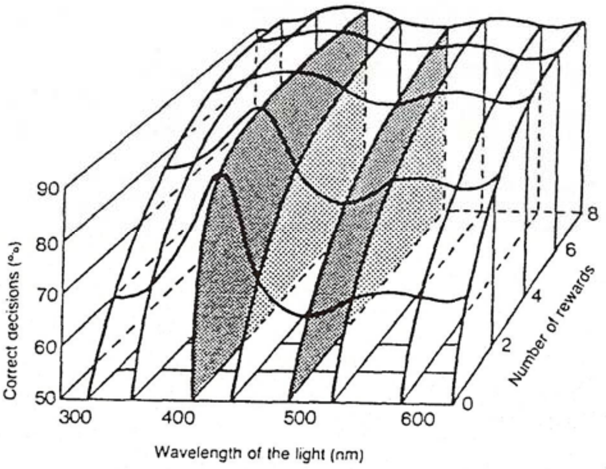


Fig. 73:
How rapidly do honeybees learn colors? They learn most quickly when the color is violet (c. 410 nm; the third curve from left rises most steeply) and most slowly when it is blue-green (c. 490 nm; the fifth curve from left rises least steeply).



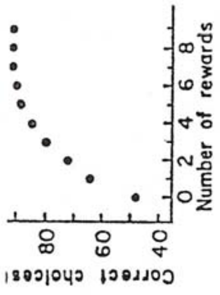
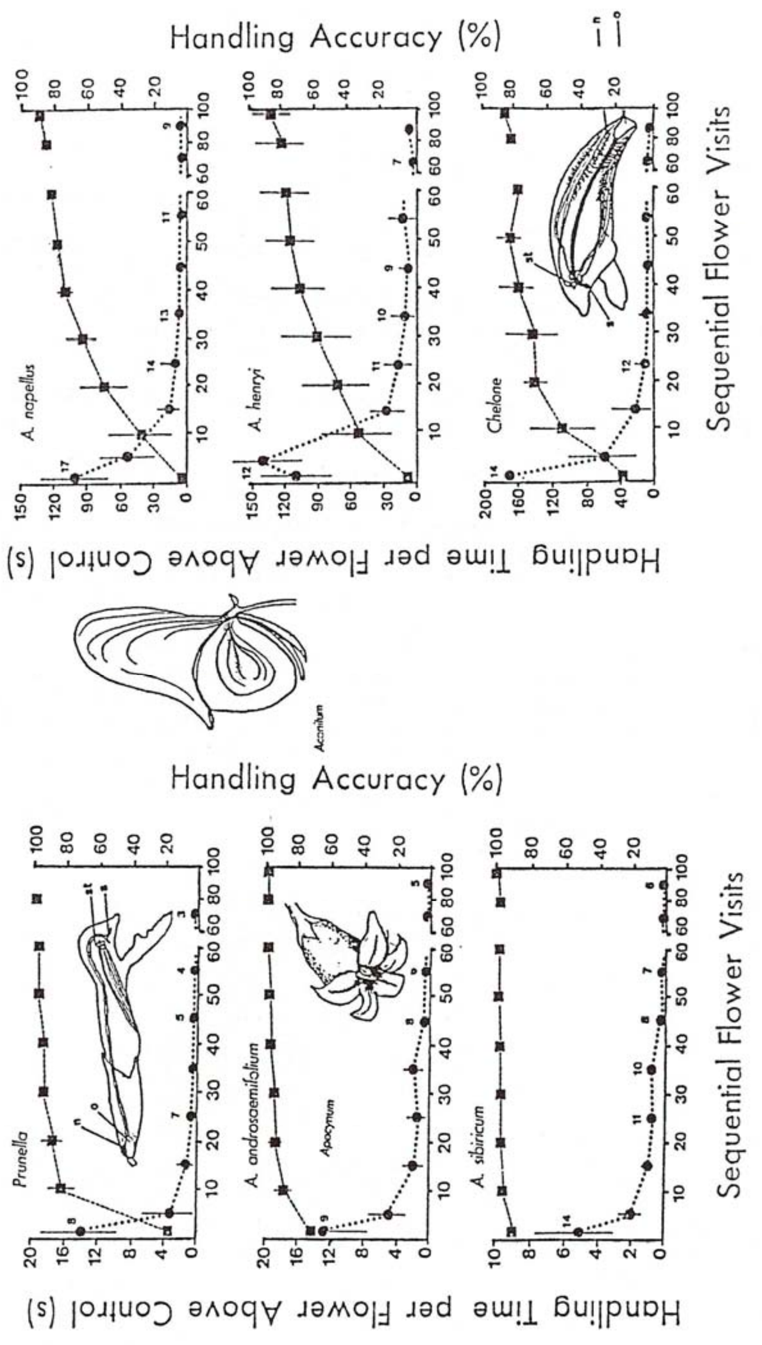


Fig. 2. Example of a honeybee learning curve. Learning improves quickly after successive reward–signal associations. After Menzel *et al.* (1974).



- Bumblebees can manipulate simple flowers (e.g. Compositae and open bowl shaped flowers) and obtain reward without practice.
- Slightly more complex flowers (e.g. *Prunella* and *Apocynum*) require little practice.
- Complex flowers (e.g. *Aconitum*, *Chelone*) require more practice.
- Some bees have innate ability to handle complex flowers with initial skill.
- E.g. *Bombus consobrinus*, a European specialist on Aconitum learns to manipulate the flowers much faster than does *B. pennsylvanicus*, a North American generalist bumblebee.

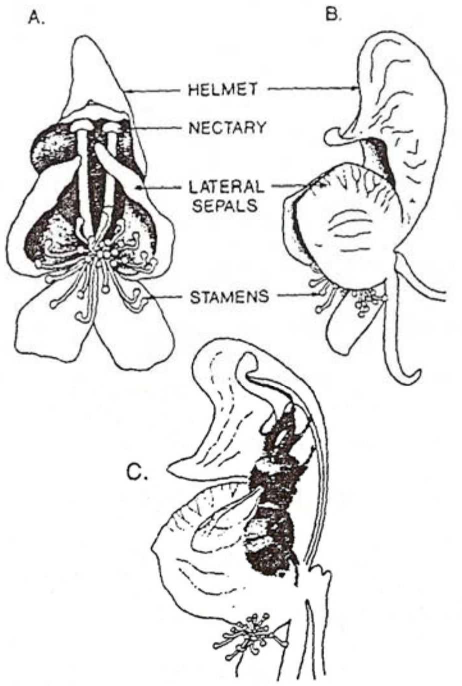


Figure 1. Flower of *Aconitum variegatum* in (A) frontal view, (B) side view, and (C) with worker bumblebee inserting tongue into nectar petal.

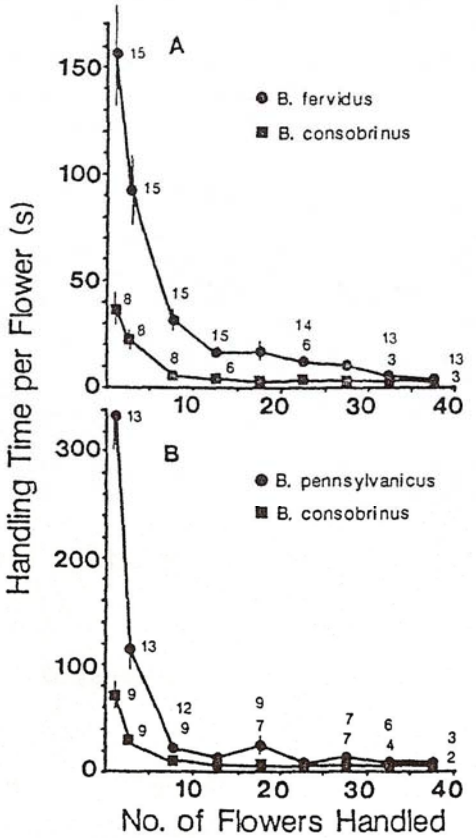


Figure 2. Standardized handling times of naive worker bumblebees visiting flowers of (A) *Aconitum napellus* and (B) *A. variegatum*. Beginning with the first flower visit, means are calculated over intervals of five visits; vertical lines indicate ± 1 SE and numbers beside plotted values give the number of bees at each point (upper numbers refer to generalists, lower numbers to specialists).

- What is the energetic value of specializing of being constant to a given species of flower?
  1. Complex flowers have greater amounts of reward, particularly nectar.
  2. There are fewer species of foragers that can obtain the reward because of anatomical or behavioural limitations.
  3. Not all con-specific foragers specialized or are constant to the same species.
  4. Once the complexity is learned, obtaining the reward is done quickly.

Thus, there is less competition for the reward and greater certainly of obtaining it.
There is also the matter of limitations of memory in floral manipulation.
Perhaps forages can remember only a few systems at once, and the more complex manipulations faster than they can perform the same number of two or more equally complex but different manipulations (as in people).

All in all: Efficiency is suggested.

- Moral: Thought Investment in Education and Learning, and then Specialization the greatest rewards can be obtained!
- Evidence: thought University degree!
- Or amongst bees:

on golden rod (*Solidago canadensis*), a plant with simple flowers an experienced bee can obtain 0.01mg sugar/min versus 11mg/min from jewell weed (*Impatiens biflora*) with complex flowers.

- Works out to 12 minutes work on jewell weed provides the same results as 1 week on goldenrod.

"Majoring" and "Minoring"

As forages proceed, forwarding on their particular specialty flower ("majoring"), they often sample flowers of the species ("minoring").

- Sampling presumably keeps forages informed about alternative resources in their environment.
- How do forages know when to switch from flowers of one species to those of another?
- How do forages know when to leave a particular patch?

Theory:

- Forages monitor the average net level of resources available to them in their environment.
- When the level of resources available to them from a particular patch, or from a particular species falls below the average, then it is time to switch patches or species.
- This average is referred to as the "Marginal Value" of the resource level, and the theory is based on the "Marginal Value Theorem" from Economics.

The Reliable of obtaining reward can be considered as Risk Assessment

Bumblebees and Paper Wasps prefer to forage when the reward levels are more or less homogeneous between stations (flowers) than in situations when there are great differences between the amounts of reward at one station and another. That, when the statistical expectation of obtaining a given amount of reward is the same in each environment.

- i.e. Patch (high variance) with 99 empty flowers and 1 with 100 units of reward is less desirable than patch (low variance) with 100 flowers each with 1 unit of reward.
- But, if high variance patch has higher average reward level, then preference above can be offset.
- Few studies along this line.

Some assumptions and considerations about Optimal Foraging:

1. An individual's contribution to the next generation (its Darwinian fitness) depends on its behaviour while foraging.
2. Components of foraging behaviour should be heritable.
3. There is a relationship between foraging behaviour and fitness.
4. The evolution of foraging behaviour is not prevented by genetic constraints.
5. The "functional" constraints (ability to learn, anatomy) can be determined.
6. The evolution of foraging behaviour should be rapid.
7. These ideas taken from G. Pyke's seminal work. Lots of overlap in the above list.

Some Figures on Foraging Energetics

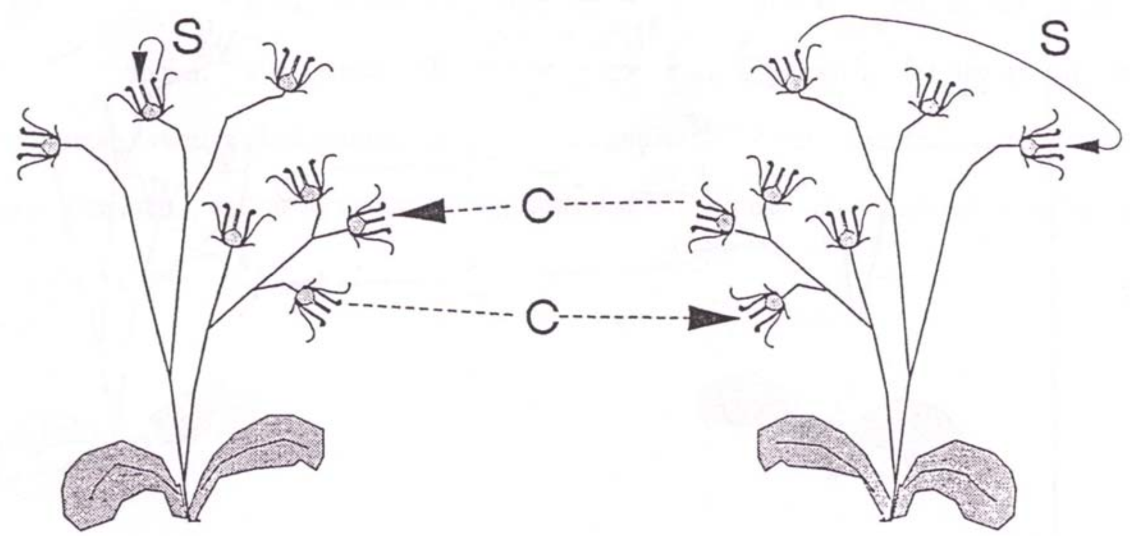
- Honeybees and Bumblebees use about 4 – 11mg sugar/hr in flight
- Sphinx moths use 9 – 840 mg sugar/hr depending on their size.
- Hummingbirds need 6 – 10 kcal/day
- Passerine birds need 10 – 50 kcal/day
- 1 mg sugar contains about 3.7 cals
- Maximum measured reward available to bumblebee 110 cal/min
- 1 kg of White Clover honey represents nectar from 19 million flowers
- Honeybees visit about 500 flowers/foraging trip
- If trip is 25 minutes, 1 kg honey represents 38,000 foraging trips and 16,000 hours of bee labour.

Wind Pollination

Introduction

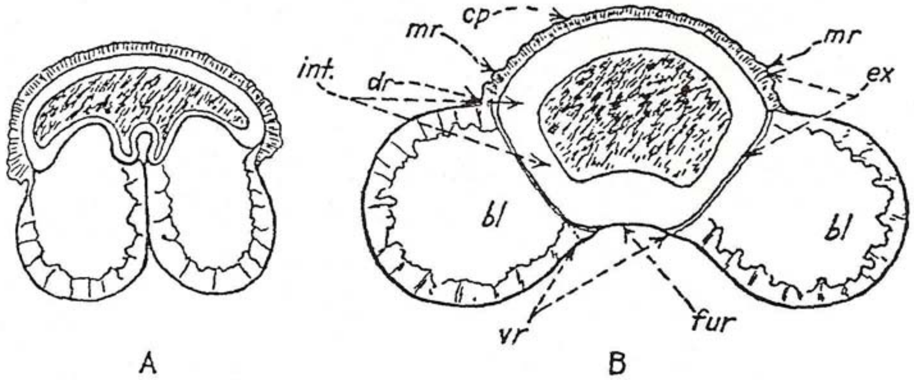
Definitions:

- Pollination: transfer of pollen from the anthers of a flower to the stigma. It is the first step in sexual reproduction which gives rise to seeds, fruit and the next generation of plants.



- Self-pollination: transfer of pollen within the same plant.
- Cross-pollination: transfer of pollen between two plants.
- Wind pollination: pollination accomplished by wind.
- Pollen: the *microgametopyhte* (microscopic) of plants.

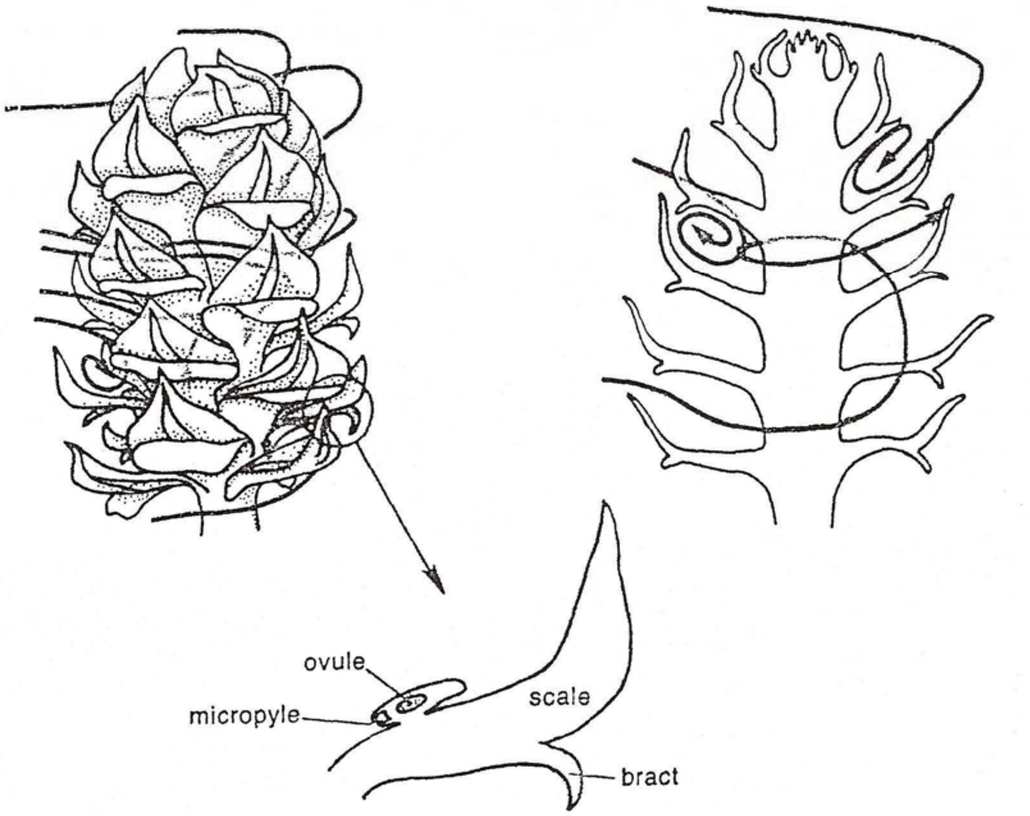
Each grain carries half the chromosomal complement of its parent plant, the *sporopyhte*.



Pollen grains of *Pinus scopulorum*, diagrammatic transverse optical sections: *A*, dry and contracted; *B*, moist and expanded; *ex*, exine; *int*, intine; *cp*, cap; *mr*, marginal ridge; *fur*, furrow; *bl*, bladders; *dr*, dorsal root of the bladders; *vr*, ventral root of the bladders.

What distinguishes wind pollinated plants

- Syndrome of anemophily:
    - Flowers unisexual, exposed before leaves come out or exposed outside of the leaf mass
    - Perianth insignificant, small or absent
    - Attractants absent
    - Anthers and stigmas exposed
    - Pollen grains small, smooth, dry produced in great quantities
    - Pollen-arresting mechanisms frequent, reduction in number of ovules.



An ovule-bearing pine cone exerts, considerable aerodynamic control over wind-borne pollen grains that pass in its vicinity. The radial symmetry of the cone enables it to deflect pollen, regardless of the wind’s direction, into airflow patterns that pass over virtually every scale-bract complex. Furthermore, the aerodynamic properties of each scale-bract complex are such that suspended pollen is directed toward the micropyles of attached ovules.

- Syndrome of entomophily:
    - Blossom in possession of an attract (real or deceptive) and means for making its existence know, generally by a large and conspicuous (sight or smell) perianth
    - Pollen grains of variable size, sculptured, sticky, in extreme cases tied together by thin viscin strands or in pollinia
    - Anthesis and production of attractants synchronized with activity of the pollinator

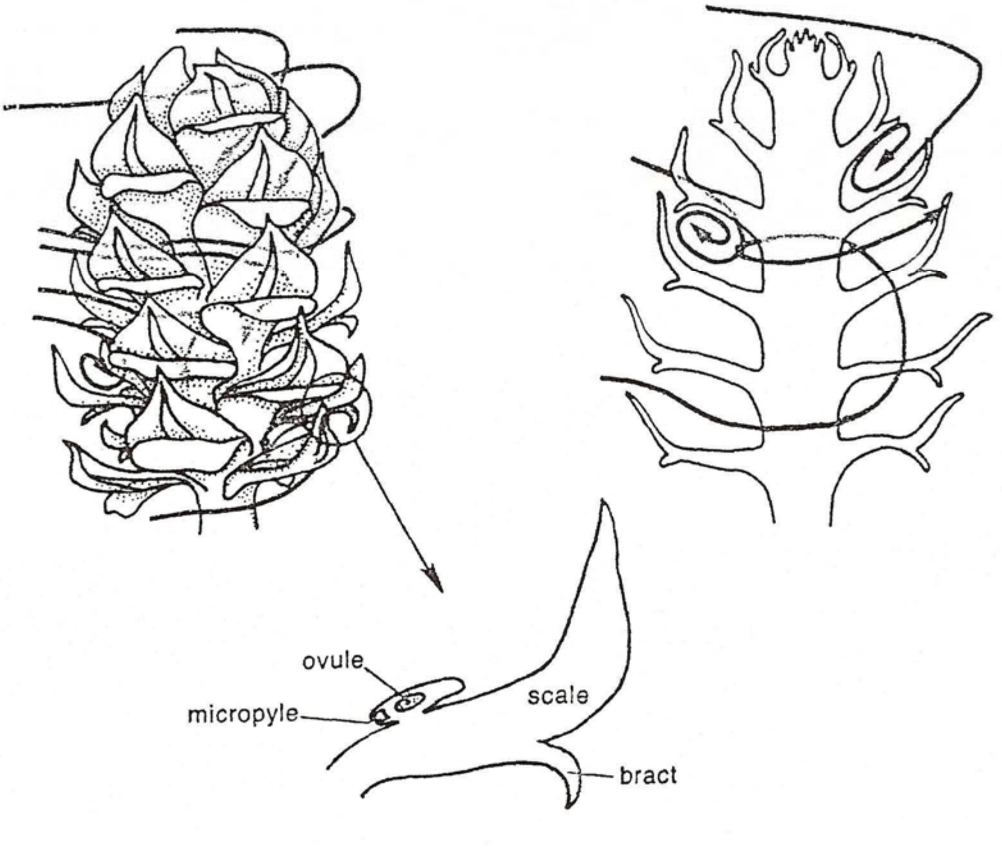
Types of environment they occur in

- Low species diversity – relatively close spacing of compatible plants
- Marked seasonality – a leafless season to reduce pollen filtration
- Low humidity and probability of rainfall – less pollen washout and greater release
- Presence of unambiguous stimuli – e.g. day length variation to co-ordinate flowering
- (Relative) Absence of potential animal vectors

Basically, environmental and climatic uncertainty leads to wind pollination.

Pollination biology

Gymnosperms



An ovule-bearing pine cone exerts, considerable aerodynamic control over wind-borne pollen grains that pass in its vicinity. The radial symmetry of the cone enables it to deflect pollen, regardless of the wind's direction, into airflow patterns that pass over virtually every scale-bract complex. Furthermore, the aerodynamic properties of each scale-bract complex are such that suspended pollen is directed toward the micropyles of attached ovules.

- No stigma
- Pollination drop mechanism
- Micropyles
- Micropylar canal
- Nucellus – fertilization a year later

Angiosperms

- E.g. *Graminieae*, *Cyeraceae* and *Juncaceae*
- Anemophily in angiosperms is generally considered a derived phenomenon
- They tend to have unisexual flowers, e.g. Acer

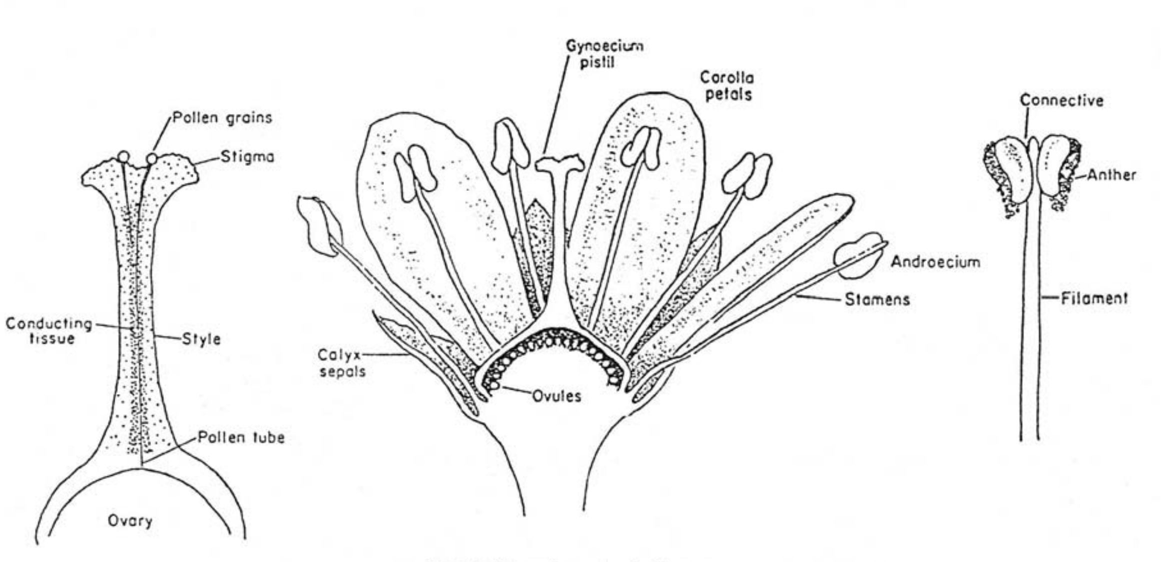


FIG. 1. The main parts of a flower.

- They have developed a whole new set of organs over and above gymnosperms:
    - Female – stigma, style and conductive tissues
    - Male – long pollen tubes

Cross- and self-pollination

- Self-pollination leads to inbreeding depression in most plants
- Therefore some plants adopt *dioecy* to combat this e.g. conifers
- Other barriers exist to self-pollination, e.g. time of pollen release versus stigma receptivity

Physics of dispersal

Pollen dispersion is dependent on the *source*, *dispersal* and *deposition* patterns of pollen grains.

Source

Liberation of pollen influenced by plant type, age, climate and other factors

- Timing
    - Pollen production can only start when the plants reach maturity, e.g. 7 years for *Pinus* ssp. and 40-45 years for many temperature hardwoods
    - Most temperate plants flower in the early spring and summer; a function of the heat accumulation units
    - *Dehiscence* takes place during dry, warm, windy weather

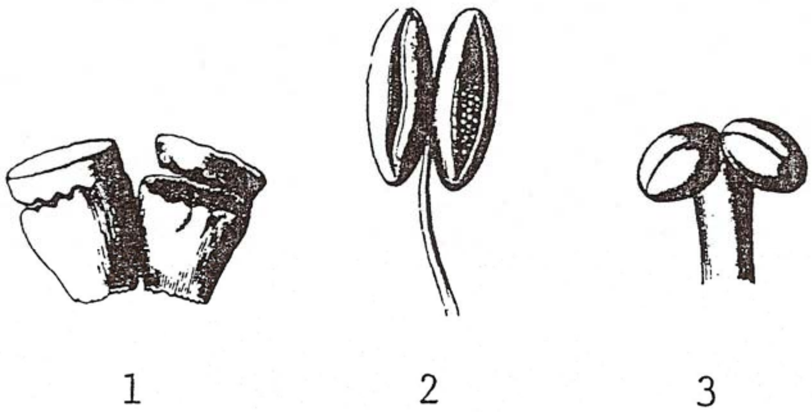


Fig. 3-1. Common dehiscence mechanisms in angiosperm anthers (KERNER, 1904). (1) Pore, circumscessile slit in *Garcina* sp.; (2) Longitudinal slit in *Calandrinia compressa;* (3) Distal slit in *Calla palustris*

- Amount
    - Quantity released is principally the results of genetic controlled adaptation, but can be influenced by the climatic characteristics of the period before and during flowering

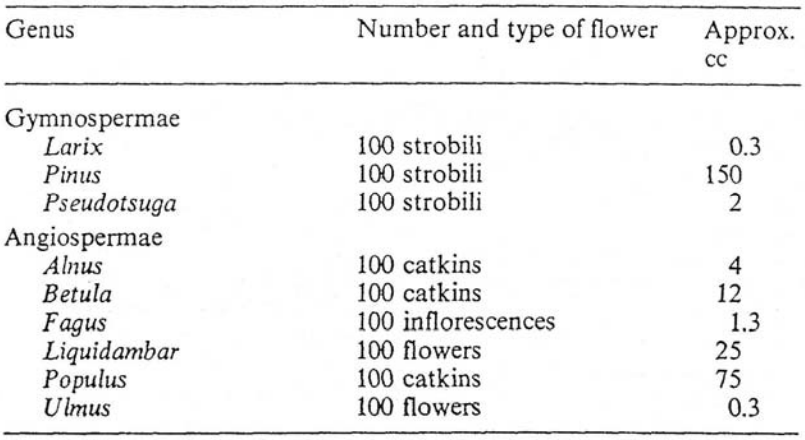


Table 3-2. Pollen yields (SNYDER and CLAUSEN, 1973)

Genus	Number and type of flower	Approx. cc
Gymnospermae		
Larix	100 strobili	0.3
Pinus	100 strobili	150
Pseudotsuga	100 strobili	2
Angiospermae		
Alnus	100 catkins	4
Betula	100 catkins	12
Fagus	100 inflorescences	1.3
Liquidambar	100 flowers	25
Populus	100 catkins	75
Ulmus	100 flowers	0.3

    - Hot, dry summer year before will increase number of flowers for the following spring in hardwoods
    - Weather during the flowering season can either allow the predetermined pollen yield to be successfully dispersed or reduction of pollen released
    - Cyclicity occurs of maximum pollen production, e.g. *Querus* 5-yr cicles, *Fraxinus* 3-yr cycles and *Betula* and *Fagus* 2-yr cycles.
- Position of pollen release
    - Important; most male flowers of conifer trees and hardwoods situated on the upper surfaces of crown and females slightly
- Wind speed
    - Also affects liberation. Many plant anthers require a *threshold speed of liberation* to move pollen away; e.g. 3 – 4 ms^{-1} for hardwood male flowers

Dispersal

- Results in scattering and downwind spread of pollen

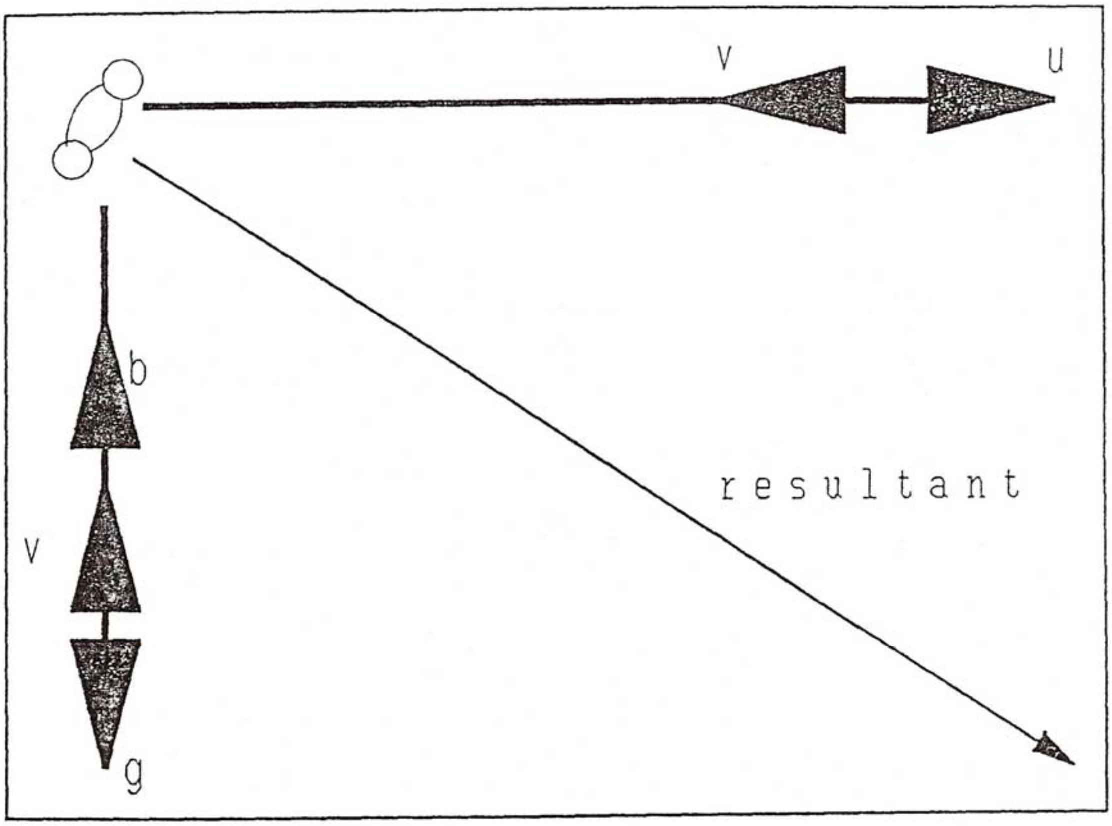
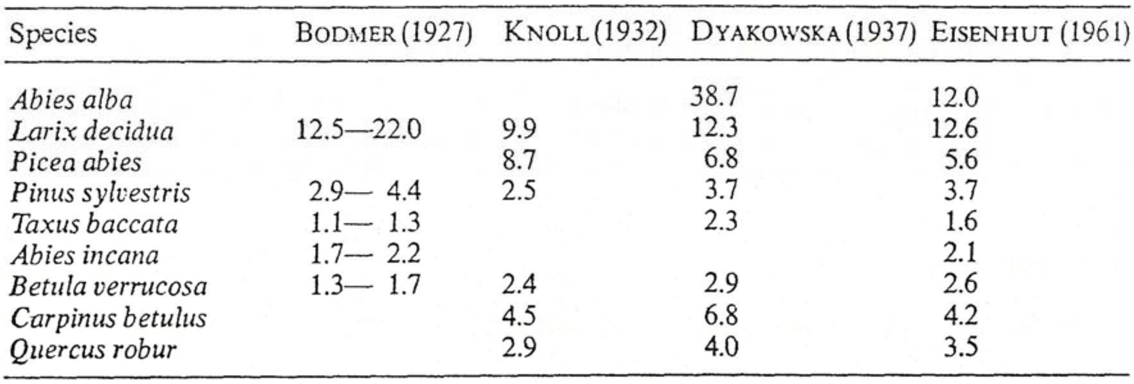


Figure 1. Laminar air flow and pollen flight. This view of the dispersal of pollen does not account for turbulence in the atmosphere and non-uniform wind flow.

u represents the mean horizontal wind speed (ms^{-1}), V is the viscosity (absolute) of the air ($Ns\ m^{-2}$), b is the buoyancy of the grain (kg) and g is the acceleration caused by gravity (ms^{-1}).

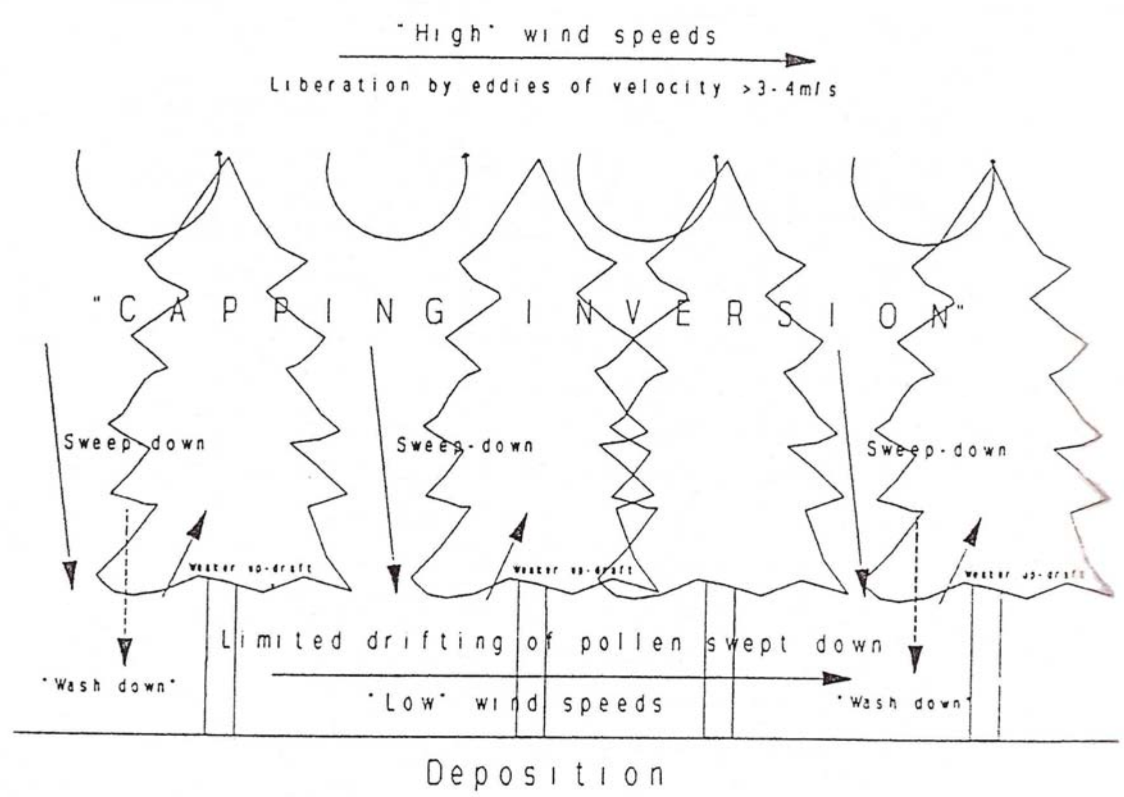
- Three main factors: *gravity*, *wind* and *turbulence*
    - Gravity
        - Free-fall velocities of grains determined by their densities, air resistance, size and form

Table 3-5. Free fall velocity of pollen (cm/sec)



Species	Bodmer (1927)	Knoll (1932)	Dyakowska (1937)	Eisenhut (1961)
Abies alba			38.7	12.0
Larix decidua	12.5—22.0	9.9	12.3	12.6
Picea abies		8.7	6.8	5.6
Pinus sylvestris	2.9— 4.4	2.5	3.7	3.7
Taxus baccata	1.1— 1.3		2.3	1.6
Abies incana	1.7— 2.2			2.1
Betula verrucosa	1.3— 1.7	2.4	2.9	2.6
Carpinus betulus		4.5	6.8	4.2
Quercus robur		2.9	4.0	3.5

-
    - Wind
        - Original estimates of pollen dispersal based on resultant of horizontal wind and free-fall velocity
        - In real situations: laminar flow close to solid boundaries only (the *boundary layer*). Therefore, turbulent flow is normal
        - Wind slower closer to boundaries/ground and faster further away/higher up. Therefore, this results in a shear of any aerial pollen
        - In vegetation wind becomes pseudo-random. Profiles of wind speed in forests indicate *blow-through*
    - Turbulence
        - Continuous fluctuations in the atmosphere
        - *Downdrafts* are the most important transport phenomenon in tall stands of vegetation, e.g. tall woodlands
        - Mechanical turbulence due to wind deviation around obstacles (greatest amongst and above tall vegetation)



Conifer pollen movements in closed-canopy stands (modified after Di-Giovanni, 1989).

        - Thermal turbulence due to convective (heat) currents in the atmosphere (mostly in the afternoon)
    - Minors effects
        - Thermophoresis particles migrate towards cold surfaces
        - Electrophoresis accumulation of electrical charges on particles influences dispersal

Deposition

- All processes by which airbone particles transferred to solid surfaces
- Major mechanisms: impaction of particles on obstacles
    - Sedimentation: free-fall velocity
    - Boundary layer exchange: diffusion of particles into the boundary layer and deposition by free-fall sedimentation in there
    - Turbulent deposition: turbulent eddies sweeping particles down onto horizontal surfaces
    - Precipitation scrubbing: rain drops capturing particles and transferring them to the ground. Also, particles caught on vegetation *washed-down* to the ground below, partly by *stem-flow*.

Impaction in the major process unless pollen in flowing over very open areas, e.g. tundra, savanna.

Modeling dispersal

- Pollen flow follows wind flow patterns and the dispersal patterns of smokes and gases except that particles the size of pollen will have an appreciable setting velocity superimposed upon its movements. Physical models have been developed which can predict air flow and smoke dispersal and therefore can be applied to pollen dispersal.
- Physical dispersion models come from two approaches:
  - Fickian diffusion – diffusion is proportional to the local concentration gradient and is Eulerian in nature (i.e. flow measured through time at a fixed poit). Gradient Transfer theory.
  - Statistical theory – Lagrangian in nature (individual particles are followed through space)
- The Eulerian approach can also include Gaussian Plume models which are simplifications to Fickian theory.
- Empirical models will also be discussed although their basis is on data collected rather than physical theories.

Empirical models

- They describe a gradient but cannot explain how it arose.

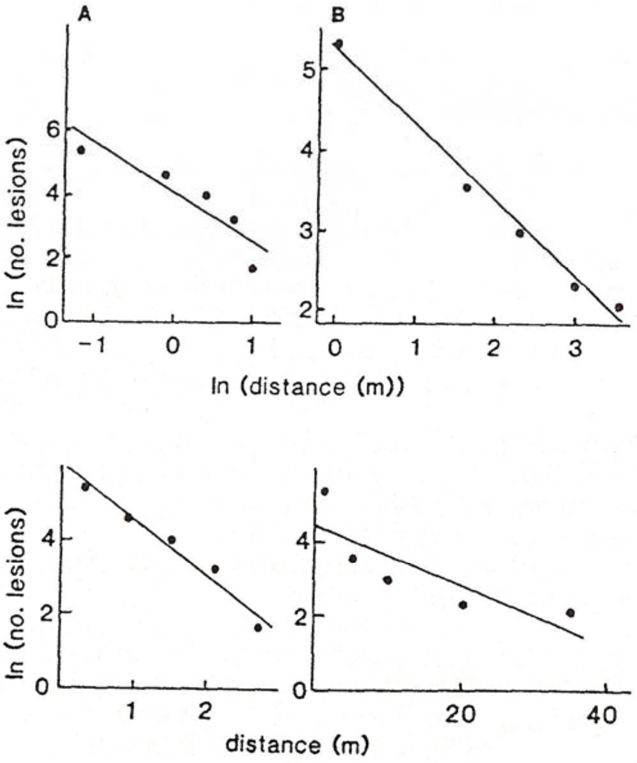
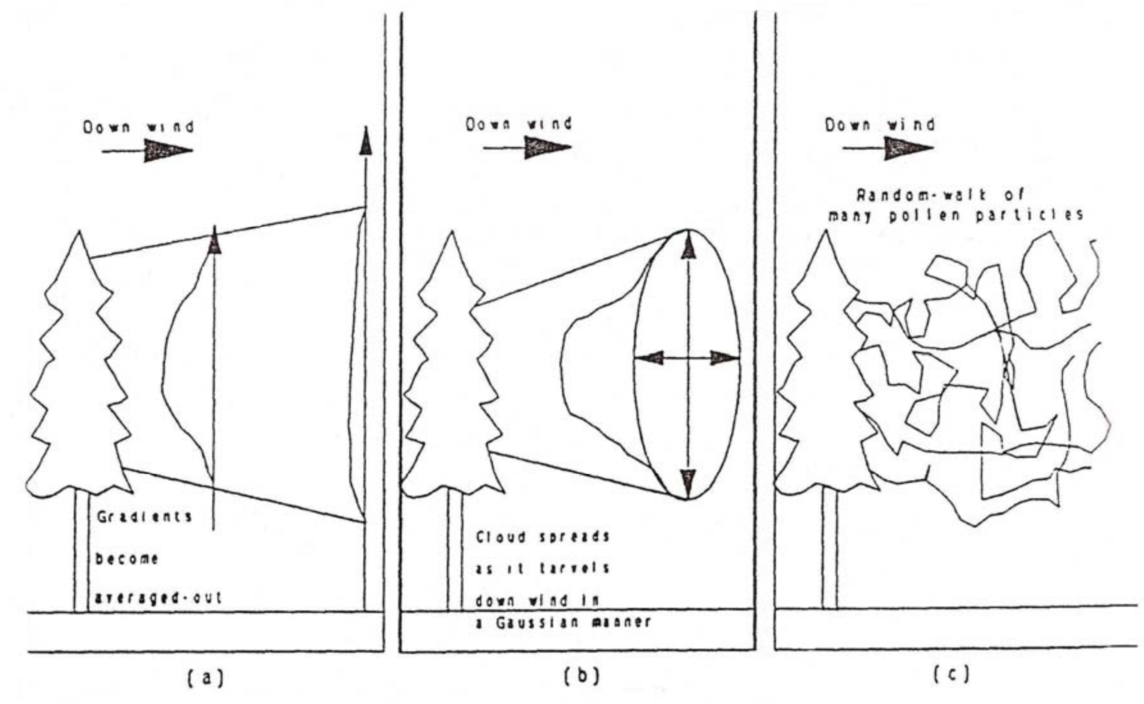


Fig. 1. Power law and exponential models of disease gradients: (A) potato blight (Limasset, 1939, focus 2); (B) eyespot (Oort, 1936).

- Data is collected, e.g. deposition versus distance and graphs made up and regression equations extracted.
- These regression equations are the models
- Not really applicable to other situations

Fickian diffusion

- Gradient Transfer theory – assumes turbulence causes movement of material down gradient of concentration



Pictorial representation of the manner in which the mathematical models mimi? pollen dispersal.
The horizontal axis of the pollen cloud curves, shown in Figs (a) and (b), represent the concentration of pollen in the air (# m^{-3}).
The diagrams denote:

(a) Gradient Transfer modeling in which pollen flows down gradients of concentration (i.e. flows from areas of high concentration to low concentration) as well as down wind.

(b) Gaussian Plume modeling, in which the relative density of the plume, as it spread down wind, will approximate the shape of a Normal distribution.

(c) Lagrangian modeling, in which each grain is seen as moving in a pseudo-random manner away from the source (and also down wind).

In simple situations (laminar air flow, no vegetation, no turbulence) all three models give similar results. However, as more and more complex situations are considered (i.e. vegetation, non-homogenous turbulence, etc.) the Gaussian Plume model and the Gradient Transfer model begin to give poorer predictions. In high complex situations, as exist at forest edges, the ----- accurate model would be the Lagrangian model. To use this model, we really need to examine the biophysics of pollen dispersal in detail.

- Need information on wind speed profile and turbulence profiles
- Breaks down within vegetation
- Gaussian Plume models
    - Simply Gradient Transfer theory by assuming particle cloud spread can be described by Gaussian curves
    - Not useful in complex situations

Statistical Theory

- Trace air parcels as they travel in a step-wise fashion through the atmosphere
- The latest and most sophisticated modeling approach
- However, equipment only recently developed which can effective measure the required parameters

Implications of wind pollination

- Wind pollination, its occurrence and effectiveness, has implications and uses in a number of fields of research

Plant Reproduction

- Reproduction in higher plants requires as extraneous agent to transport pollen from male to female parts
- Aerial dispersal used by anemophiles
- Problem in cross-fertilization is relation of distance between the plants and number of pollen grains produced
- For successful pollination among plants placed at arithmetically increasing distances, logarithmically pollen quantities are required. Pollen limited, therefore distance critical. Anemophiles usually clumped and dispersal distances are short
- "If effective pollination requires 1 pollen grain to reach a stigma of 1mm^2, every square metre of the plant's habitat must receive about a million grains"

Pollen Contamination

- Fields of agronomic crops and conifers are set up to produce genetically superior seed
- Seed used for replantation (forestry) or crop production (arable farming)
- Agronomic seed production areas should be isolated from other cultivars
- Conifer seed orchards should be isolated from "wild" pollen influx
- Some agronomic crops (e.g. corn) wind pollinated and most economically important conifers are wind pollinated
- Modeling and examining pollen flow can help management decisions on reducing contamination in existing orchards and designing new orchards in a manner conductive to minimal foreign influx

Pollinosis

- Much pollen is in the air – we all inhale it
- Particular species – some people are allergic to them

- Two categories:
    - Pollen of common grasses, e.g. Timothy (U.K.) and Ragweed (U.S.A.)
    - Pollen of weeds and ruderal species
- Some hardwoods (e.g. *Betula*) cause allergic reactions
- Diagnosis by scratch test on patient's skin
- Relief by anti-histamines or desensitization

Pollen analysis

- Outer layer (exine) of pollen grains are very resistant to decay
- Pollen falling on lakes or peat-bogs become incorporate into accumulated sediments and preserved under anaerobic conditions
- Pollen can be chemically extracted from such sediments; the proportions of different pollen grains present (ascertained by identification under a microscope) gives a great deal of information about the vegetation surrounding the lake or bog at the time the sediment was laid
- It is also a useful geological technique for dating rock strata
- Usually a number of pollen spectra from successive levels are combined into a <u>pollen diagram</u> which shows variation over time
- In NW Europe, this technique shows the course of forest history since the last glaciation

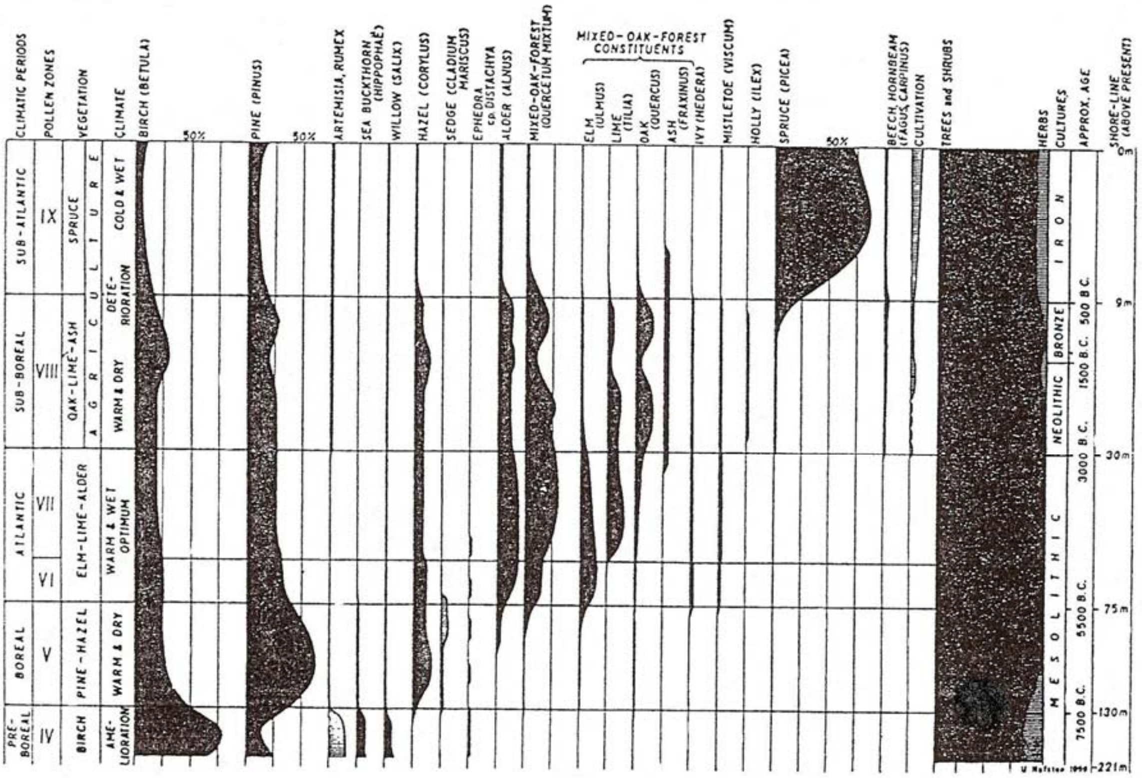


Fig. 12. Schematic diagram summarizing the results of investigations within an area (S. E. Norway). Hatching in this case indicates curves of NAP representatives, of which only a few, significant types have been included. At the extreme right an AP/NAP total diagram. From HAFSTEN (1960).

Introducing the practicum

Objectives

- To trace the dispersal of an artificial marker downwind of a point-source and derive appropriate biological conclusions

Methods

- Divided into 3 groups
- Each group works as a team (submit 1 report per group)
- Pollen released artificially, twice if possible
- Downwind of release point, pollen traps will be set-up configuration to be decided by the group
- Release over open ground or amongst vegetation (to be decided by group)
- Slides from pollen trap to be counted by the group

Analysis

- Frequency of pollen versus distance graphs
- Regression equations computed and compared between groups
- Discuss the effects of affects of wind, turbulence, vegetation and other factors on the dispersal of pollen

Time-table

1. After lunch – experimental set-up
2. After lunch – carry out experiments
3. Next day (?) – count pollen and analyze data
4. Before end of course – hand reports into me. Reports should follow format of scientific journals, e.g. Agricultural and Forest Metereology

The Evolutionary Ecology of Pollination

The Evolutionary Ecology of Pollination

Evolutionary events of major importance are usually preceded by trends which may seem rather trivial.

- These trivial events may be represented in the fossil record by the most subtle of hints to overt occurrence.
- Interpretation of the fossil record in palaeoecology is a relatively new discipline. The fossil assemblage of spores and pollen tells of floral diversity. The fossil assemblage of animals tells of the faunistic diversity. But how can the fossil record tell us about mutualistic systems such as pollination?
- Mostly, we much interpolate from present day ecological processes to conjecture about ecology in the past.

Charles Darwin described the origin of the Angiosperms as an abominable mystery, yet it is assumed that they originated and burgeoned in Cretaceous time along with insects and insect pollination.

- Are there hints in the fossil record that would suggest a predisposition of plants and insects to become mutualists through the former's producing material of value to the latter, and the latter providing a spore dispersing service to the former?

Answer: Yes!

- Soon after terrestrial plants and arthropods had evolved, mutualisms can be postulated.
- In Devonian time, c.a. 450 Million years ago plant spores show
- Ornamentation including hooks and barbs with presumed dispersal function
- Heterospory with mobile microspores and immobile megaspores
- Megagametophytes appear in the fossil record by the end of Devonian
- Some megagametophytes had pollination droplets at a micropyle

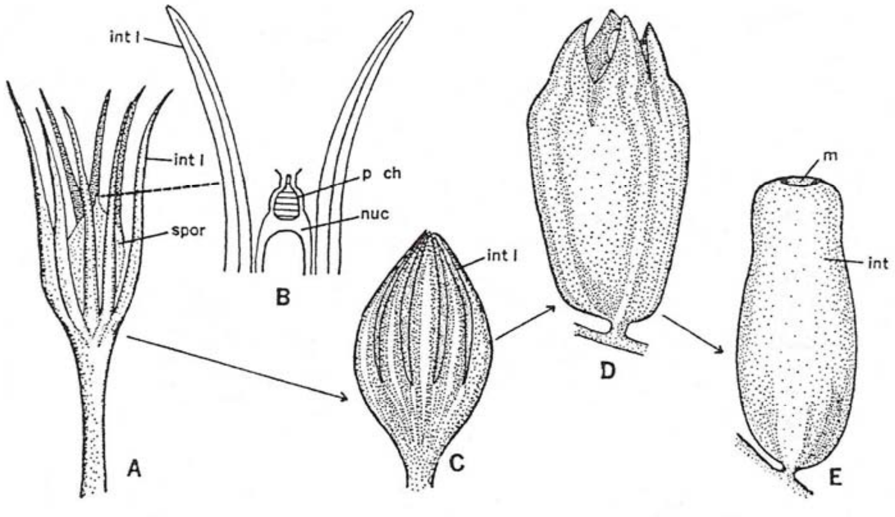
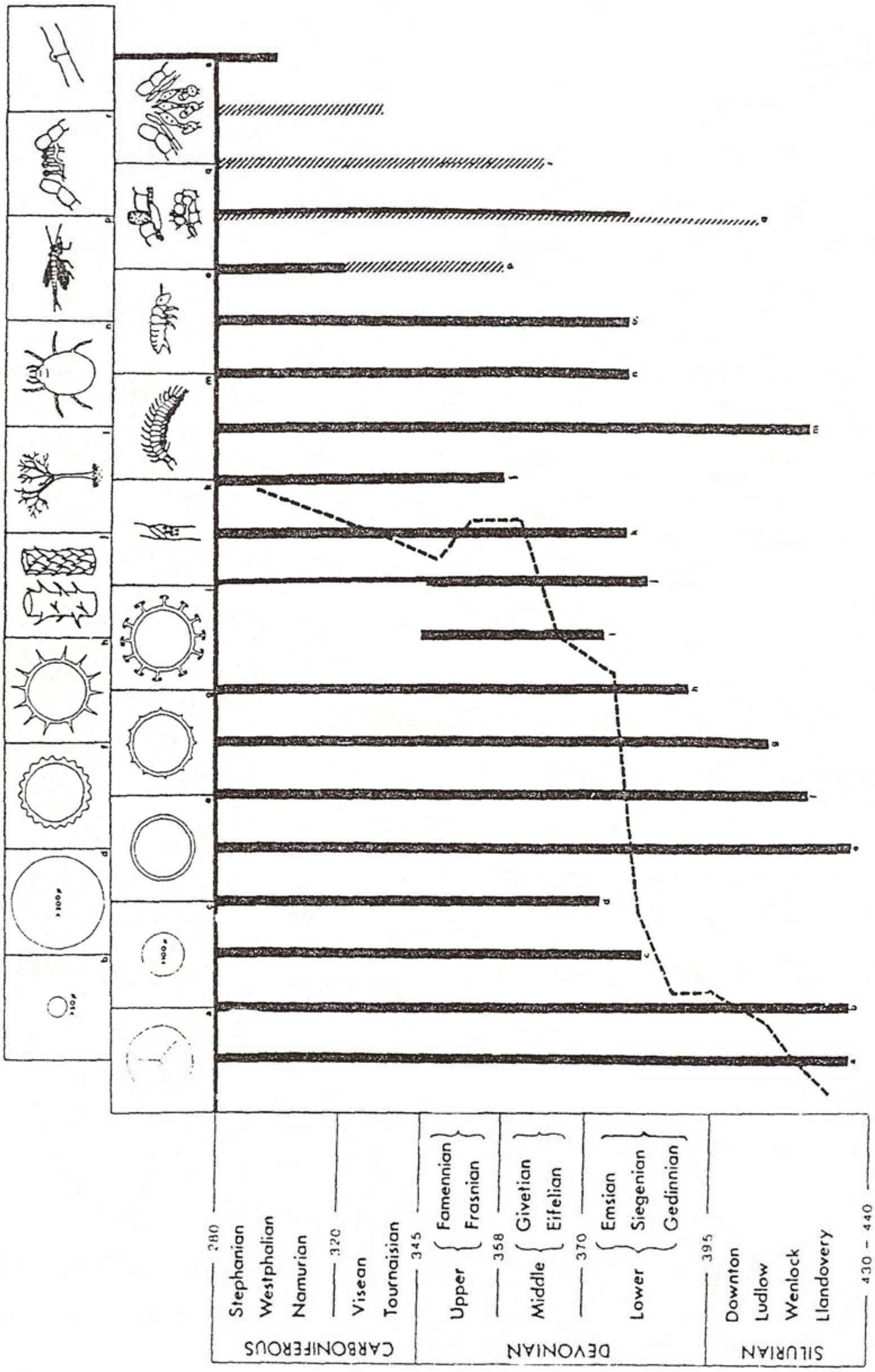


FIGURE 18–8 Series of early Carboniferous seeds attributed to pteridosperms, showing degrees of fusion of integumentary lobes leading to a true micropyle in E. B shows the development of the pollen chamber in the nucellus of the seed in A. *int*, integument; *int l*, integumentary lobe; *m*, micropyle; *nuc*, nucellus; *p ch*, pollen chamber; *spor*, sporangial wall. (A, C–E, after Andrews, Vol. 142, pp. 927–928, copyright 1963 by the American Association for the Advancement of Science; B, after Long with permission of the Royal Society of Edinburgh.)



- All suggest role for arthropods in microspore dispersal
- Appropriate arthropods of the time were Collembola and small Arachnida.

- By Carboniferous time, there were arborescent plants and winged insects, some found with pollen on their sucking mouthparts and on their bodies.
- Fossil feces (coprolites), presumed to have come from arthropods of the time contain lots of pollen grains. Very good evidence for pollenivory.
- Over Carboniferous, Jurassic, Triassic, and Permian times the Cycadoidea (including Cycadales with extant insect pollinated representatives) and Mesozoic Bennettitales (some of which had showy “flowers” that were up to 20cm across).

B. *Williamsoniella*, reconstruction. A, B: Jurassic. (Photographs courtesy of the Field Museum of Natural History, Chicago.)

- The sorts of insect thought to have been the first pollinators would have been
- Flying insects with folding wings
- Probably a general predator with high demand for protein (pollen)
- Insects like this are known from the fossil record. They also have wing venation which suggests that they cryptically blended in with the vegetation of the plants they foraged.

The diversity of insect Orders was well established by Permian time, but it was not until the middle of the Mesozoic and later that the recognizable families of the higher Orders became established.

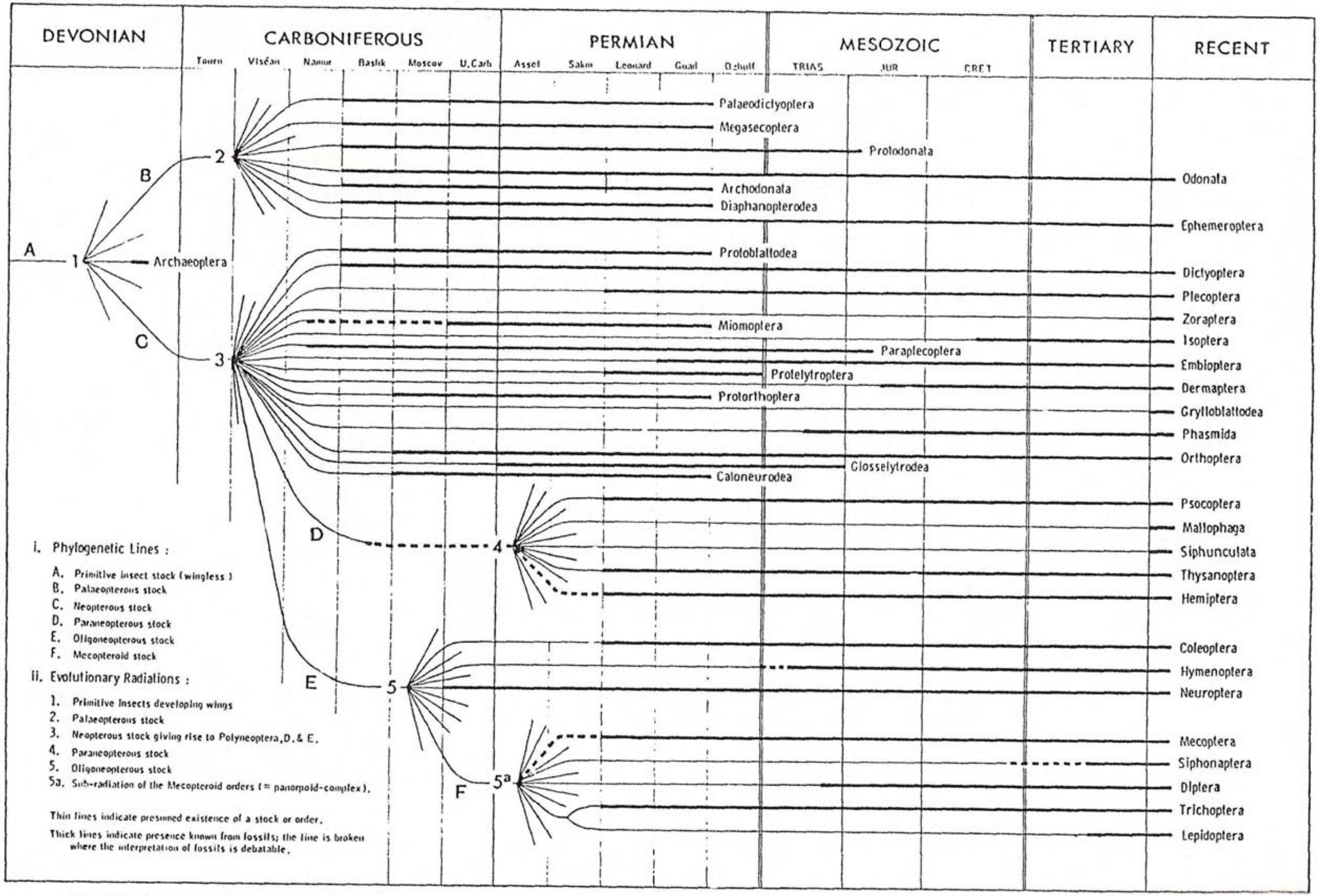


FIG. 1. The fossil record of insects and their phylogeny (modified from Smart (1963), with data from Crowson, Smart & Wootton (1967)). This figure, unlike Figs 2, 3, is not scaled for time

In Permian/Triassic time there were major floral and faunal changes.

Insect pollination seems to have been well established at the beginning of the Permian in dioecious and monoecious taxa.
Plants had protected ovules (perhaps against herbivorous insects). Perhaps insect pollination offered an evolutionary escape to already well-adapted plants at a time of great evolutionary upheaval.

- Evidence from the fossil record is scant, but quite convincing.
- The Cycadeoidophyta (e.g. Cycadeoidea) show well preserved sporangia (cones) through to mid and late Mesozoic which trend from open and exposed (early) to closed and protected (late).
- The trend corresponds to fossil evidence on the levels of insect damage to the cones. Beetles are suspected.
- Most studies in Palaeocology of pollination start with events of the Cretaceous, about 130 Million years ago.
- Angiosperm origins are still a mystery.
- Generally thought to have arised from the Pteridosperm (seed ferns).
- Angiosperm pollen is known from early Cretaceous time.
- Their radiation followed soon after their appearance.

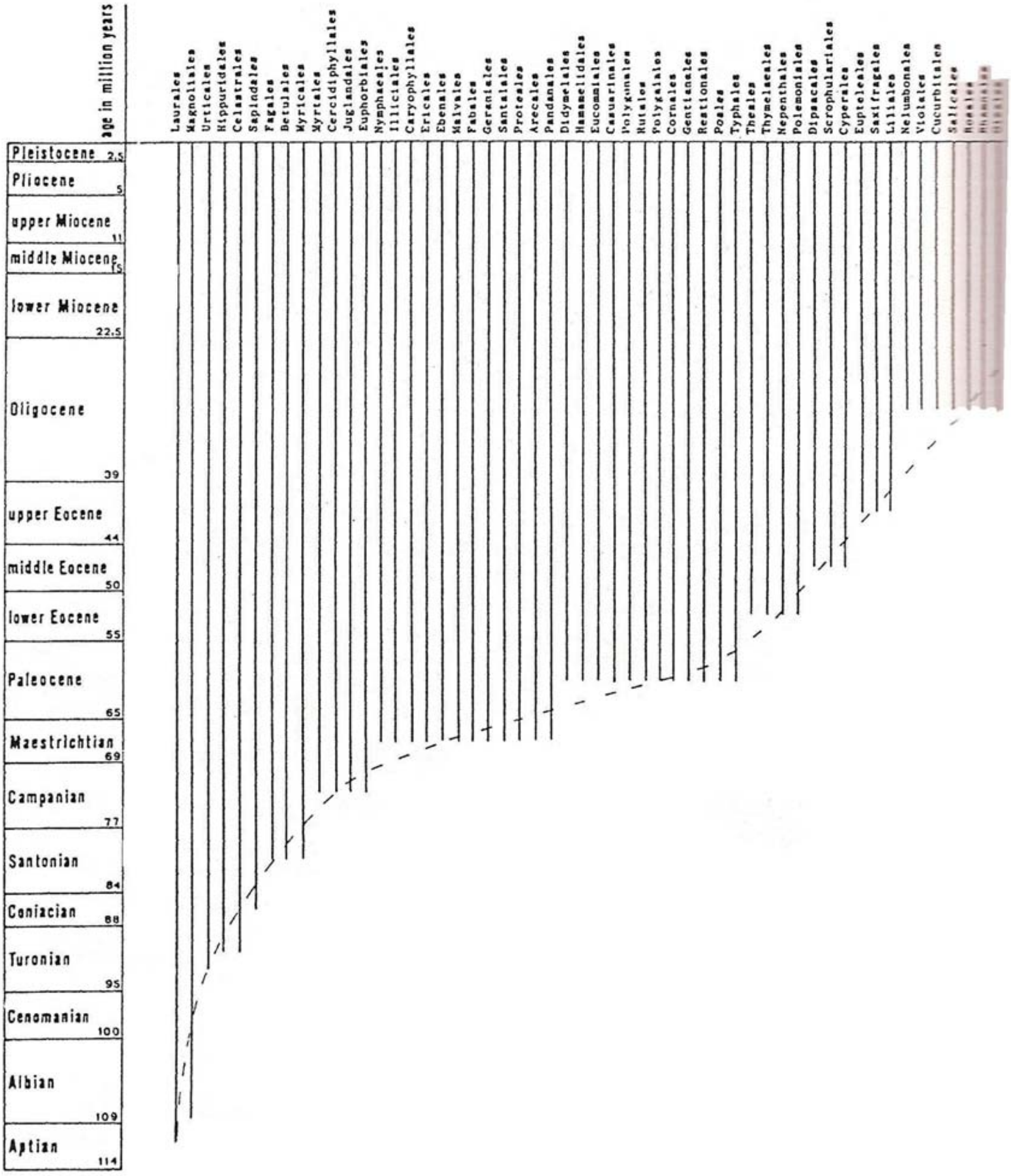


FIGURE 3. Pollen records for angiosperm orders.

Muller, J. 1984

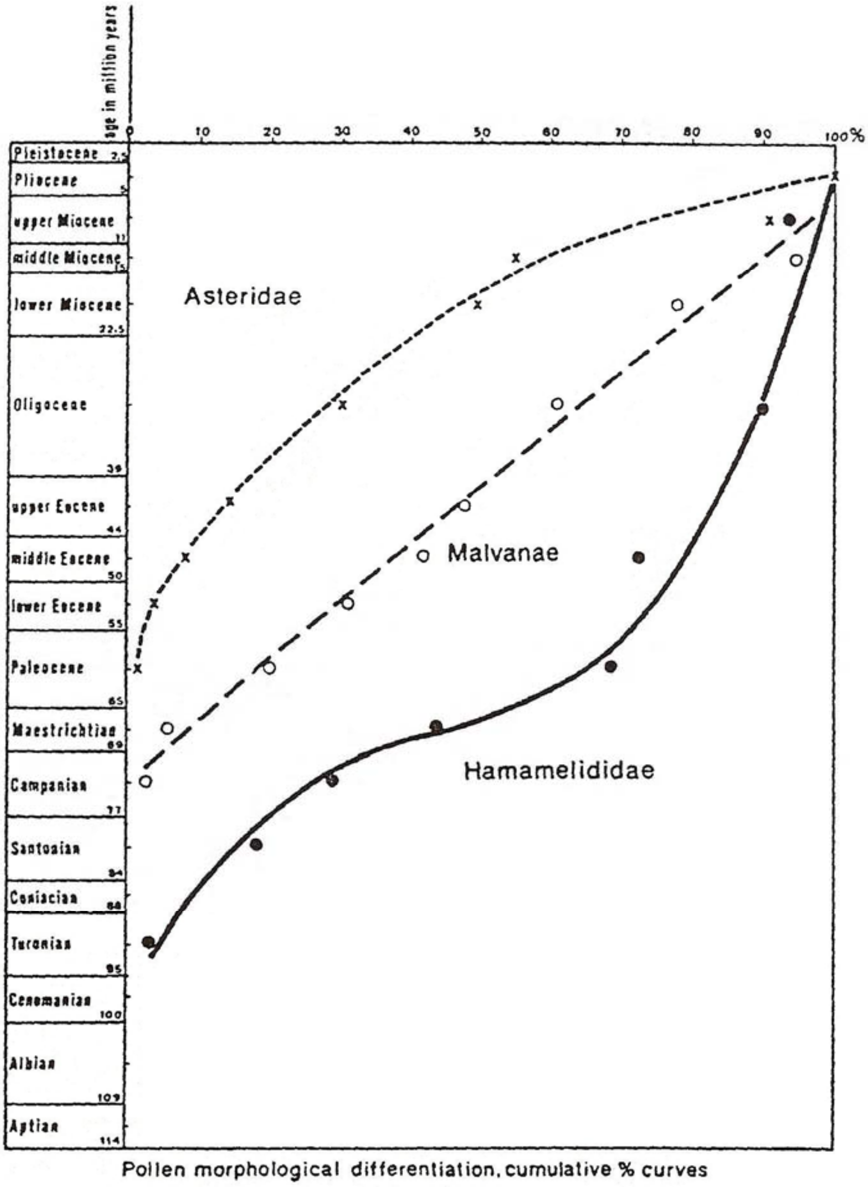


FIGURE 7. Cumulative % curves for Hamamelididae (dots), Malvanae (circles), and Asteridae (crosses).

Primitive angiosperm flower is generally regarded to have been:

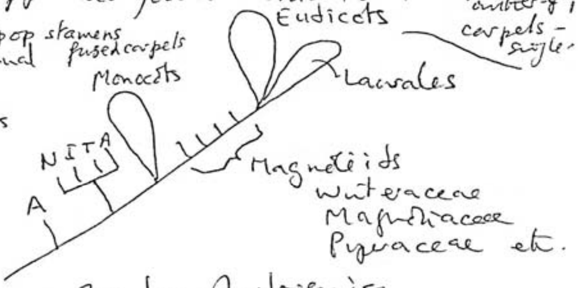
- Radially symmetrical
- Many-parted
- Hermaophroditic
- Dish- or bowl-shaped
- Possibly with intergradation from sepals to petals to androecial sporophylls.
- E.g. *Nuphar*, *Magnolia*

FIGURE 70. *Archaeanthus linnenbergeri*. Reconstruction of leafy twig and flower.

Basal angiosperms

Jurassic – 140-145 x 10⁶ yrs follicle
then → C † – 110-120 x 10⁶ fragments – unisexual (not bisexual)
pollen fossil Winteraceae
[illegible]ized [illegible]imp. [illegible]gel → C † – 110 Gippsland fossil – unisexual
C * – 90-100 lollipop stamens fused carpels
Archaeanthus – bisexual
C ⊙ – 80-70 x 10⁶
carbonized flowers
C – T § – 65-55 modern flora

stamens that leaf-like anther-ʄ, carpels – single.



molecular phylogenies

early flowers –
v. small – 1/16 - 1/8 inch Diam Oce
unisexual
v. little ~~[illegible]~~ fusion of organs
† no typical perianth
scale/scalelike tepals
not in buds
– per in bract-like

A = Amborellaceae
N = ~~Neta~~ Nymph
Ilich
Trimeni
Austrobal
} ANITA

(Magnoliids used to incl ANITA gp)

Chloranthaceae like † ; tetrad grains = Winteraceae
monoporate c̄ collar,
(times ∃ at same time of course)

* bisexuality – big tepals, etc.
~~[illegible]~~ fusion, inferior ovaries
5 partite etc... = major design forms

No monocots yet!

⊙ Aridization – fires forest, smoulderers, tiny flowers - shrunken head effect
mummified, 1/4" - 1/8" diam – nectaries seem ∃
Sweden, Spain, Portugal also some parts in 3's = monocots
= Triuridaceae

§ - symmetry - recognizable modern form.

4 kinds of organs in the same flower

Vogel – nectarioles in ANITA group – resemble stomates

- Early Magnoliaceaen-type flowers originally confused with Cycadeoidean flowers. However, parallel events, not phylogenetic events.

The diversity of floral forms is presumed to have evolved from those beginnings.

- But the advances are also associated with the evolution of faithful pollinators (the higher orders and higher families o insects, then later the vertebrates).

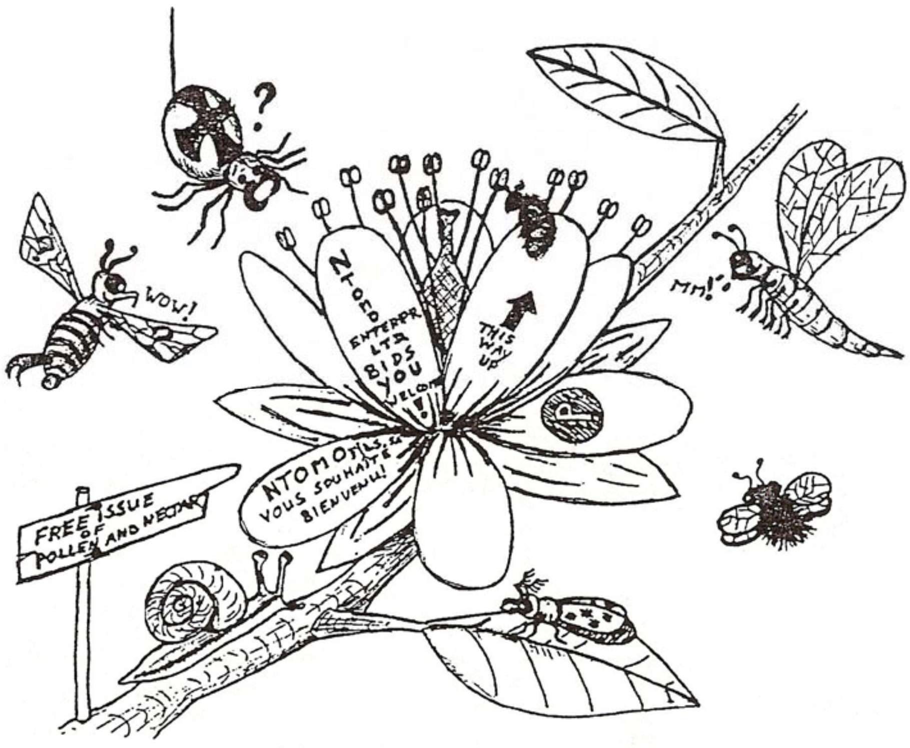


Fig. 7. A Cretaceous Employment Office.

What sort of Evolutionary/Ecological Process would have driven the radiation of the Angiosperms and their Pollinators?

- Already we have looked at the dimensions of pollination which hint at the dynamics of the processes of pollination in evolutionary ecology.

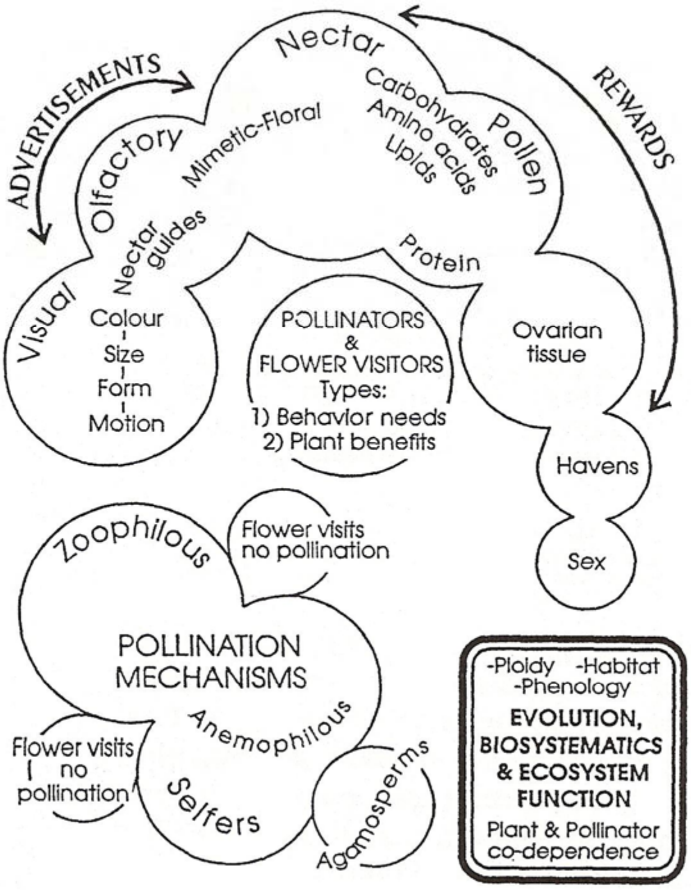


FIGURE 20.1 The dimensions of pollination. This entomocentric view shows the relationships of floral attractants and rewards on pollinators and insect visitors and the roles of the latter on plant reproduction. The processes involved (see Figure 17.2) lead to understandings of evolution, ecology, and biosystematice.

The DYNAMICS are depicted as follows and which will be explored through examining each component.

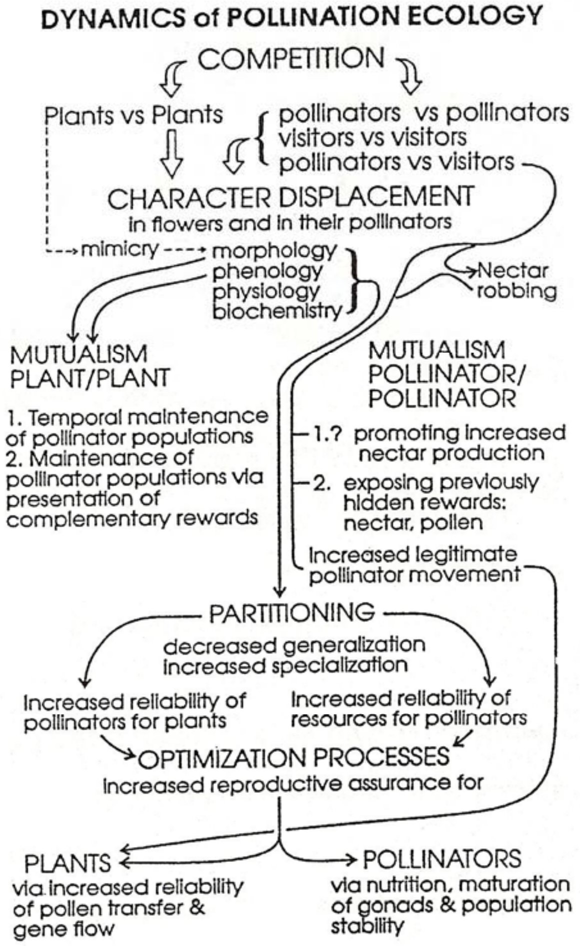


Figure 20.2 The dynamics of pollination. This flowchart starts with aspects of competition in pollination systems and follows their consequences through main-stream processes of character displacement, partitioning, and optimization, all of which heighten the mutualism which is basic to evolution in pollination systems. Side issues of mutualisms between plants and mutualisms between anthophiles may heighten the effectiveness of the basic mutualism in assuring the reproductive success of both plants and pollinators.

two flushed for
flowering ~
Med.
spring
autumn)
crocus
cycle

Competition

- The term competition has its problems. It is vague and has been dismissed as a “panchreston” by some ecologists.
- Competition must be qualified somehow.
- Here as Competition of plants with plants for pollinators and anthophiles with anthophiles for floral rewards (anthophiles need not be pollinators).
- Competition among plants for pollinators.
- This area of pollination has not been well documented.
- Examples are of dandelions (*Taraxacum officinale*) drawing pollinators from other blossoms blooming at the same time.
- Dandelions have been described as having “cornucopian” flowers, having easily accessible and goodly amounts of rewards.
- That has been invoked as an argument for removal of dandelions from orchards.

Losers in the fray should become increasing reliant of self-pollination or shift their flowering times out of competition.

- An insidious means of inter-plant competition in pollination is their production of pollen by some plants which is allelopathic to pollen of other plants when on the stigma of the latter plant as a pollinator-vectored contaminant pollen. This phenomenon is known for hawkweed (*Hieraceum*) pollen on stigmas of other plants.

Inter-plant competition for pollinators may be only a week force.

- Fertile area for research.

Competition among anthophiles is better documented.

- At feeding dishes in Sri Lanka, honeybees rank in dominance according to size: *Apis dorsata*, *A. cerana*, *A. florea* but small *Trigona* would drive off any of them.
- Interspecific dominance rankings in studies on Japanese herbs order insects as follows: Bumblebees, Syrphidae, Butterflies in general, but with variations within and between groups dependent on the sizes of the flower visitors.
- Others have shown competitive behaviour in bumblebees and in hummingbirds.
- For a community of 1 hummingbird (*Archilochus colubris*) and 2 bumblebee species (*Bombus fervidus* and *B. impatiens*) all foraging at *Impatiens biflora*, the following results were seen:

The hummingbird foraged on the outer, exposed flowers of the plant which grow in dense patches. It would be unable to penetrate the patch and fly at the same time.

The bumblebees foraged within the patch at flowers protected from hummingbird exploitation.

If hummingbirds were rare, *B. fervidus* expanded its foraging to the edges of the patches.

The bumblebees foraged at different times of day, *B. vagans* early and *B. fervidus* later.
But, it *B. fervidus* rare, the *B. vagans* would forage longer.

- The Africanized honeybee is strongly suspected of out-competition native bees in the Americas.

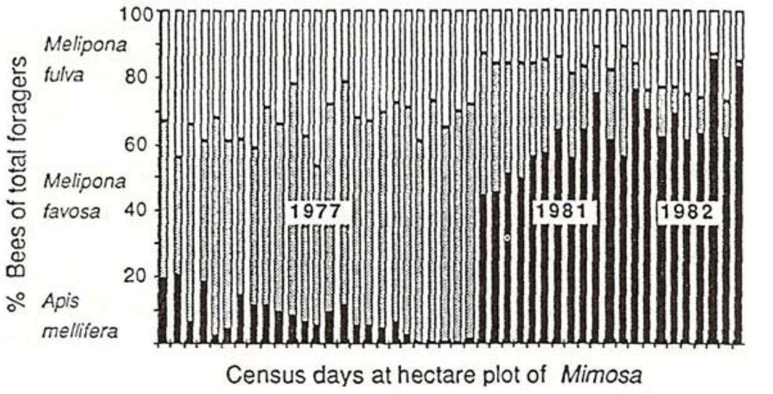


Figure 4.12. Changing relative bee abundance following invasion by Africanized honeybees in lowland forest of French Guiana. The two native bees visiting flowers of *Mimosa* are *Melipona* (Apidae) censused in a hectare plot (after Roubik 1987a).

- A concern for conservation, also in Australian National Parks versus Beekeepers.

Losers in the competition either suffer demise or have to switch to other resource bases.
The Outcome of Competition (Plant-Plant and Pollinator-Pollinator) has been thought to be represented in CHARACTER DISPLACEMENT AND RESOURCE PARTITIONING.

Character Displacement

- This may be morphological, phonological (above), physiological, or biochemical.
- Most of the morphological evidence comes from studies on Bumblebee tongue lengths and corolla depths.

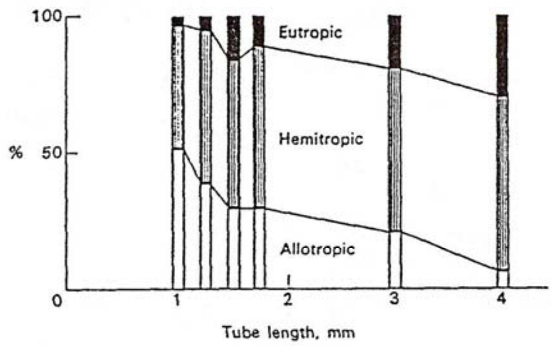


FIG. 3. Harmony between blossom and pollinators: the diagram shows how, with increasing length of the corolla tube in North American *Aster* species, the number of allotropic visitors goes down, because they cannot reach the nectar. At the same time, the number of eutropic increases, indicating their preference for the long-tubed flowers. The example is important because the blossoms are otherwise very similar to each other (after Graenicher 1909; cf. also Brian 1957).

- And similarly for hummingbirds

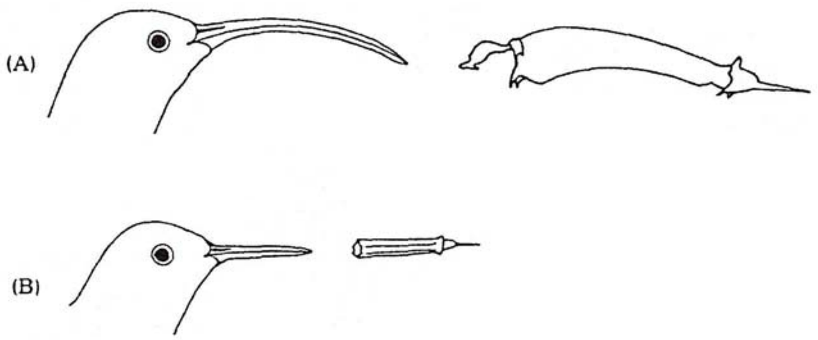
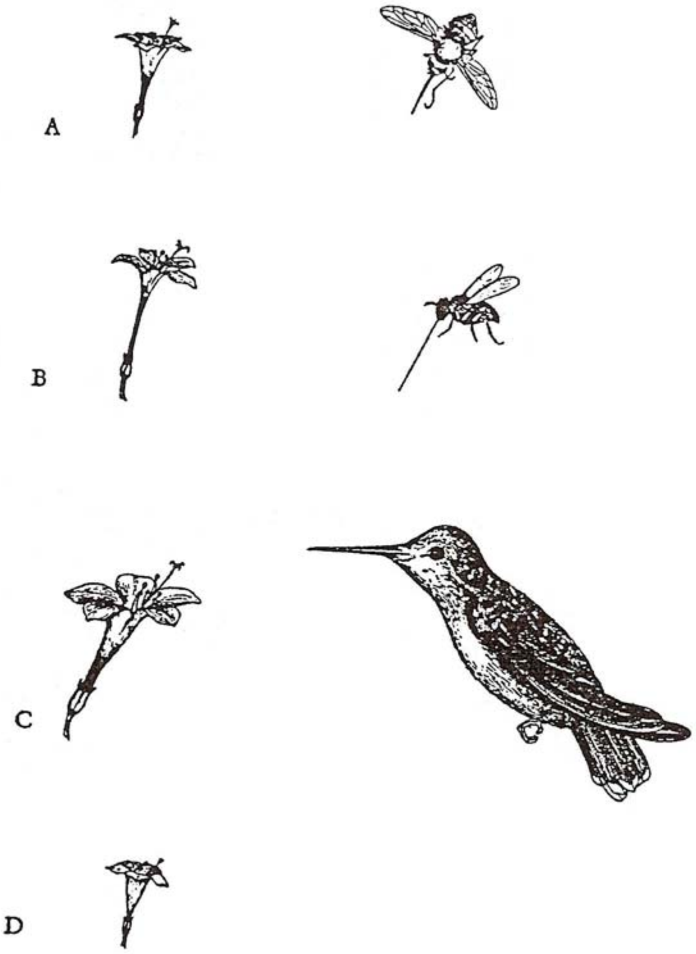


FIGURE 5. The two groups of hummingbirds and bird-plants. (A) A representative "hermit" hummingbird and rich flower. (B) A representative short-billed hummingbird and moderate flower.

- Or even within the same genus of plants and large differences in pollinator types.



- Competition and Partitioning can be seen to act between pollinators at the same flowers,
- And can be inferred to act between flowers for the same pollinators.
- In sympatric species of *Dalechampia* (with resin rewarding flowers for 4 species of bees) the various species are pollinated by different times of the day. The bees, Euglossines, *Trigona* and *Hypanthidium* use the flowers of numbers of numerous other species for pollen and nectar.

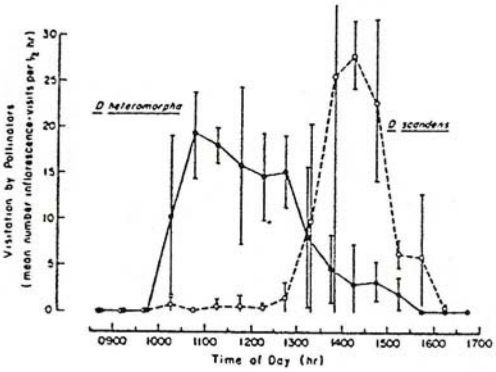
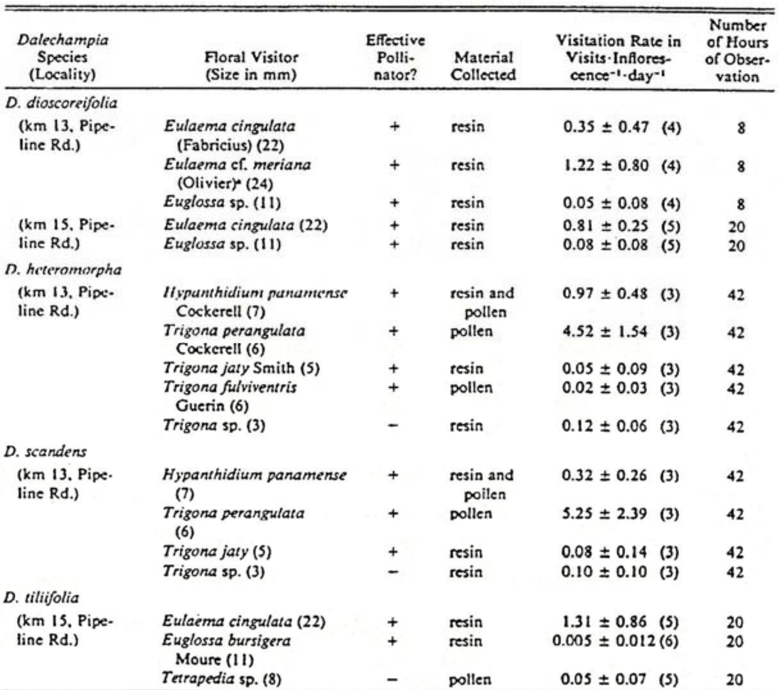


FIGURE 5. Rates of effective visitation by pollinators of *Dalechampia heteromorpha* and *D. scandens* at km 13 Pipeline Road, Canal Zone, Panama, 13–26 January, 1980. Bars are ± one standard deviation.

TABLE 5. Floral visitors to Panamanian *Dalechampia*. Visitation rates based on observations from 9–27 Jan. 1980. Numbers in column 5 are means ± s.d. with N in parentheses.



Dalechampia Species (Locality)	Floral Visitor (Size in mm)	Effective Pollinator?	Material Collected	Visitation Rate in Visits·Inflorescence⁻¹·day⁻¹	Number of Hours of Observation
D. dioscoreifolia					
(km 13, Pipeline Rd.)	*Eulaema cingulata* (Fabricius) (22)	+	resin	0.35 ± 0.47 (4)	8
	Eulaema cf. *meriana* (Olivier)* (24)	+	resin	1.22 ± 0.80 (4)	8
	Euglossa sp. (11)	+	resin	0.05 ± 0.08 (4)	8
(km 15, Pipeline Rd.)	*Eulaema cingulata* (22)	+	resin	0.81 ± 0.25 (5)	20
	Euglossa sp. (11)	+	resin	0.08 ± 0.08 (5)	20
D. heteromorpha					
(km 13, Pipeline Rd.)	*Hypanthidium panamense* Cockerell (7)	+	resin and pollen	0.97 ± 0.48 (3)	42
	Trigona perangulata Cockerell (6)	+	pollen	4.52 ± 1.54 (3)	42
	Trigona jaty Smith (5)	+	resin	0.05 ± 0.09 (3)	42
	Trigona fulviventris Guerin (6)	+	pollen	0.02 ± 0.03 (3)	42
	Trigona sp. (3)	–	resin	0.12 ± 0.06 (3)	42
D. scandens					
(km 13, Pipeline Rd.)	*Hypanthidium panamense* (7)	+	resin and pollen	0.32 ± 0.26 (3)	42
	Trigona perangulata (6)	+	pollen	5.25 ± 2.39 (3)	42
	Trigona jaty (5)	+	resin	0.08 ± 0.14 (3)	42
	Trigona sp. (3)	–	resin	0.10 ± 0.10 (3)	42
D. tiliifolia					
(km 15, Pipeline Rd.)	*Eulaëma cingulata* (22)	+	resin	1.31 ± 0.86 (5)	20
	Euglossa bursigera Moure (11)	+	resin	0.005 ± 0.012 (6)	20
	Tetrapedia sp. (8)	–	pollen	0.05 ± 0.07 (5)	20

* This bee was only observed with binoculars. Due to extreme similarity of mimetic euglossines, we cannot be certain that this is *E. meriana* (cf. Dressler, 1979).

- Pollinator guilds for a given plant species may be different in different parts of the plant's range.
- Floral guilds for pollinators have not been well analyzed, except in terms of floral calenders for honey production by managed honeybees.
- Examples from evolutionary ecology come from systems with long-lived pollinators, such as hummingbirds and bumblebees.

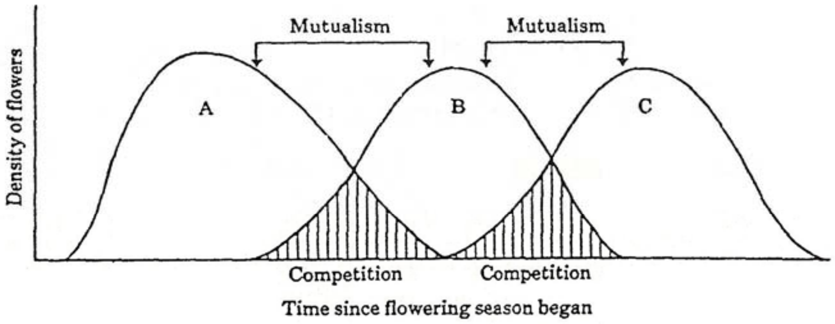


FIGURE 4. Phenological relationships within a "replacement set" of three plant species, A, B, and C, pollinated by bumblebees. (After Heinrich, 1975a; Waser and Real, 1979; Thomson, 1980.)

The interesting question circles back to point of origin:

- Did competition force character displacement in flowering time, so that original competitiors are now mutualistis?

The some other questions arise:

- Is "pollinator/pollinatee niche separation" the only expected outcome of community level evolutionary and ecological processes?

And

- Are observed instances of "pollinator/pollinatee niche separation" the outcome of evolutionary and ecological processes?

One can imagine that the appearance of subtle differences in either flowers or pollinators could provide for increased reliability of pollination and reward availability and lead to specializations.

- Specializations may be in floral morphology, colour, scent, etc. and in pollinator morphology, nutritive requirements, behaviour, etc.
- In both situations, maximization of fitness is the "aim" of the selfish genes.

The processes of co-evolutionary ecology are probably not smooth and linear, nor always in the same general direction. Other pressures impinge on maximizing fitness, and over-specialization can be detrimental.

- Resource reliability is important to both partners (plant and animals) in pollination.

- Thus, if pollinators of a certain species are rare, the plant’s reproductive capacity would be jeopardized unless it had alternative pollinators or could be independent of them.
- The plant’s strategy would be to have a guild of pollinators (as Impatiens above) or be self-pollinating.
- The pollinator’s strategy would be to have a guild of floral resources or be independent of them.
- Pollinator guilds may be highly diverse (over 100 species of bees for lowbush blueberry in Eastern Canada), or very small in highly specialized plants (e.g. some Orchids).

Pollinator Community Ecology

Pollinator community ecology

Carlos F. Greco

1. Introduction

In this chapter we will address the problem of how pollinator communities are organized and how such knowledge can help us to elaborate management measures either to increase crop production, to preserve native flora or even to control weeds.

The first of this chapter, *General Concepts*, explores some of the most current issues in theoretical community ecology such as stability, competition and organismal theories of communities. The following section, *Examples of studies of pollinator communities*, examines the impact of those theoretical concepts on specific studies on pollinator ecology. By means of some examples with bumblebees, it is shown how a paradigm in community ecology such as competition is utilized as a major hypothesis in pollinator community organization. As well, it is shown how alternative hypothesis are generated in the light of a new interpretation of communities. Finally, in the last section, *Applied community ecology of pollinators*, the application of community ecology studies to specific problems in crop production is exemplified with two cases in pollination of blueberry heaths in Canada.

2. General concepts

2.1 Definition

A community can be defined as the ensemble of species in some area, whose limits are determined by the practical extent of energy flow (Drake, 1992). Pollinators are unquestionably energetically related to plants. In turn, some herbivores are related to these plants and these herbivores are preyed and parasitized by a complex of predators and parasitoids. Then, according to Drake’s definition constitute, rather than a community *sensu stricto*, a group of species that exploit the same class of environmental resources in a similar way, more commonly known as *guild* (Simberloff & Dayan, 1991).

Studies involving communities focus on properties of a whole not identifiable in parts (emergent properties). Those properties are, for instance, relative abundance, stability, diversity, topology, food web patterns and productivity. Some of these properties, in turn, are applicable to some parts of the whole such as guilds, which are complex units in themselves.

Nevertheless, the determination of the community according to the definition above, is a difficult endeavor which has not been surfaced yet. Because of its unwieldy complexity, understanding organization at the community level has been an elusive, often frustrating enterprise.

On the other hand, guilds are more easily delimited in the system and are less complex in their organization. Furthermore, the concept of guild is useful in comparative studies of communities since it enables us to concentrate on specific groups with specific functional relationships. This is preferable to study taxonomic groups within different species may perform unrelated roles (Root, 1967).

Something that is often articulated for the study of guilds is that they might represent the basic building blocks of communities *sensu* Drake (1992) (Hawkins & McMahon, 1989). Hence, the study of pollinator guilds can be parallel to the study of the reproductive anatomy and physiology of an organism, considering that pollinators are related to the reproduction of plants, which are the basic energy producers of the whole system. Them, on the line of this analogy, by studying properties such as the organization of the guild and its species composition, we are actually studying the *anatomy* of that part of the community and, when we refer to the guild internal dynamics and relationship to the reproduction of plants, we are studying the *physiology* of the "organ". We are going to put our further discussions on pollinators into this conceptual frame and talk about *pollinator guilds* throughout.

2.2 Assembly rules or… "Does God shoot dice?"

At this point we have to put a caveat. The analogy of the organ presented above, must be simply taken as a hypothesis. This is actually matter of fervent discussion nowadays, although this problem has been in the ecological literature for a long time now: *can guilds and even communities be regarded as organisms?* However, before considering the organismal hypothesis, a more proximate question must be brought up: are there any kind of assembly rules in community or they are randomly formed from a general pool of species in a given area? In this respect, we can cite for instance, the renowned controversy between Diamond and Gilpin on one side, and Connor and Simberloff on the other. Diamond (1975), studying a bird community in Bismarck, concluded that these manifest the following patters:

a) "If one considers all the combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature"
b) "Permissible combinations resist invaders that would transform them into forbidden combinations"
c) "A combination that is instable on a large species-rich island may be unstable on small or species poor island"
d) "On a small or species-poor island, a combination may resist invaders that would be incorporated on a larger or more species-rich island"
e) "Some pairs of species never coexist, either by themselves or as part of a larger combination"
f) "Some pairs of species that form an unstable combination by themselves may be form part of a sable larger combination"

g) “Conversely, some combinations that are composed entirely of stable subcombinations are themselves unstable.”

Connor and Simberloff (1979), rebutted Diamond’s paper by constructing a *null hypothesis* that started that the distribution found in the islands were generated by species randomly and individually colonizing the archipelago. Some years latter, Diamond and Gilpin (1982) replied Simberloff’s paper by saying that the null hypothesis suggested in their paper, was inappropriate because:

1. from the biological point of view, they added competition in it and,
2. from the statistical point of view, the authors did not give all the cases the same probability or at least a frequency distribution to compare.

The “Achilles’heel” in Diamond’s argument was that he relied too much on competition as a structuring force, without having actually strong evidence to prove either its present or past existence in his communities.

Competition is a difficult concept to deal with, mainly because it is difficult to prove in natural guilds or communities. The reason why Diamond, like other researchers, clung so much to the competition concept is because competition was largely the more accepted structuring factor of communities at the time. Indeed, for a long time, studies on community organization and dynamics focused on limiting resources, whereas trophic exploitations (predation and parasitism) were not equally much appreciated. Emphasis on resource limitation and competition could be espoused, assuming that the bulk of plant biomass is not potential food for herbivores and that most herbivores are free of predators. Nevertheless, the credibility of these assumptions is eroding fastly. The idea of competition as the foremost structuring force is being questioned, and increasing attention is paid to predation and parasitism as alternatives (Oksanen & Ericson, 1987).

2.3 Stability

The behaviour of isolated components (populations, guilds or taxocenes) may not reflect the dynamics of the entirely (Drake, 1992). Drake, clearly expounded some of the reasons why communities as a whole should be studied, rather than their separated components. Understanding stability is one of them. A hazy delimitation of the community can mislead us towards fallacious conclusions about how stable the community is. For instance, let us suppose that we want to study a forest ecosystem and we define our community as the one made up by birds and butterflies. Let us suppose too, that the populations of the species appertaining to these two groups oscillate significantly in time. We might conclude then, that the community is unstable. Instead, if our view of the community included all species in the system that are in one way or the other energetically related, we might think that the system is overall stable, with some variations among some of the components. The difficult task is, however the identification of spurious links among the species present in the system, which can be stated in other words, as the quantification of Drake's qualitative definition. Truly, another laborious task is to study the whole ensemble of species present in the community. Probably, to choose some *key species*, a particular guild for instance, could be a methodological solution to this problem. Unfortunately, this is "catch-22" because the only way to define functional and appropriate key species is by knowing the organization and dynamics of the whole system. That is to say, key species are not useful in primordial steps of a project in community ecology; they certainly are useful elements in practical diagnosis in ecosystem management, once a meaningful amount of information about the structure and dynamics of the community was culled.

All in all, stability has been historically an important issue in community ecology because of its practical consequences. For instance, stable pollinator communities imply sustainable yields in crops. The assessment of the status of stability of the community, may contribute to more reliable management protocols, either to maintain stability or to restore it.

One of the more controversies about stability of large complex systems such as communities is the relationship between the diversity of the system and stability. An empirical investigation of the problem concluded that the more diverse a system is, the more stable it should be (McNaughton, 1977). Antithetically, theoretical studies previously made by May (1972) following the suggestion by Gardner and Ashby (1970), demonstrated analytically that the stability of a system is more related to the *connectance* than to the number of species it has. Connectance is defined as follow:

$$c \; \alpha \; \frac{M}{M(M-1)} = \frac{1}{M-1}.$$

where M is the number of species present in the system, and M(M-1) is the number of possible links between the M species. This theoretical studies involving the concept of connectance, concluded that systems with more interespecific interactions *per* species (higher connectance), or strong interactions, are not as likely to be stable as systems with fewer of these attributes (King & Pimm, 1983). Despite the attempt of some researchers to reconcile both positions (King & Pimm, 1983), the controversy still remains and more empirical studies are needed to spawn a strong theory.

The stability issue is also related to the idea of the existence of assembly rules in communities mentioned in point 2.2. In this respect, it was shown that "plausible community matrices" drawn up to reflect the patterns of real world, were more likely to be stable than comparable random webs (Nee, 1990).

Another interesting approach to stability is the idea of *local and global stability* and associated with it, the concept of *persistence* (Nee, 1990). Some feel that persistence is more relevant than local stability to a community. Some "point" equilibria can be unstable and yet to be possible for all the species in the system to persist as stable cycles or even as bounded chaotic *fluctuations* generated by strange attractors in the stability topography (planetary orbits are actually chaotic, yet this does not mean that planets are about to whiz off into space!).

2.4 Community organization

Lately, a growing number of theoretical studies and experimental evidence are firmly conveying towards an *organismal hypothesis of communities*. As mentioned in previous paragraphs, this new conception in communities is primarily built on the idea that communities are not random ensembles of species but that assembly rules and mechanisms are involved in their genesis (Drake, 1990, 1992; Nee, 1990). Opponents to this theory argue that an organism, to be deemed as such, must evolve. However, the evolution of functionally organized communities encounter a fundamental problem: adaptation at any level requires a process of natural selection operating at that level (Dubar, 1960; Lewontin, 1970; Slatkin & Wilson, 1979; Wilson & Sober, 1989) and for a natural selection to operate variability is indispensable. Theoretical formulations, endorsed by some experimental evidence, of alternative states of a community (Drake, 1990, 1992) might probably surmount this hurdle. Additionally, the ideas of Robinson and Dickerson (1987) and Wilson (1992) hint that variability is possible. Robinson and Dickerson (1987) showed that the sequence of invasion to a system by species coming from a general species pool, determines the composition of the final community. This means that in a given area where a general pool of species is present, several different communities can be found, which differ in their qualitative and quantitative diversity. This, in turn, determines the quality of emergent properties of the communities thus formed.

Based on these general ideas, Wilson (1992) developed a model in which several communities, patchily distributed and with distinctive initial conditions, conformed what he called a metacommunity. Although just a model, the idea has merit: the "dynamical cloud of variation" proposed by Wilson has an important implication in the concept of communities as organisms. The complex interactions inside each sub-community provide a new source of variation upon which natural selection can operate at a patch level (Wilson, 1992). This might respond, as least theoretically, to one of the predominant critics against the superorganism theory.

3. Examples of studies in pollinator communities

As mentioned in previous sections in this chapter, the pollinators inside a system constitute, rather than a community *sensu* Drake, a component of the whole system known as guild. We can consider a guild such as the one of pollinators, in a narrow taxonomic range (bumblebees, for instance) or in a broad sense, including different groups such as all kinds of bees, butterflies, beetles, flies, etc.

Particularly, bumblebees guilds were extensively studied in an attempt to ascertain the factors affecting their structure and organization of this s0-called community in the literature (Ranta & Vepsalainen, 1981; Ranta and Taiainen, 1982; Obeso, 1992; Inouye, 1977, Ranta, 1982). Most of these studies, emphasize competition as the structuring force to be tested. Competition seems to be the paradigm in community ecology still in the 80's and way into the 90's. Guilds are particularly vulnerable to this unilateral analysis because of their nature. By definition they represent a group of species exploiting the same kind of environmental resources. As such, it is enticing to hypothetisize that the components of the guild are kept within the guild by a competition process which is either taken place or took place in the past, shaping the present structure of that portion of the whole community. Although this might be the case, some of these bumblebees studies showed that other forces must be considered in order to understand thoroughly, first the structure and then the dynamics of pollinator guild.

Alternative explanations to competition where posed in some of the investigations conducted with bumblebees. Given a limited food resource, there is expected to be a more even (equidistant) packing of species in a niche space (in the case of bumblebees, measured by spacing along the proboscis length axis) than in a random subset of bumblebees from the species pool of the arena (Ranta and Tiainem, 1982). Some studies (Ranta and Tiainem, 1982; Ranta and Vepsalainen, 1981) did not substantiate this hypothesis, showing that the guilds studied had species composition which did not deviate from the ones drawn randomly from the regional species pool. This, however, does not imply that those communities are a fickle drove of species. In this particular studies, environmental heterogeneity and stochasticity were proposed as feasible forces affecting the species composition of bumblebees found. As food resources are patchily distributed and temporarily changing, the different colonies are liable to suffer energy problems in different time. Hence, the competitive situation, if any, among colonies and species changes continuously allowing a larger number of species coexisting in the same area than expected on the basis of merely competitive hypothesis (Ranta and Vepsalainen, 1981).

The importance of actually determining the forces shaping a particular guild within a community such as pollinators, lies on the fact that the dynamics of the whole system (community) can not be otherwise understood. Furthermore, a precise discernment of the dynamics of pollinator guilds is dispensable for management purposes. However, other emergent properties of guilds and/or communities should not be overlooked, since they may serve as well as suitable answers to some questions about the status of the system and its management requirements.

4. Applied community ecology

All the theoretical considerations succinctly presented in the first section on this chapter are certainly reflected in studies on pollinator communities as it was shown in the second section. All these purely theoretical (section 1), and applied findings (section2), cascade down towards strictly technological investigations conducted in order:

a) To improve cash crop yields
b) To control weeds in cash crops
c) To preserve native flora in order to enhance biodiversity and,
d) To preserve adventitious flora to promote diversity of biological control.

Example 1: *Environmental risk assessment*

A sequence of studies started in 1975 by Kevan (1975, 1977), Kevan and Opperman (1979), Kevan and LeBerge (1979) and Kevan and Plowright (1989) explored the influence of pesticide application in nearby woodlands, on the guild of native bees in blueberry fields in New Brunswick, Canada. This research culminated in 1995 in a study in which a “symmetry concept” was applied to determine the incidence of the pesticide on the pollinator guild (Kevan, et al. in press). In this study the diversity pattern of the pollinator guild was assessed, applying the log-normal distribution methodology (Preston, 1948). On both spatial (different fields) and temporal (different years) basis, fields unaffected by the pesticide fitted well to the log-normal model of species diversity, whereas fields affected by the insecticide departed significantly from that model. The log-normal relationship linking species diversity and abundance proved to be an objective norm (technological tool) against which to test ecosystemic integrity, disruption and health.

Example 2: *Crop yields*

In an investigation conducted by the Nova Scotia Agricultural College (Nova Scotia, Canada) and Enviroquest Ltd. (Ontario, Canada), the structure and dynamics of the pollinator community of blueberry fields in Nova Scotia was studied in order to understand the contribution of the different components of the community to the yields of blueberries.

The first step of this project was to try to understand the relationship among the different components of the pollinator guild (Greco, 1995a,b; 1996). In this particular case, the guild studied included four groups of native pollinators (large bees, medium bees, small bees and “others” (any insect that were observed working blossoms)) and honeybees. No significant pattern of correlation, either instantaneous or lagged was found among the groups of anthophiles. No temporal replacement or exclusion of the groups on one another could be concluded from that study. As well, no clear trend could be concluded as to any spatial replacement or exclusion pattern. Thus, no intrinsic cohesive forces seemed to be present in the pollinator community sampled. Even though honey bees might represent one of the most troublesome components as an introduced element in a system such as wild blueberries, impairing the normal activities of native pollinators, it was not the case in this study since that hypothesis was not substantiated by statistical analysis.

Further in this project on community ecology of blueberry pollinators, some studies on plant-insects interactions were made (Greco, 1995c; 1996). The main objective of this analysis was to assess the possible influence of three botanical parameters (blossom density (blossom/m^2), blossom/stem and plant architecture (height) on the variation of the abundances of the five groups of anthophiles defined in this study. As a result of the analysis, the following conclusions were drawn:

1) The parameter height was not enough to find any significant influence of plant architecture on the structure of the pollinator guild.
2) “Intragroup” competition was suggested as a possible explanation for the relationship found between the abundances of each group of anthophiles and the density of flowers. However, this hypothesis does not constitute a formal competition hypothesis because no formal competition study was actually conducted.
3) The intragroup competition may imply qualitative changes in the composition of the group. The lower numbers for a group with a given density of flower may connote either an even decline of all components of the group or the disappearance of some of them.

The final analysis used all the preceding information to ascertain the contribution of each component of the community to the blueberry yields. In each year different results were obtained (Greco, 1995d; 1996). For instance in 1994, solitary bees and honeybees contributed equally with almost 38% respectively of the total harvest, whereas large bees only were important in 25% of the cases studied. On the other hand, in 1995, in 50% of the fields sampled, honeybees accounted significantly variation in yield of berries. This swelling in the relative contribution to the production by honeybees in 1995, is likely consequence of higher abundances of these pollinators in this year in 1994 (close to three times as many hives as in 1994 were distributed in the blueberry fields in 1995). Solitary bees, once again in 1995, accounted for 38% and large bees with 12,5%. Although honeybees seem to play a prime role in berry production, in neither of the two years they were fully responsible for the blueberry yields. The fact that honeybees are not the group to which the production of blueberry can be altogether attributed is not new as it has been previously documented.

The result above, which consider the contribution to production by each group of pollinators separately, are surely of practical value to start adaptive management in blueberry heaths in order to improve yields, yet they did not permit any conclusive generalization as to the link between pollinators and berry production. However, one of the most interesting findings of this research was the general trend discovered in the relationship between the blueberry production and the *proportion* of different groups of native bees in the pollinator guild (Figure 1). Presumably, rather than a particular group of anthophiles, the proportion in which the different anthophiles are present in the community, is more liable to explain what happens with the blueberry fruit set and the pollinator guild.

Still, more detailed studies on the dynamics and interaction among anthophiles are needed. The importance of the relative abundances (*proportion*) of the different groups to explain production of berries could be more understandable if any significant association had been found among the five groups of pollinators studied. However, considering that this was not the case in this investigation, another variables might be required to attain an explanation. A multitrophic model, in which some information in included about, for instance, the nectar and pollen production of the blueberry flowers, the blooming dynamic of the plant in the season, etc., and even information about the influence of climatic factors on the physiology of the plant, might certainly contribute towards unraveling this question.

References

Connor, E. and Simberloff, D. 1979. The assembly of species communities: chance or competition. *Ecology 60(6): 1132-1140.*

Diamond, J.M. 1975. Assembly of species communities. *In*: M.L.Cody and Diamond ed. Ecology and evolution of communities. Harvard University Press, Cambridge, pp:342-444.

Diamond, J.M. and Gilpin, M.E. 1982. Examination of the “Null” Model of Connor and Simberloff for Species Co-Ocurrence on Islands. *Oecologia, 52:64-74.*

Drake, J.A. **1990**. Communities as assembled structures: do rules govern patterns? *Trends in Ecology and Evolution 5:159-163.*

Drake, J.A. **1992**. Communities as assembled structures: do rules govern patterns? *Trends in Ecology and Evolution 5:159-163.*

Dunbar, M.J. 1960. The evolution of stability in marine environments: natural selection at the level of the ecosystem. *American Naturalist 94:129-136.*

Gardner, M.R. and Ashby, W.R. 1970. Connectance of large dynamic (cybernetic) systems: critical values for stability. *Nature, 228:794.*

Greco, C.F. 1995a. Pollinator communities in blueberry fields in Nova Scotia, Canada. I. Descriptive ecology of the community structure. *Enviroquest Ltd. Technical Report Nº2.*

Greco, C.F. 1995b. Pollinator communities in blueberry fields in Nova Scotia, Canada. II. Community organization. *Enviroquest Ltd. Technical Report Nº3.*

Greco, C.F. 1995c. Pollinator communities in blueberry fields in Nova Scotia, Canada. III. Plant-Insect Interations. *Enviroquest Ltd. Technical Report Nº4.*

Greco, C.F. 1995d. Pollinator communities in blueberry fields in Nova Scotia, Canada. IV. Contributions of the different groups of anthophiles to the fruit setting of blueberry. *Enviroquest Ltd. Technical Report Nº5.*

Greco, C.F. 1996. Pollinator communities in blueberry heaths in Nova Scotia, Canada – Second Year. *Enviroquest Ltd. Technical Report Nº8.*

Hawkings, C.P. and MacMahon, J.A. 1989. Guilds: the multiple meanings of a concept. *Ann. Rev. Entomology 34:423-451.*

Inouye, D. 1977. Species structure of bumblebee communities in North America and Europe. *In:* Mattson, W.J. ed. The role of arthropods in forest ecosystem. Springer, Berlin pp 35-40.

Kevan, P.G. 1975. Forest applications of the insecticide fenitrothion and its effects on wild bee pollinators (Hymenoptera: Apoidea) of lowbush blueberries (Vaccinium sp.) in southern New Brunswick, Canada. *Biol. Conservation 7:301-309.*

Kevan, P.G. 1977. Blueberries crops in Nova Scotia and New Brunswick – pesticide and crops reduction. *Can.J.Agric.Econom. 25:61-64.*

Kevan, P.G. and Oppermann, E.B. 1979. Blueberry production in New Brunswick, Nova Scotia and Maine: A reply to Wood et al. *Can.J.Agr.Econom. 28(1):81-83.*

Kevan, P.G. and LaBerge, W.E. 1979. Demise and recovery of native pollinator populations through pesticide use and some economic implications. *Proceedings of the 4th International Symposium on Pollination, MD. Agric. Exp. St. Misc. Publ. 1:489-508.*

Kevan, P.G. and Plowright, R.C. 1989. Fenitrothion and insect pollinators. *In: W.R. Ernst; P.A. Pearce and T.L. Pollock eds.: Environmental effects of fenitrothion use in forestry. Impacts on insect pollinators songbirds & Aquatic Organism. Environment Canada. 166.*

Kevan, P.G.; Greco, C.F. and Belaussoff, S. (in press). Biodiversity and abundance in diagnosis and measuring of ecosystem health: pesticide stress on pollinators on blueberry heaths. *J.Appl.Ecol.*

King, A.W. and Pimm, S.L. 1983. Complexity, diversity and stability: a reconciliation of theoretical and empirical results. *Am. Nat. 122:229-239.*

Lewontin, R. 1970. The units of selection. *Ann. Rev. Ecol. Syst. 1:1-18.*

May, R.M. 1972. Will a large complex system be stable? *Nature 238:413-414.*

McMnaughton, S.J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *Am. Nat. 111:515-525.*

Nee, Sean. 1990. Community construction. *Trends in Ecology and Evolution, 5(10):337-339.*

Obeso, J.R. 1992. Geographic distribution and community structure of bumblebees in northern Iberian peninsula. *Oecologia, 89:244-252.*

Oksanen, L. and Ericson, L. 1987. Preface: Why should we care about predation and parasitism? *Oikos, 50:3,274-275.*

Ranta, E. 1982. Structure of North European bumblebee communities. *Oikos, 43:189-196.*

Ranta, E. and Tiainen, M. 1982. Structure in seven bumblebee communities in eastern Finland in relation to resource to resource availability. *Holarct. Ecol. 5:48-54.*

Ranta, E. and Vepsalainen, K. 1981. Why are there so many species? Spatio-temporal heterogeneity and northern bumblebee communities. *Oikos 36:28-34.*

Robinson, J.V. and Dickerson, J.E. 1987. Does invasion sequence affect community structure. *Ecology 68, 587-595.*

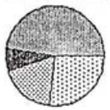
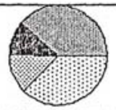
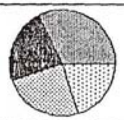
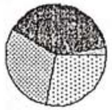
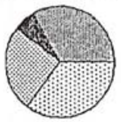
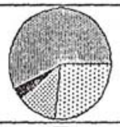
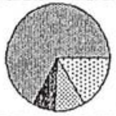
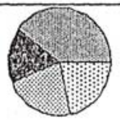
Root, R.B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr. 37:317-350.*

Simberloff, D. and Dayan, T. 1991. The guild concept and the structure of ecological communities. *Ann. Rev. Syst. 22:115-143.*

Slatkin, M. and Wilson, D.S. 1979. Coevolution in structured of demes. *Proceedings of the National Academy of Sciences (USA) 76:2084-2087.*

Wilson, D.S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology 73(6):1984-200.*

Wilson, D.S. and Sober, E. 1989. Reviving the superorganism. *J. Theor. Biol. 136:337-356.*

Field	hives / hectare	Field size (hectares)	% of pollination Fruit set / blossoms x 100	pollinators total abundance	community composition	
					▨ honey bees ▩ medium bees ■ large bees ⬚ others	Native pollinators MB:LB:Oth
N.S.B.I	2.46	2.43	38.64	1562		1:0.41:1.50
Mt. Thompson	4.11	9.71	33.52	749		1:0.90:2.96
Murray Siding	9.88	8.09	50.58	1814		1:0.92:0.96
North River	0.00	5.46	47.74	857		1:1.15:0.97
West Brook	2.46	4.86	29.83	696		1:0.26:1.41
Diligent River	20.42	14.64	37.29	2009		1:0.30:2.19
Pigeon Hill	4.11	9.71	88.21	1494		1:0.75:1.71
Glenmore	8.24	3.64	42.88	1644		1:0.78:0.97

Pollination and Conservation

Pollination and Conservation

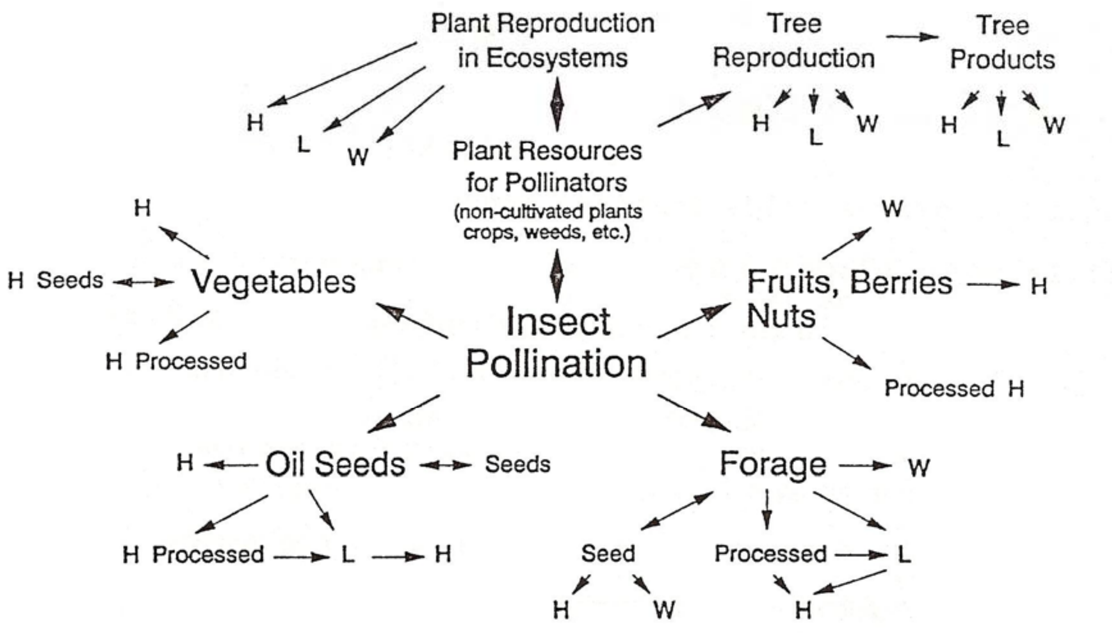
Angiosperms and insects make up:

1) Most of the world’s terrestrial biomass
2) Most of the world’s diversity
3) Most of the world’s productivity

Angiosperm and Pollinator (mostly insects) are inextricably linked through pollination.

- Pollination is the first step in Angiosperm sexual reproduction.
- Flowers provide nutritive and other rewards for pollinators.
- The mutualism have evolved over at least 130 Million years, and probably have their beginnings before there were angiosperm and true insects at the start of terrestrialization (450 Million years ago in Silurian time).
- Zoophilous pollination is basic to life as we know it in:
  a) Completely wild natural environments
  b) Unmanaged and managed forest ecosystems
  c) Systems of agroforestry from “primitive” slash and burn to “modern” approaches
  d) Sustainable, or ecological agriculture, and
  e) Intensive agricultural systems to even hydroponics and tomatoes or melons.

INSECT POLLINATION & THE CONSUMER
(human, livestock & wildlife)



The long process of co-evolution makes the system of pollination well buffered against perturbations, but

How much perturbation can the system stand before it starts to break down?

Recent major issues:

- Ozone depletion
- Acid rain
- Deforestation
- Global warming
- Ocean pollution
- Should pollination be included?

Demise of pollinators and pollination systems.

- Pesticides
- Habitat destruction
- Nesting sites
- Alternative food
- Available food
- Mating sites
- Diseases
- Competition

Pesticides

Dangers are well understood, but this is a perennial problem world-wide.

- Accidents
- Carelessness
- Ignorance
- Deliberate mis-use

An example from Canada in the Lowbush blueberry (Vaccinium spp.) ecosystem.

- Result: 0.67 Million kg of blueberries not produced each year

Effects in the forest:

- Bumblebees and other pollinators locally extirpated or severely reduced.
- Remaining bumblebees did very well from underutilized floral resources. Competition was reduced.
- Wide variety of plants reduced seed-set.

Habitat destruction

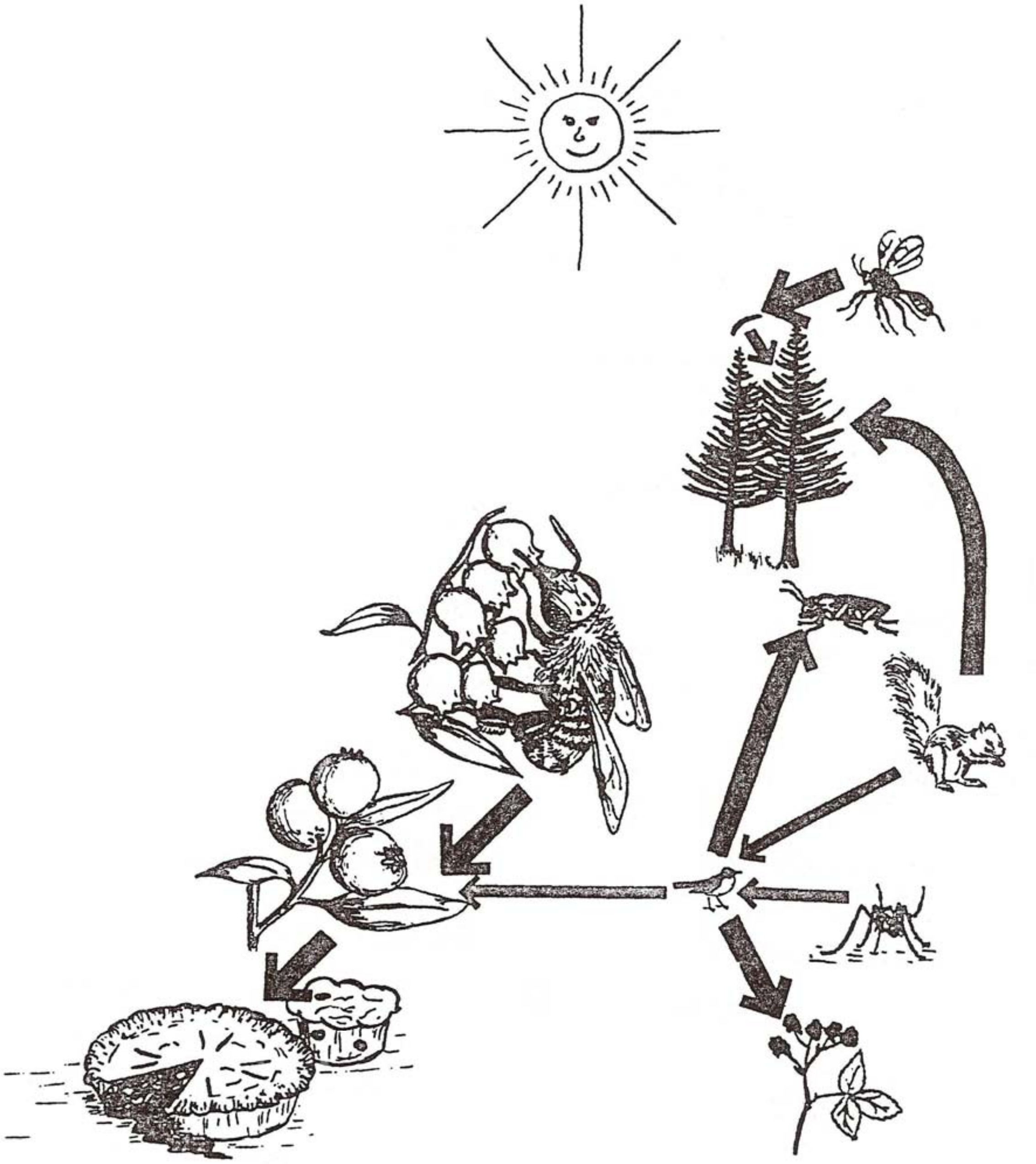
Nesting sites removed

- Widespread, but poorly appreciated.
- Bumblebee and solitary bee populations have declined in Europe from removal of hedge-rows, intensive land management, etc.

- In western Canada, the expansion of alfalfa fields resulted in declines in populations of native pollinating bees. Pollination was good around the field margins, but lacking in the interior.
- In Brazilian Cacao plantations, overly fastidious removal of debris caused lack of breeding sites for pollination midges.
- Removal of Alternative Food for Pollinators.
- Example from blueberry cultivation in Maine in the U.S.A.

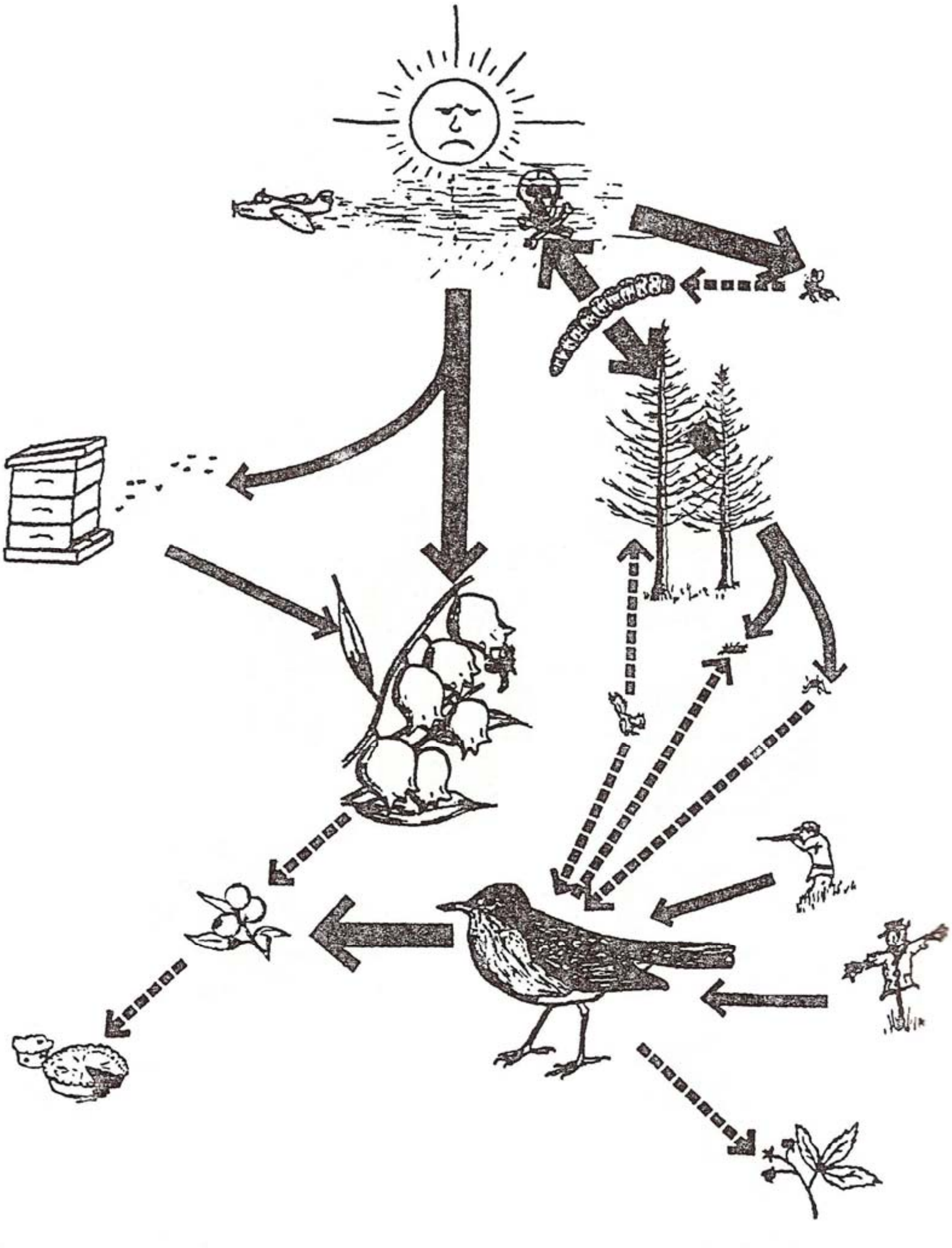
Herbicides used to control weeds eliminated most of the alternative forage for pollinating bees. Bees starve before and after the blueberries have bloomed. Populations have declined.

- Weeds may not be all bad!



A

Comparison of the "Blueberry-pie ecosystem" under <u>A</u> natural conditions (left) and under <u>B</u> disrupted conditions (right). In the forest natural control agents (represented by parasitoid wasp-top right) keep budworms (above trees) in check, trees remain healthy; whereas the spray disrupts the system by reducing natural biotic control agents. The budworms now control spray program (double ended arrow in <u>B</u>), and remain a major pest defoliating trees. At the same time the spray program disrupts the natural system operating on small birds (here, a robin). Comparing <u>A</u> and <u>B</u> the roles of predators (represented by the squirrel) and disease (represented by a vector, mosquito) are reduced and disrupted: animal (represented by beetle or cricket) and plant (represented by blackberries) is reduced and the food chain disrupted. The starving, but otherwise unnaturally healthy small birds, turn to blueberries and become a major pest (compare A and B). Man steps in with guns and scaring devices (here, a scare-crow) to protect his crop, the blueberries. The



B

spray, however, has severely reduced the wild bee pollination (compare A and B and note also the same cause applies to the wild berry (blackberry) crop reductions (lower-right)), so supplemental pollinators (honeybee hive in B) are introduced. The spray also affects them. Not enough can be introduced to economically maintain good crops, which are reduced. The net result fewer blueberries are harvested (represented here by blueberry pie and muffin).

Solid arrows represent the direction of direct effects, wide being major paths, narrow being minor. Dashed arrows represent disrupted pathways.

Removal of Available Food

- Dan Janzen has voiced the concern more or less as follows for tropical ecosystems:

Cutting of forest and leaving a few trees standing removes habitat and food for pollinators. Pollinator populations decline. Remaining trees fail to set fruit. The ecosystem fails as the vicious cycle finishes.

Mating sites

- Some pollinators have special mating, or male resting, site requirements.
- Destruction of the sites would spell the demise of the pollinators.

Diseases

- This has been mostly studied for domesticated honeybees.
- Example comes from agriculture.
- *Varroa* come from Southeast Asia, tracheal will cause the colony to die out.

Effects now seen in U.S.A.

- Insufficient numbers of pollinating colonies of honeybees for fruit production in several states.

Competition

Roubik has drawn attention to the reduction in native bee species in the Americas in the face of competition with the Africanized honeybee.

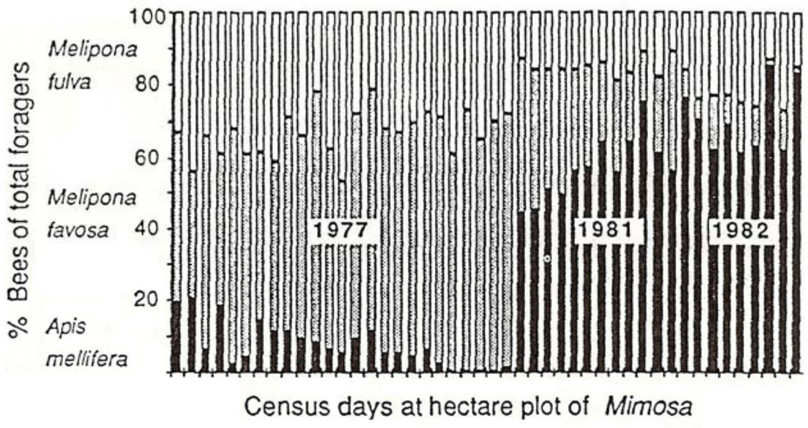


Figure 4.12. Changing relative bee abundance following invasion by Africanized honeybees in lowland forest of French Guiana. The two native bees visiting flowers of *Mimosa* are *Melipona* (Apidae) censused in a hectare plot (after Roubik 1987a).

- It will be a long time before the whole story unfolds.
- The pollinating activities of Africanized honeybees have not been seriously researched.
- In Australia has been some concern about the effect of honeybee-keeping in national parks. Many plants not pollinated by honeybees, but honeybees are nectar thieves. That leaves no nectar for legitimate pollinators, which have a reduced (inadequate) floral food base to prosper.

Conservation and Environmental Issues must Recognize Mutualisms

- pollination
- fruit/seed dispersal
- mycorrhizal associates
- etc.

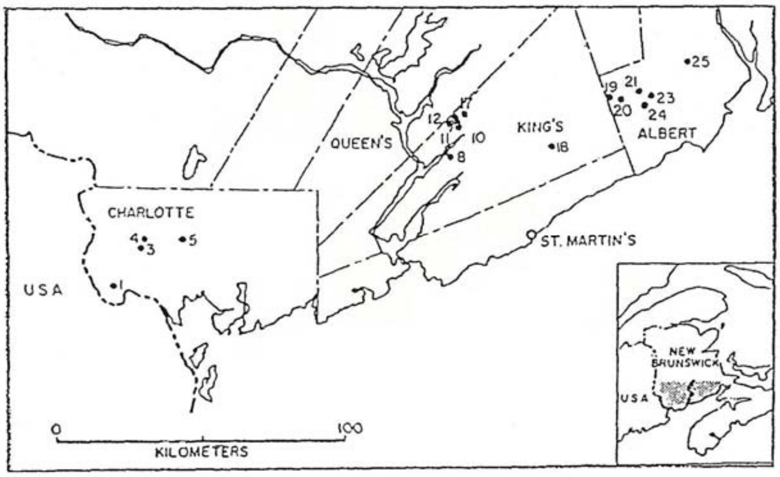
Is Pollination an Endangered Process?

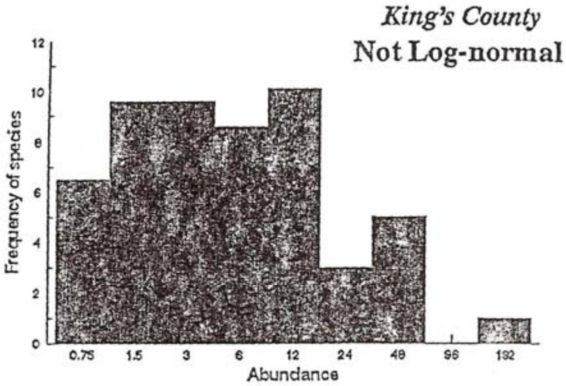
- Yes.

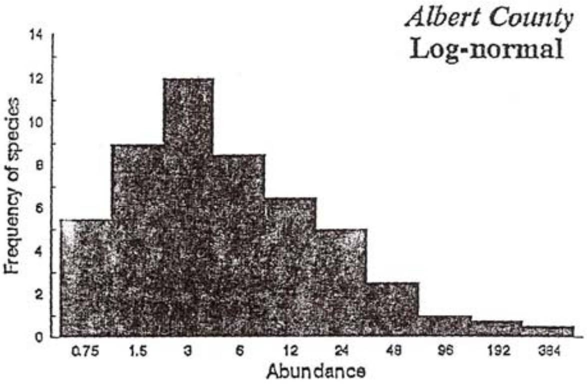
Is the Endangerment local, regional, continental, or global?

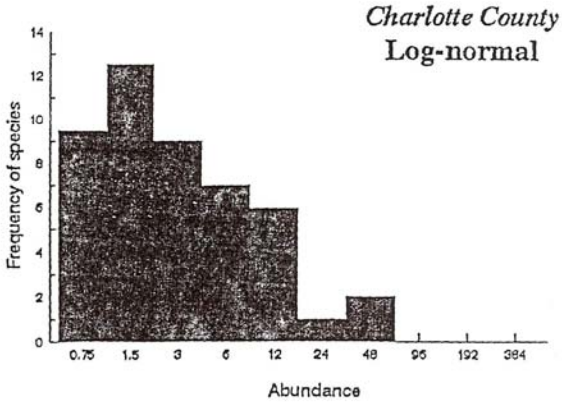
Summary

1. Data from sampling pollinating bees over eight years in thirteen blueberry fields in New Brunswick, Canada, were used to test the log-normality of the species diversity and abundance relationships in regard to disruption of communities by applications of the insecticide, fenitrothion to nearby forest
2. Ecosystemic integrity (health) of the lowbush blueberry fields was assessed by using species diversity and abundance in Sugihara's (1980) sequential breakage model to test the log-normality of data sets from affected and non affected fields.
3. On both spatial and temporal bases, fields unaffected by the pesticide fitted well to the log-normal model of species diversity and abundance, whereas affected fields departed from that pattern. Thus, the relationship is useful because the samples from fields affected by fenitrotuion presumably represent compromised integrity and decline in health.
4. Shannon-Wiener's hierarchical diversity indices and Jaccard's indices of similarity were found to have little value in measuring ecossistemic health. For the former, none of the indices calculated (total diversity (H(GS)), mean intragenic diversity (H_G(S)) and generic diversity (H(G)) showed any difference between communities with a log-normal patterns of species diversity and abundance and those without it. The Jaccard index of similarity was low and similar in all the cases.
5. In general, ecosystem health should not be narrowly assessed through biodiversity but must include taxonomic and population changes together. The log-normal relationship linking species diversity and abundance is an objective norm against which to test ecosystemic integrity, disruption, health, ill-health, and reconstitution




King's County
Not Log-normal


Albert County
Log-normal


Charlotte County
Log-normal

Plant Breeding And Reproductive Systems

Self-pollination versus Cross-pollination

- Characteristically, in flowering plants (Angiospermae), fertilization is “double”
- The process, in general, is as follows
    - A pollen grain is transferred to a stigma (pollination occurs).
    - If the stigma and pollen are compatible, the pollen grain germinates.
    - The pollen grain is actually a multicelled (2 or 3 cells usually) microgametophyte (i.e. a small plant that produces gametes).
    - The megagametophyte (i.e. a relatively larger plant that produces gamete(s)) is the embryo sac within the ovule and typically contains 8 cells without walls: 3 antipodal cells at one end (chalazal) of the embryo sac, 3 cells (synergids) at the other end (micropylar) of embryo sac and 2 cells (the egg cell and another) in association with those 3).
    - As the pollen germinates it produces a tube (pollen tube) that penetrates the stigma and grows down through the style and into the ovary. Leading the growth is the tube nucleus from the pollen grain.
    - Following the tube nucleus is the generative nucleus. As it passes down the pollen tube, it divides into two sperm nuclei.
    - The sperm nuclei are liberated into the embryo sac one sperm nucleus unites with the egg nucleus, and the other sperm nucleus unites with primary endosperm nucleus.
    - The sperm and egg nucleus together restore the diplid condition and develop to form the embryo.
    - The primary endosperm nucleus has arisen through the prior union of two haploid cells (one associated with the egg cell and the other one of the synergids in the embryo sac). Thus, the union of a sperm cell with this cell, forms a triploid primary endosperm cell. This gives rise to the endosperm of the seed.

Double fertilization has occurred!

- The cells not involved in nuclear unions start to disintegrate during the process of embryo sac maturation and soon disappear.

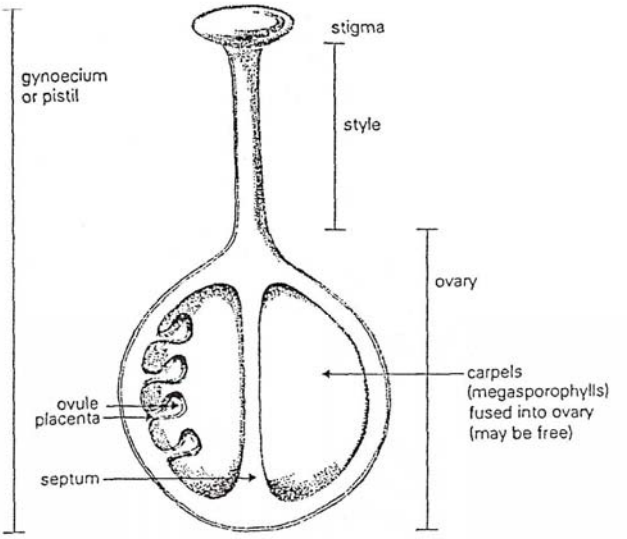


Figure 3.6 Conventionalised diagram of a gynoecium in an Angiosperm in the family Cruciferae (Brassicaceae).

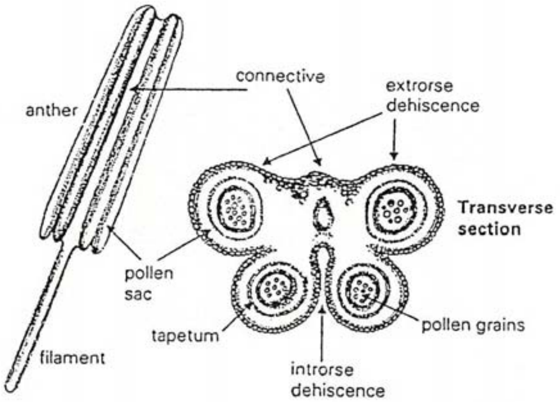


Figure 3.7 Conventionalised diagram of a stamen in an Angiosperm

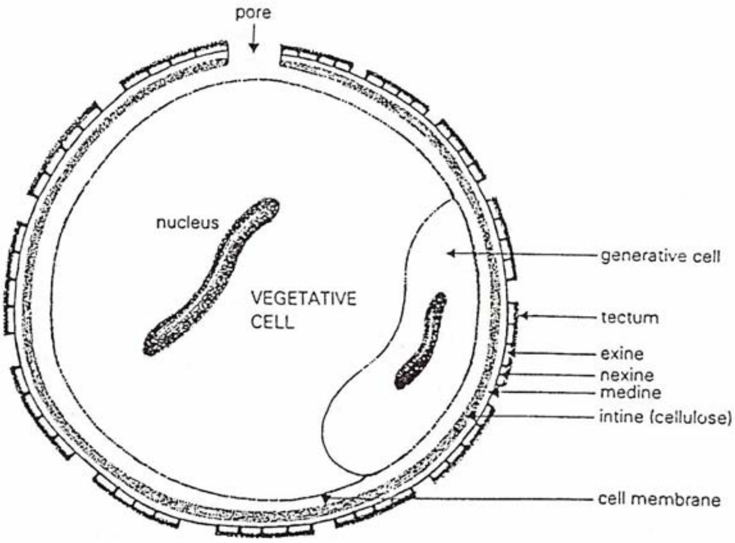


Figure 3.8 Anatomy of a conventionalised typical Angiosperm pollen grain. The gametophyte may contain two or three cells.

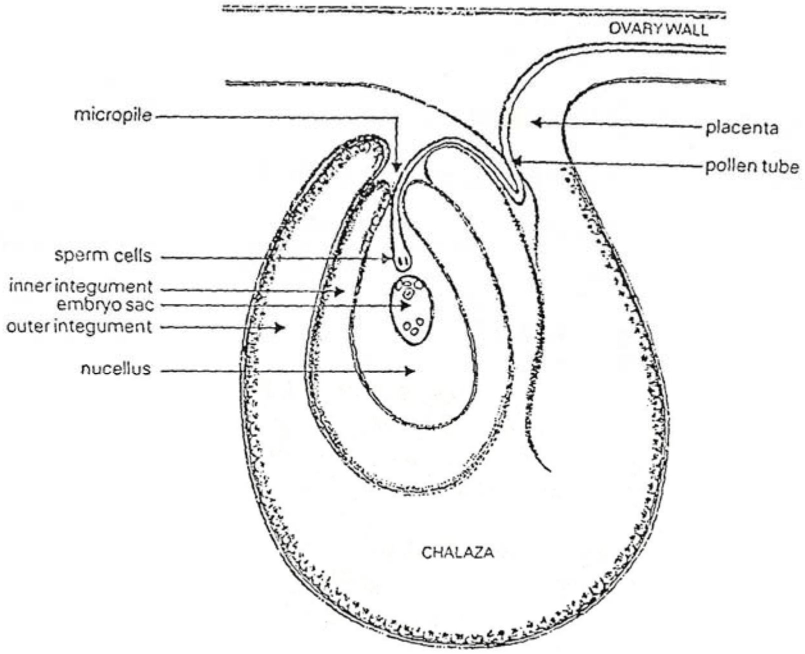


Figure 3.9 Diagram of the path of the pollen tube in the ovary and ovule of an Angiosperm.

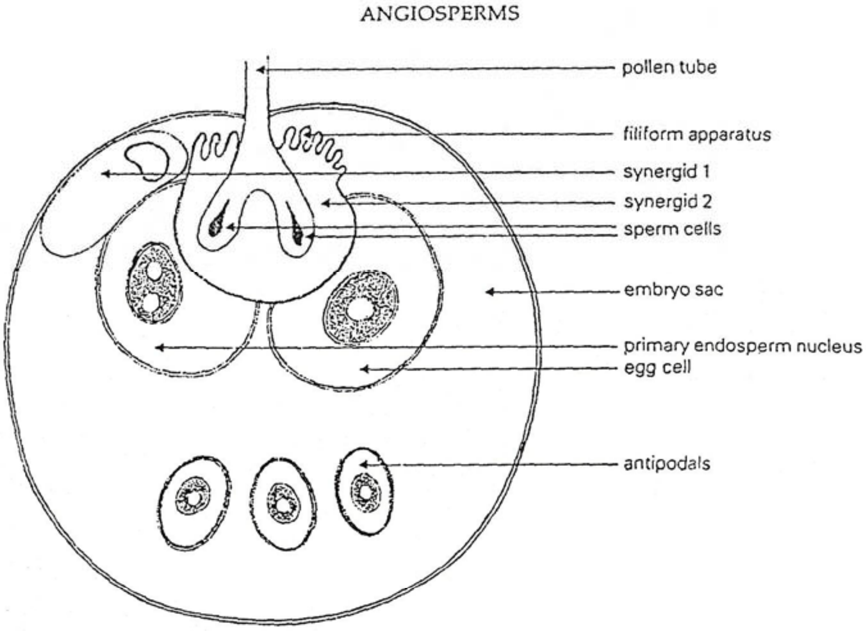


Figure 3.10 Diagrammatic representation of the process of double fertilisation in an Angiosperm embryo-sac. The pollen tube has entered the embryo-sac by means of one of the two synergids that now engulfs it. The pollen tube has bifurcated, with one sperm cell in each branch, and the synergid leads one pollen tube branch and sperm cell towards the egg cell and the other towards the primary endosperm nucleus (fused polar nuclei). The nuclear membranes of the primary endosperm nucleus and the egg cell will shortly break down, admitting the degenerating synergid and the respective sperm cell.

Cross and Self Fertilization

- For self-fertilization to occur, the plant must be self-compatible.

Patterns of Pollen Transfer

- Autogamy: transfer within the same flower (selfing) (in-breeding)
- Allogamy: transfer between flowers.
- Geitonogamy: allogamy on the same plant or between vegetative ramet (genetically identical) of the same parent plant (selfing) (in-breeding);
- Xenogamy: allogamy between flowers of genetically different plants (genets) (out-crossing) (out-breeding).

Self-incompatibility and Self-compatibility:

- Incompatibility come about because the pollen's growth is curtailed or inhibited when the pollen is polaced on the stigma or after it gas germinated and started to grow through the style.
- Genetic control of incompatibility may be di-allelic at a single locus or multi-allelic at single to multiple loci.
- Self-incompatibility may be sporophytic or gametophytic.
    - In sporophytic incompatibility, it is the genotype of the anther witch is important (the anther being the part of the sporophyte generation of a plant). Pollen tube growth is inhibited at the stigma surface.

Examples of multi-allelic, sporophytic incompatibility come from Brassicaceae and Asteraceae. Examples of di-allelic, sporophytic incompatibility are seen in plants showing dimorphism of flowers (distyly).

- In gametophytic incompatibility, it is the genotype of the pollen (the microgametophyte wich is important. Pollen tube inhibition takes place in the style.

The number of alleles at a single locus for gametophytic incompatibility ranges between 3 and 400!

Systems of up to 4 loci have been worked out.

Gametophytic incompatibility is widespread among plants.

- Clearly, the whole issue of self-incompatibility is complex.
- In pollination biology, the concern is for the ultimate effect. If plants are self-incompatible, self-pollination does not result in seeds' being formed.
- If groups of plants are self-incompatible, cross-pollination within the group does results in no seed' being formed (example for apples and other pome crops).

Incompatibility can fail (e.g. in buds, old flowers, senescing plants, effects of high temperature, salt spray, carbon dioxide, irradiation, mixing with other compatible pollen (mentor effect)).

Self- fertilization:

- Assurance of sexual reproduction.
- Must be self-compatible and have floral form and development allowing for self-pollination in the bud. Autogamy is obligate. Some plants have both cleistogamous and chasmogamous (fully opening to allow for pollination) flowers (e.g. Viola).
- In some herkogamous flowers, positions of parts may change with time to allow for autoamy. In some dichogamous flowers, sexual parts may remain receptive until autogamy can be achieved.

Advangages of selfing:

reproductive efficiency
reduced allocation of resources to reproductive structures
reduced genetic variation and highly adapted genotypes

Disavantages:

reduced capacity for adaptation
inbreeding depression

Sexual Arrangements of Plants in Space and Time:

Dioecy	Sexes on separate plants	Xenogamy
Gynodioecy	Some plants with hermaphroditic flowers Some plants with felmale only flowers	Xenogamy Genitenogamy Autogamy
Androdiecy	Some plants hermaphroditic Some plants male only	as above
Monoecy	Plants hermaphroditic but flowers unisexual	Allogamy Geitenogamy Xenogamy
Gynomonoecy	Plants hermaphroditic but some flowers bisexyal and some female only	as above
Subgynoecy	Gynomonoect + some male only	as above
Andromonoecy	Plants hermaphroditic but some flowers bisexual and some male only	as above
Subandroecy	Andromonoecy + some female only	as above
Hermaphrotity	Plants and flowers hermafroditic	Autogamy Allogamy Geitenogamy Xenogamy

Dicliny	Not all genets in a population are hermaphroditic. Includes dioecy, gynodioecy, androdioecy. Correlations in dioecy with animal dispersed fruits and seeds, island habitats, early seral stages. Evolutionary advantages of resource allocation and ensuring out-crossing.
Polygamy	Genets of various sexual expression occur in the population: some male, some female, some hermaphrodites, including co-existence with gynomonoecy or andromonoecy or both. (a rather vague category without further descriptions applied).
Trioecy	Plants in three sexual forms, male only, female only, and hermaphrodites.
Dichogamy	Perfect or imperfect flowers: anthers and stigmata mature at different times so that autogamy is prevented or discouraged: protandry for anthers maturing first; protogyny for stigmata maturing first.
Homogamy	Simultaneous maturation of anthers and stigmata.
Herkogamy	Perfect flowers: anthers and stigmas spaced apart so autogamy is prevented
Heteromorphy	Two or more forms of flowers, each on separate plants (genetically controlled) as in heterostyly.
Heterostyly	Perfect flowers but with differences in the lengths of the styles between plants. Two forms (pin and thrum): distylu; Three forms: tristyly.

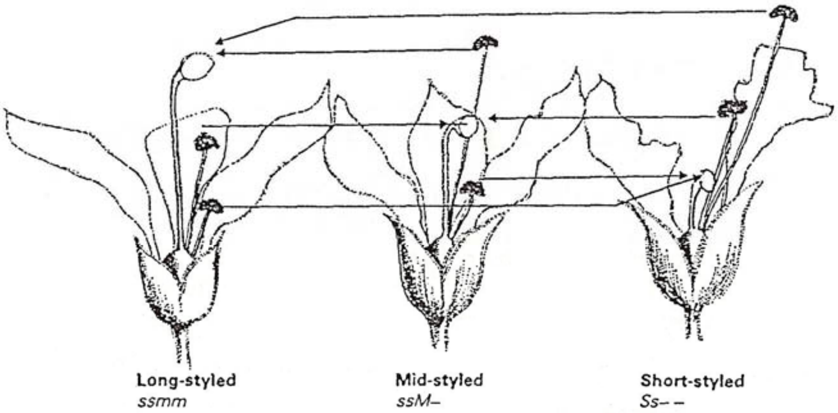


Figure 7.9 Tristyly in *Lythrum salicaria*. Stigmas are pale and anthers dark. Arrows indicate compatible pollinations between morphs.

Parthenocarpy:

Formation of a fruit without seeds. E.g. commercially grown bananas, some citrus, salad cucumbers, commercially grown figs.

Asexual Reproduction:

- Agamospermy is the formation of seeds without sexual reproduction. Pollen mostly is not involved.
- Gametophytic agamospermy involves cells of the embryo sac. There are at least 7 inter-related processes which can gibe rise to a mature seed and endosperm without the egg cell being fertilized.

- One, pseudogamy, requires pollination to take place because pollen cell fertilization of endosperm nuclei.
- Sporophytic agamospermy results when cells of the sporophyte develop into the seed. The endosperm may be fertilized independently

Vegetative Reproduction:

- Fragmentation: many aquatic plants, some shrubs and trees from broken twigs.
- Branch tip rooting: various shrubs (Roses)
- Stolons: specialized above ground stems (Strawberries)
- Rhizomes: specialized below ground stems (various weeds, especially grasses).
- Corms: short, swollen underground stem (Crocus, Anenome);
- Bulbs: short, swollen mass of leaves underground (Allium).
- Bulbils: axillary buds of the inflorescence of the leaves.
- Suckers: growth from the true roots (Populus, etc).
- Budding: thallus budding as in Lemna (pond weed).
- Turions: bulbils of some aquatic plants.
- Vivipary or Floral proliferation: Flowers mature to become the equivalent of bulbils (Poa alpina).

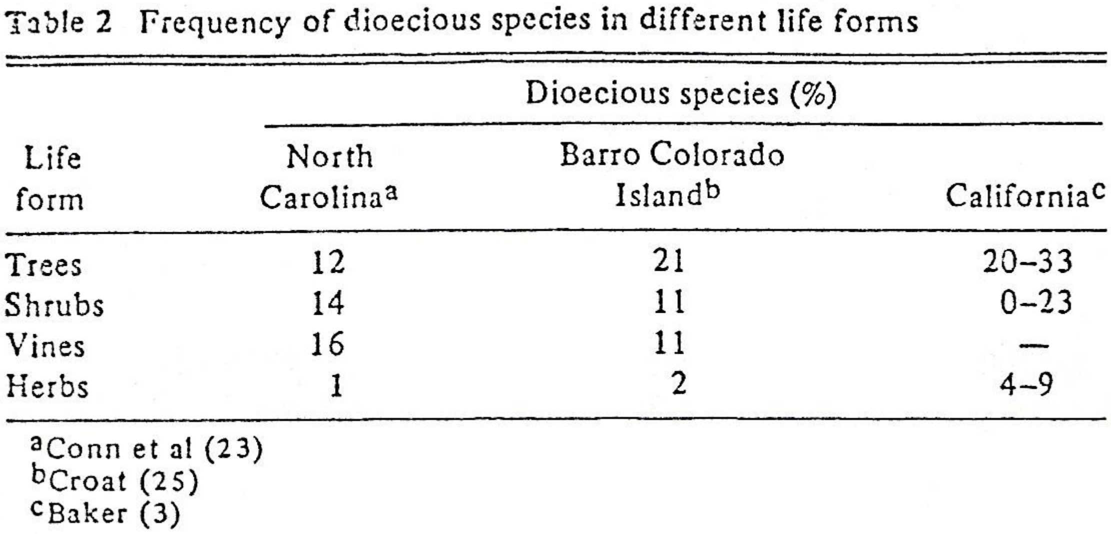


Table 2 Frequency of dioecious species in different life forms

	Dioecious species (%)		
Life form	North Carolina[a]	Barro Colorado Island[b]	California[c]
Trees	12	21	20–33
Shrubs	14	11	0–23
Vines	16	11	—
Herbs	1	2	4–9

[a] Conn et al (23)
[b] Croat (25)
[c] Baker (3)

Table 3 Correlation between dioecy and pollination systems in a dry forest in Costa Rica

	Percentage of tree species	
Pollination systems[a]	Hermaphroditic/ Monoecious (N = 94)	Dioecious (N = 28)
Medium-Large bee[b]	25	1
Small bee or opportunistic[c]	26	80
Beetle	14	3
Fly	1	2
Wasp	3	2
Moth	19	9
Butterfly	1	0
Hummingbird	3	0
Bat	8	0
Wind	0	3

[a] Pollination systems are modified from Frankie (38), based on the "most probable pollinator" type. The exact figures are subject to revision, but the revision is not likely to modify the observed trends.

[b] Mostly Anthophoridae, some Xylocopids.

[c] Mostly Halictidae, Megachilidae and/or Meliponini (Apidae).

Table 4 Correlation between breeding systems and modes of dispersal

		Number of species[a]		
Locality/taxonomic group	Breeding system	Animal-dispersed	Wind-dispersed	χ^2
Tropical lowland dry deciduous forest	Dioecious	30	3	5.8[c]
(Palo Verde, Costa Rica)	Hermaphroditic and monoecious	60	26	
Tropical lowland wet evergreen forest	Dioecious	66	0	8.4[c]
(La Selva, Costa Rica)[b]	Hermaphroditic and monoecious	222	29	
Meliaceae	Dioecious,	16	0	13.5[c]
	Hermaphroditic and monoecious	9	12	

[a] For Meliaceae read number of genera. Also, in Meliaceae, genera containing both dioecious and hermaphroditic and/or monoecious species are excluded from the analysis, but the number of such genera is only 12.

[b] Tentative figures for dioecious species, the number of which may increase; however all the wind-dispersed species are known to be hermaphroditic and/or monoecious.

[c] $P < 0.05$.

Table 5 Correlation between dioecy and fruit morphology in gymnosperms[a]

	Number of genera[b]		
Breeding system	Fleshy fruits or seeds or cone axes	Winged seeds	χ^2
Dioecious	28	2	54.6[c]
Monoecious	2	38	

[a] Data from Givnish (46)

[b] Six genera containing both dioecious and monoecious species excluded from analysis; also excluded one genus with monoecious species having wingless seeds in dehiscent cones, and one genus with dioecious species having seeds in cones.

[c] $P<0.01$

BIBLIOGRAPHY

Arita, H. T. & C. Martinez del Rio, 1990. Interacciones Flor-Murcielago: Um Enfoque Zoocentrico. Publ. Esp. No. 4 Inst. Biologia, UNAM, Mexico DF, Mexico.

Barth, F. G. 1985. Insects and Flowers: The Biology of a Partnership. Princeton University Press, Princeton, NJ, USA.

Bawa, K. S., 1980. Evolution of dioecy in flowering plants. Annual Review of Ecology and Systematics, 11: 15-40.

Dafni, A. 1992. Pollination Ecology: A Practical Approach. IRL Press of Oxford University Press, Oxford, UK.

Faegri, K. & L. van der Pijl, 1980. The Principles of Pollination Ecology. Third Revised Edition. Pergamon Press.

Frankel, R. & E. Galun, 1977. Pollination Mechanisms, Reproduction and Plant Breeding. Springer-Verlag, Berlin, Germany.

Free, J. B. 1993. Insect Pollination of Crops (2nd Edition). Academic Press, London, UK. & New York, USA.

Grant, K. A. & V. Grant, 1968. Hummingbirds and Their Flowers. Columbia University Press, New York, USA.

Jones, C. E. & R. J. Little (Editors), 1983. Handbook of Experimental Pollination Biology. Scientific and Academic Editions, Van Nostrand, New York, USA.

Kearns, C. A. & D. W. Inouye, 1993. Techiniques for Pollination Biologists. University Press of Colorado, Niwot Ridge, CO, USA.

Kevan, P. G. & H. G. Baker, 1983. Insects as flower visitors and pollinators. Annual Review of Entomology, 28: 407-453.

Knuth, P. 1906-1912. Handbook of Flower Pollination. Volumes I to III. The Clarendon Press, Oxford, UK.

Lovett Doust, J. & L. Lovett Doust (Editors), 1988. Plant Reproductive Ecology; Patterns and Strategies. Oxford University Press, Oxford, UK.

McGregor, S. E., 1976. Insect Pollination of Cultivated Crop Plants. US Dept. Agriculture Handbook No. 496, Washington, DC, USA.

Meeuse, B. & S. Morris, 1984. The Sex Life of Flowers. Facts on File, New York, USA.

Pijl, L. van der & C. H. Dodson, 1966; Orchid Flowers: Their Pollination and Evolution. University of Miami Press, Coral Gables, FL. USA.

Proctor, M. & P. Yeo, 1973. The Pollination of Flowers. Collins Sons & Co., Ltd., Glasgow, U.K.

Real, L. (Editor), 1983. Pollination Biology. Academic Press, Inc., Orlando, Florida, USA.

Richards, A. J. (Editor), 1978. The Pollination of Flowers by Insects. Linnean Society of London, Academic Press, London, UK.

Richards, A. J. 1986. Plant Breeding Systems. Allen & Unwin, London, UK.

Roubik, D. W., 1989. Ecology and Natural History of Tropical Bees. Cambridge University Press, Cambridge, UK.

Sedgley, M. & A. R. Griffin, 1989. Sexual Reproduction of Tree Crops. Academic Press, London, UK and New York, USA.

Willson, M. F., 1983. Plant Reproductive Ecology. John Wiley-Interscience, New York, USA.