



Each species of *Yucca* relies on a mutualist species of yucca moth of genus *Tegeticula* for pollination. The moth's full life-cycle plays out on the yucca; the adult moth actively carries pollen from stamen to stigma, and then uses a long ovipositor to lay eggs in some of the developing ovules (seeds) of the yucca flower. Parasitized ovules don't make viable seeds. Unpollinated flowers abort, killing any moth eggs. Flowers where too many ovules are parasitized are aborted by the plant before developing into a fruit, killing any developing moth larvae. While this is a true mutualism (each party benefits from presence of the other) – even an *obligate* one (neither can persist without the other) – it is not far from parasitism. It can be thought of as a balanced, mutual exploitation. Selection presumably acts on each party to gain as much fitness benefit from the other with as little investment (fitness reduction) as possible. In this case, if either species were to overcome the regulatory actions of the other (e.g., if moth could lay more eggs per flower with impunity, or if flower could get pollination services without allowing moth to lay eggs successfully), this would presumably be selected for in the short term, even though it might destabilize in the long run – even drive both species to extinction. Mutualisms are vulnerable to exploitation and likely not very stable in many cases. Think about when they're likely to be particularly vulnerable to exploitation....



Yuccas and moths and developing seed pods with larvae

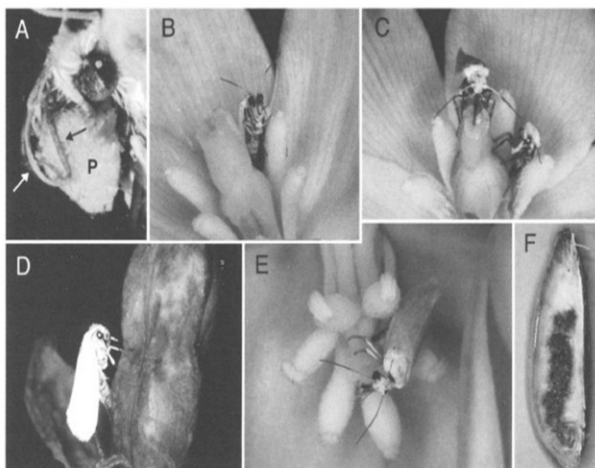


Figure 5. —A. Head of *Tegeticula carnerosana* female. Large pollen load (P) held below the head, with left tentacle and proboscis indicated by black and white arrows. Cross section of tentacle 1.0 mm. —B. Female *T. yuccasella* compacting pollen just collected from a *Y. filamentosa* stamen. —C. Females of *T. yuccasella* pollinating (top) and ovipositing into (right) a *Y. filamentosa* ovary. —D. Female *T. intermedia* ovipositing into a ca. 8-day-old *Y. filamentosa* fruit; note constriction caused by *T. yuccasella* ovipositions. —E. *T. treculeana* female pollinating *Y. treculeana* Carrière flower. Moth wing length in panels B–E 10–11 mm. —F. Longitudinal section through locule of mature *Y. carnerosana* (Trel.) McKelv. fruit, showing feeding path of *T. carnerosana* larva that has destroyed seven seeds; fruit length 73 mm. For a set of color pictures of *T. yuccasella* behavior on *Y. filamentosa*, see Murawski (1997).



Fig. 240.—Transport of Pollen by Egg-laying Insects.

1 Branch from the inflorescence of *Yucca whipplei*; the middle flower open, that beneath it was open the previous night and is now closed again, the rest of the flowers in bud. 2 Single flower of the same plant visited by a moth of the species *Pronuba yuccasella*; the three front perianth-leaves removed. 3 Stigma of *Yucca whipplei*. 4 *Pronuba yuccasella* flying to a flower of *Yucca whipplei*. 5 Head of *Pronuba yuccasella* with a ball of pollen held by the coiled maxillary palp. 6 Twig with inflorescence of *Ficus pumila*; the umb-shaped inflorescence (or synconium) cut through longitudinally. 7 Single female flower from the bottom of the synconium of *Ficus pumila*. 8, 9 Stamens of the same plant from the upper part of the synconium. 10 Synconium of *Ficus cariosa* full of gall-flowers produced by *Elastophaga*, cut through longitudinally; near the mouth of the cavity is a Fig-wasp (*Elastophaga grossorum*) which has escaped from one of the galls. 11 Synconium of *Ficus cariosa* full of female flowers, cut through longitudinally; near the mouth of the cavity are two Fig-wasps, one of which has already crept into the cavity whilst the second is about to do so. 12 Male flower. 13 Long-styled female flowers of *Ficus cariosa*. 14 Gall produced from a short-styled gall-flower. 15 *Elastophaga grossorum* escaping from a gall. 16 A liberated *Elastophaga*. 17 The same niggulfed. 1, 2, 4, 6, 10, 11, 16, natural size; 3 × 2; 5 × 20; 7, 8, 9, 13, 14 × 5; 15, 16, 17 × 8.

Figs and fig wasps have a similar relationship, but even odder; females hatching within developing fig mate with flightless males (their brothers, usually; as might be expected, sex ratios are extremely female-biased...). Females enter developing fig to lay eggs; they do not escape. You can read more on the details. In some cases, the fig plant appears to successfully exploit pollinators without allowing them to parasitize flowers...



Figs and barely visible fig wasps



Not all pollination systems involve animal pollinators; maples and oaks (above) are mostly *wind-pollinated*. Consider adaptive trade-offs with respect to investment in flower and attractants vs. investment in pollen; precision of pollination vs. risks of not getting serviced by pollinator. What circumstances might favor animal pollination vs. wind pollination? Consider properties of environment as well as distributions in space.



Generalized insect pollination syndrome. Flowers are attractive to a wide range of potential pollinators and provide an easily accessible nectar reward. Consider trade-offs between a generalized relationship



And a more specialized one. In the upper case, nectar is at bottom of long floral tube, accessible only to insects that can hover and have long proboscis; flowers open only at night. In passion flower (right), only certain sizes and shape of insects can access nectaries. In both cases, flower is designed to 'place' pollen precisely on body of insect, where it will be deposited on stigma of next flower.

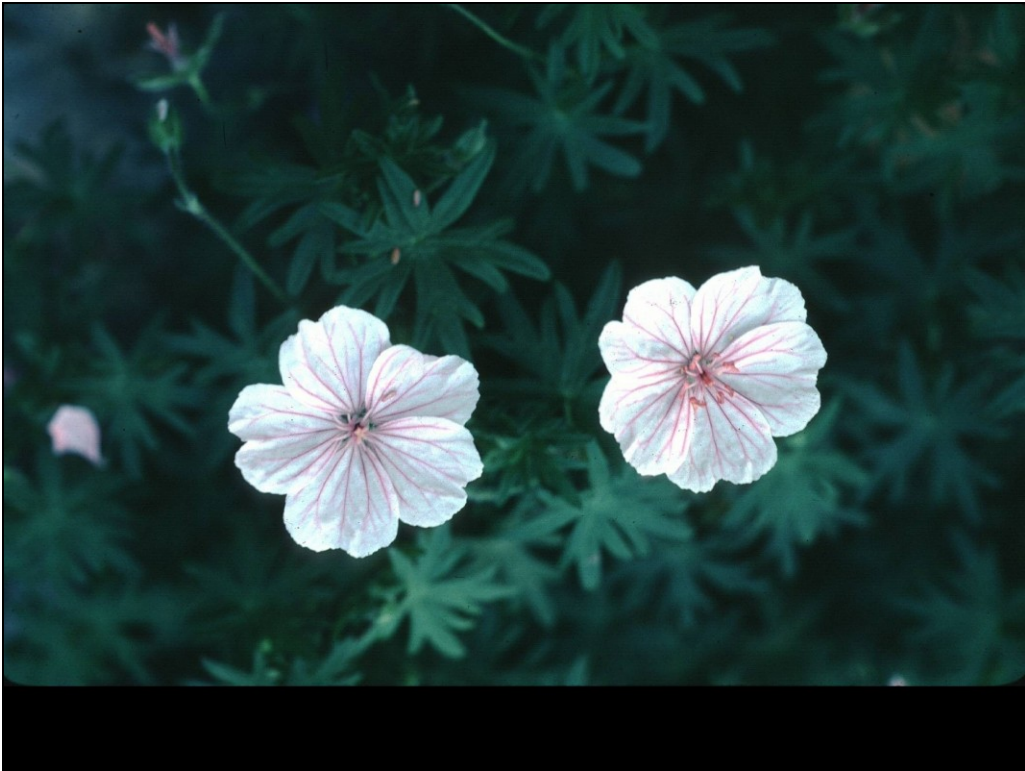


Extreme specialization: Malagasy orchid *Angraecum sesquipedale*, pollinated only by a hawk-moth with 12-inch proboscis matching 12-inch spur of flower... Fitness benefits and risks for each?

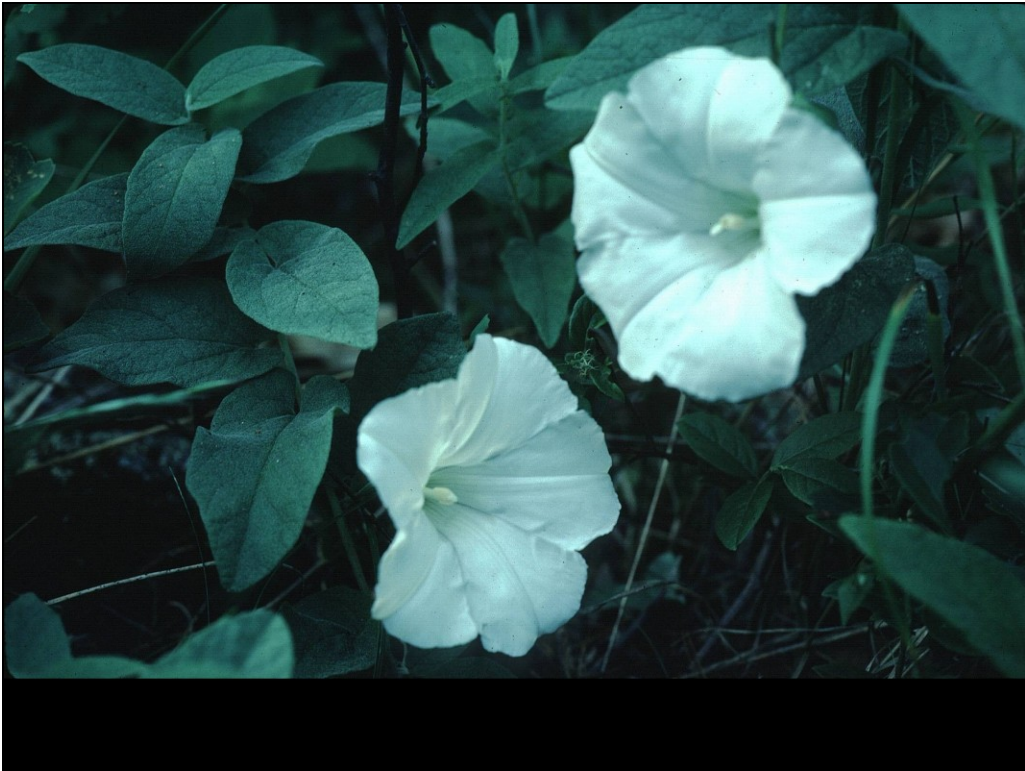




Even generalized flowers will have traits that promote efficiency of pollination; radiating patterns in flowers help pollinators go directly to where the nectar is – and where plant 'wants them' to be (where the pollen is); less time per flower means more flowers get visited. This would seem to be fitness enhancing for both parties? No conflicts of selective interest? But note that some flowers don't put nectar in every flower...



More pronounced radial pattern (lines are called 'nectar guides")



Some white flowers have nectar guides visible in the UV only. These also are highly fragrant



A night-blooming cactus with very large flowers accessible only to flying pollinators. Here, bats: note the arrangement of stamens. Very large quantities of nectar – so expensive. What are fitness advantages of using larger, warm-blooded vertebrate pollinators to counter balance these costs?





Many tropical plants have highly coevolved relationships with hummingbirds; as with bats, flowers produce large quantities of pollen. Plants also tend to produce blooms over long period. They're also typically rather scattered in distribution. Why is this a particularly adaptive pollinator arrangement for plant? Bird?







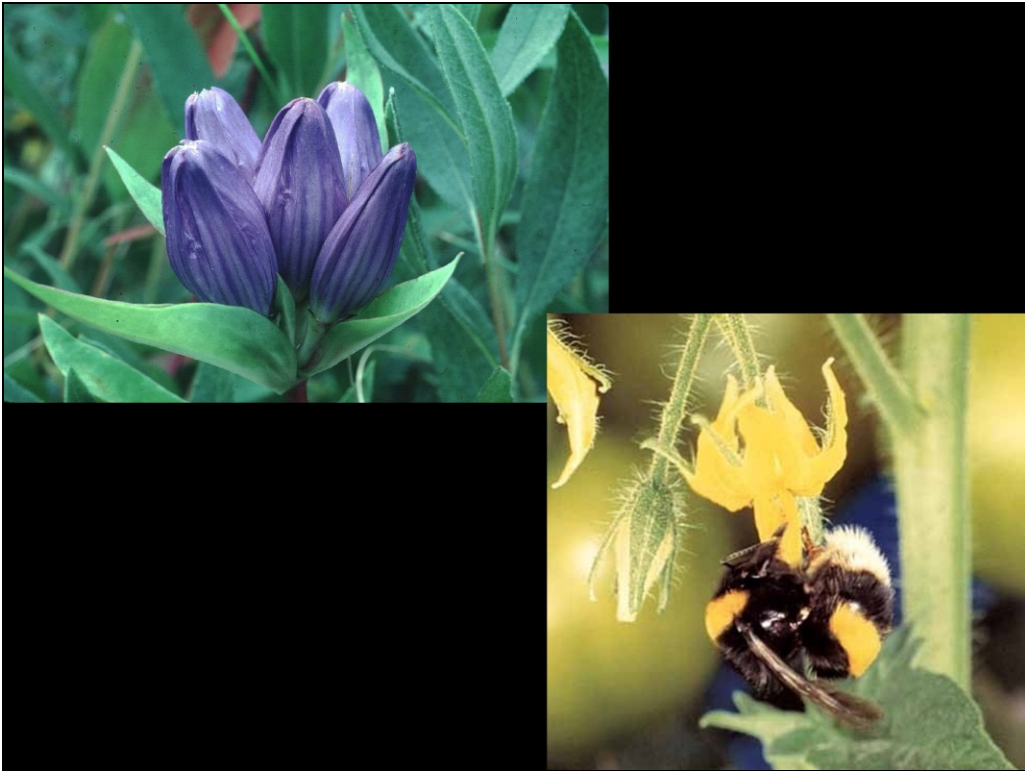
Evolutionary convergence; sunbirds in Africa are much like hummingbirds in behavior and in coevolutionary relationships with plants – but they can't hover; flowers must have perches...



Marsupial pollinator: honey-glider (size of small mouse, but glides like flying squirrel) pollinating *Banksia* shrub. As with bats and hummingbirds, plant provides very large amounts of nectar (here the structure is actually many flowers combined...)



Lupine flowers: the 'standard' – upright petals on flower – changes color after flower is pollinated. Those flowers no longer produce nectar. A signaling game that 'works' for both parties – presumably stabilizing the pollination mutualism?



Oddities: Some flowers have to be pried open by specialized pollinators. Tomatoes are 'buzz-pollinated'; they'll shed pollen only when vibrated at a particular frequency...



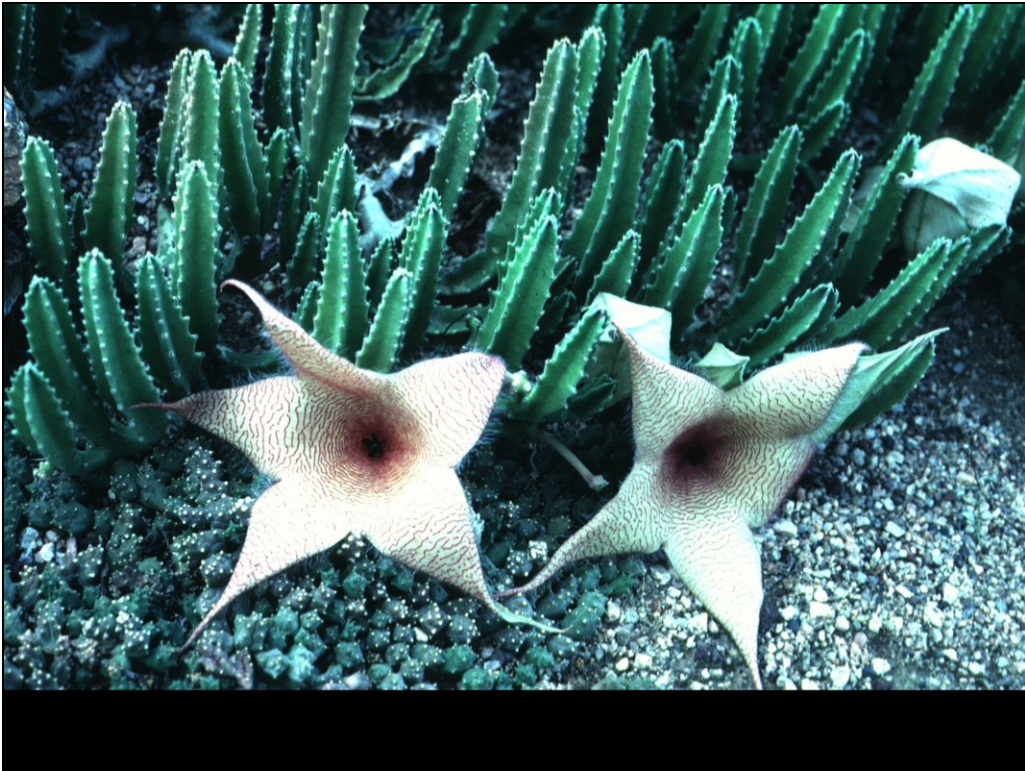
Early-spring-blooming 'pasque flower". No nectar, but flowers act as a parabolic solar oven, keeping plants germ cell warm, but also attractive to insects. Still mutualism, but 'reward' much cheaper for plant than nectar – works as long as it's chilly weather and nobody else is blooming...



But things can turn perverse – the mutualism can go to asymmetry or exploitation. Wild 'gingers' (not really gingers) of genus *Asarum* are pollinated by beetles and slugs; they offer no reward – presumably just smell good...



Even more devious: Plants with flowers that smell like carrion; flies are attracted by same chemicals as produced by rotting flesh. They lay eggs which hatch and die – but pollinate plant. This is parasitism of the flies by the plant. Seems like selection should favor flies that avoid it – but is there a way that they can



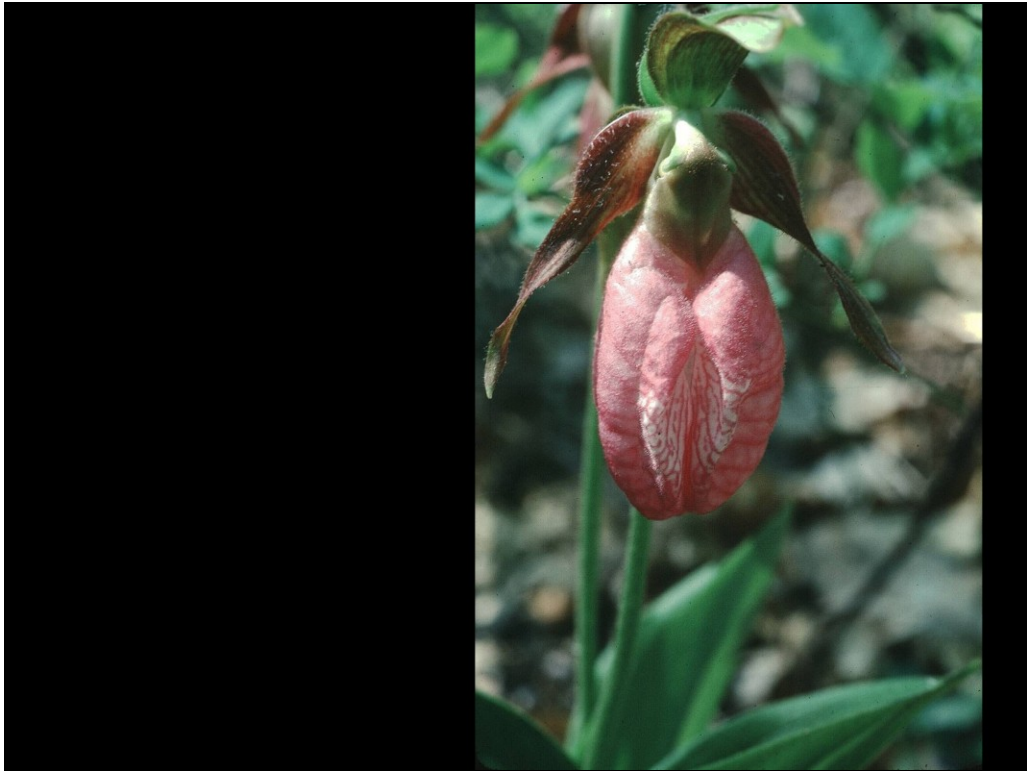
Another corpse flower – an African *Stapelia*. There are hundreds of species of plants, in many families, that have converged on the same trick... this seems to be a mutualism that has 'broken'...



The largest single flower on the planet – *Rafflesia* – is a corpse-flower. Genus is from southeast Asia. The plant itself lives as an internal parasite on the roots of other plants, acting more like a fungus than a plant...



Other organisms can exploit pollination mutualisms by accessing rewards offered by plant to pollinators – but without actually pollinating. Nectar thieves (a name suggesting plant-centrism...). These are all instances where insects have penetrated the flower by 'non-standard' routes, bypassing the stamens and stigma. Flower structures often show adaptations against this – structures shielding access to nectar. Such exploitation of a mutualistic 'reward' may be costly to plant fitness if it impedes pollination, and lead to selection on the plant to 'drop' the production of a reward if there are alternative pathways to pollination



Specialized relationships can involve risks. This pink lady's slipper orchid (native to this area) is pollinated by bees that are enticed into a sort of pit-fall trap (in the pouch of the orchid) from which they can escape only by a route that effects pollination. There is no reward. Apparently insects once tricked are not very readily tempted to do it again, and the orchids are, in fact, not very frequently cross-pollinated. Most flowers do not end up producing seeds (although when they do, there are many thousands per fruit). This may be an 'evolutionary trap' for the flower; no available variation on existing phenotype able to drive more effective pollination...



Another local native forest wild-flower, 'jack-in-the-pulpit' (*Arisaema triphyllum*) is pollinated by randomly bumbling fungus gnats who are trapped in the funnel of the inflorescence (where the flowers are located). The plant is dioecious – individual plants are either all male or all female. Male plants have an 'escape route' by which gnats can eventually exit the trap. Female plants lack this small tunnel, and gnats trapped there may eventually die – but the fitness of the female plant is optimized by keeping gnats as long as possible to ensure that any pollen grains they carry are deposited on stigmata of the multiple flowers in the inflorescence. Seed-set (= 'female fitness component') appears to be limited, in most cases, by inefficient pollination.



Another of the many deceptive plants that have 'broken' the presumed ancestral mutualism – another orchid, *Calopogon pulchellus*. The yellow-tipped white hairs on the upper lobe of the flower look like stamens and may attract insects seeking protein-rich pollen. They are, however, just hairs. The weight of an insect landing on the structure releases a hinge that drops the insect onto the true pollen-bearing structure and stigma. Again, no reward (though little cost) to the insect; the relationship is more accurately a mild form of parasitism by the plant on the insect, but selective cost to insect is probably not enough to select for avoidance.



There is a vast array of flowers – especially orchids – that exploit insect pollinators by chemical cues – for example, using scents that mimic insect sex pheromones. The bee orchids of Europe go a step further and mimic both scent and appearance of a female bee. Male insects attempt to copulate with the flower, effecting pollination. There is presumably an energetic cost to the plant in producing the scents, but amounts are tiny compared to cost of producing sugar-rich nectar...



Even coevolved, true mutualisms have risks. Here, an orchid introduced to Hawai'i attracts bees (also introduced) that are not the coevolved pollinators. The bees get stuck in the flowers where they die; no pollination, dead bees. Lose-lose...



Similar dynamics apply with respect to animal dispersal of seeds. Plants produce fruits as reward (bright red berries are usually designed to attract birds). Fitness of the plant depends on dispersal of seed, so fruits need to be consumed without destruction of seed. In the case of bird-dispersed fruits, the seeds are usually simply very tough with thick walls that survive passage through bird gut and gizzard (birds don't chew). But, again, other animals may exploit the reward intended for disperser and may also destroy/digest the seed (which is typically pretty nutritious, too, since it contains reserves for germinating seedling...)





Mistletoes are parasites on woody plants; many are non-photosynthetic. Their seeds have to find their way to a branch or twig of a host plant species where they can immediately penetrate the tissues of the host plant for sustenance. Mistletoe berries on this species in the desert southwest are eaten by birds; when the seeds emerge from the birds cloaca, their sticky outer coat adheres to the bird's feathers and apparently causes some irritation, which the bird soothes by scraping against perches (branches), where the seeds are deposited. The photo on the left is of mistletoe seeds attached to a dead cactus stem – a failure for the plant...



Many forest herbs are ant-dispersed; they provide a temptation/reward in the form of a small parcel of oil- or protein-rich tissue (called an elaiosome) attached to each seed. The seed is often carried to the ant nest where the yummy stuff is consumed and the seed (too tough/big for ants to consume) is tossed in the compost.



Elaiosomes



As with pollination, dispersal mutualisms are at risk of breakage, either by exploitation by one 'partner', or loss of the partner. Some American trees (osage-orange, top right, Kentucky coffee-tree other photos) are thought to have coevolved with large mammalian browsers as dispersers. They have large fleshy fruits with large, very tough seeds. When most large mammals (think giant ground sloths, mammoths...) went extinct about 14,000 years ago (probably due to over-hunting), they lost their capacity to travel significant distances and were 'stranded' in the southern part of their potential range.

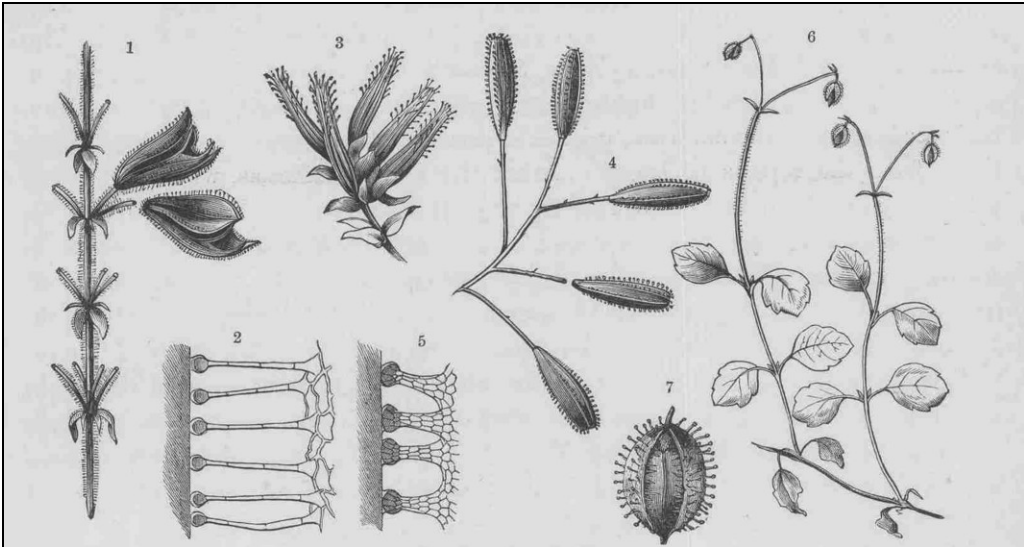
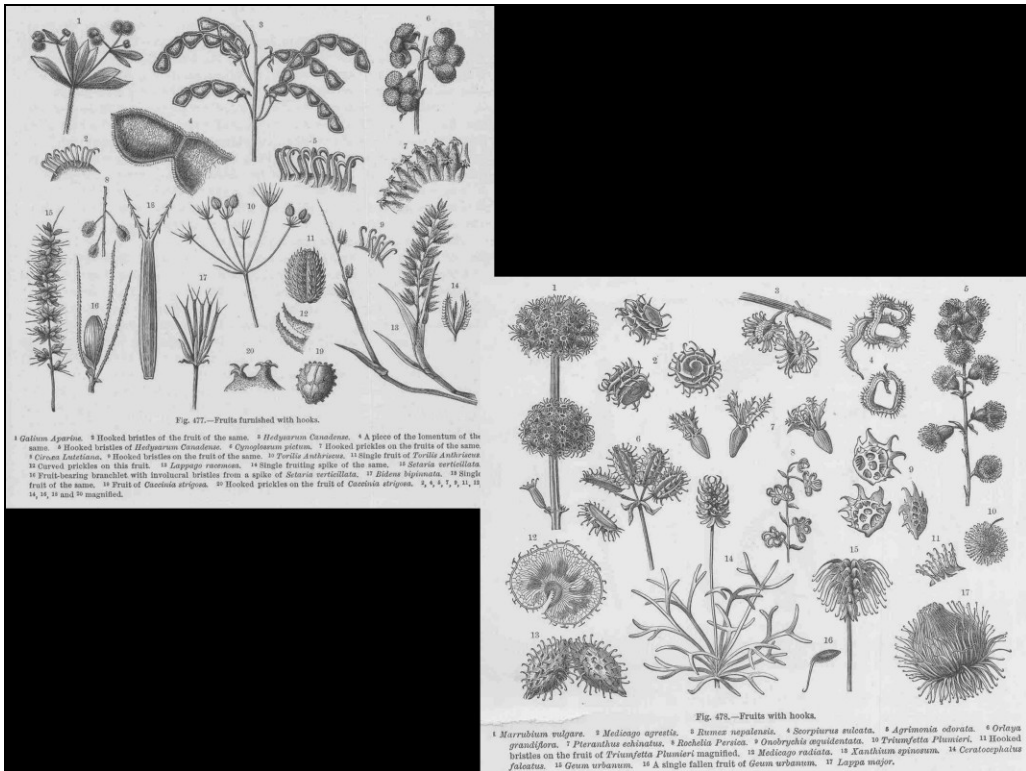
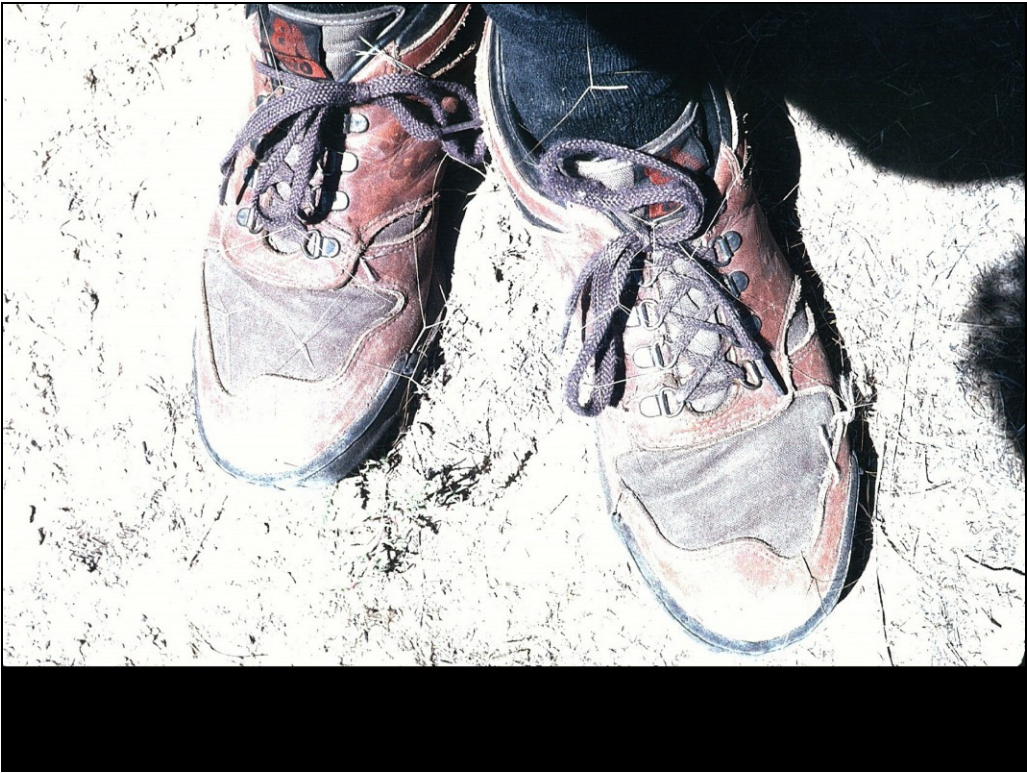


Fig. 476.—Sticky fruits.

1 *Salvia glutinosa*. 2 Stalked adhesive glands on the fruiting calyx of the same; $\times 60$. 3 *Plumbago Capensis*. 4 *Pisonia aculeata*. 5 Stalked adhesive glands on the fruit of the same; $\times 60$. 6 *Linnæa borealis*. 7 Fruit of the same; $\times 5$.



Many seeds/fruits have evolved to attach to the fur or feathers (or socks or shoes) of animals for dispersal, and can travel great distances (these are typically the plants to colonize remote islands). This isn't a mutualistic relationship, but probably evolved from ancestral states involving a mutualistic dispersal syndrome.





The risk of seeds being eaten is often countered by producing highly toxic seeds in tasty fruits.